https://doi.org/10.35662/unine-thesis-2990

Université de Neuchâtel

VOCAL COMMUNICATION IN CHIMPANZEES: A TOOL FOR SOCIAL COHESION

PhD thesis submitted to the Faculty of Science

Institute of Biology

University of Neuchâtel

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Defended on the 18th of October 2022

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Titre:

"Vocal communication in chimpanzees: a tool for social cohesion"

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Neuchâtel, le 17 novembre 2022 Le Doyen, Prof. R. Bshary

Abstract

In some animal species, individuals develop strong and enduring social bonds, which promote cooperation and usually offer significant fitness advantages. In these highly social species, individuals need to be able to coordinate and negotiate their complex social relationships but how do they do so? Does high sociality promote the evolution of specific communicative signals to manage these relationships? These issues becomes even more problematic for species with fluid social structures, where cohesion between group members varies constantly. Chimpanzees are an ideal model species to study these questions, as they present a high degree of fission-fusion dynamics. In this species, males are more gregarious than females and form highly strong and stable bonds with unrelated individuals of the same sex. These bonds, which can manifest in various contexts, such as grooming and intragroup conflicts, play a crucial role in establishing dominance relations between males and have a significant impact on their reproductive success. However, how do males choose their social partners and how do they maintain their relationships with their preferred partners? By empirically investigating the vocal communication and social cohesion of male chimpanzees in various contexts, this thesis aimed to elucidate how males use vocalisations to manage their social relationships.

I first explored specific contexts where social bonds are under strain, i.e., when the social composition of the subgroup is likely to change. Hence, I studied the vocal production of short and long distance calls (i.e., 'pant hoots' and 'rough grunts') by male chimpanzees upon their arrival at food trees, an socially challenging event, as it is particularly prone to outbreaks of aggression but also offers opportunities for cooperation. I showed that vocal communication in this context appeared to have a dual function to mediate both cooperative and competitive interactions, with males producing 'pant hoots' to cooperatively inform absent social partners about the presence of food whereas 'rough grunts' seemed to be produced as part of competitive interactions, to avoid aggression. Secondly, I investigated the vocal production of 'rest hoos', a context-specific vocalisation given while resting, another context during which the subgroup composition is threatened due to forthcoming travel. My findings provided evidence that 'rest hoos' were produced intentionally to prolong resting bouts with desired partners, and that their function would thus be to help manage social cohesion. Furthermore, I discovered that low-ranking males who did not groom often produced 'rest hoos' more frequently than other males, hence suggesting that vocal communication could serve as an alternative cohesion strategy to tactile-based bonding. Finally, I described the patterns of dyadic short-term associations between males (i.e., periods of time during which males stay in each other's visual range) and showed that these associations were mostly determined by dominance relations, as high-ranking males were more effective in prolonging associations when producing a 'hoo' and were also more likely to terminate the associations. I also specifically investigated whether males used vocal signals (i.e., production of 'hoo' vocalisations) or tactile behaviour (i.e., grooming) to manage these associations and found that 'hoo' vocalisations but not grooming had a significant impact on association patterns, suggesting not only that males produced these calls strategically to ensure social cohesion but also that vocalisations may be a more reliable predictor of short-term affiliations than grooming.

Overall, these findings provide evidence that vocalisations have various social functions, including mediating social cohesion and managing both cooperative and competitive interactions, and are therefore playing an essential role in chimpanzee fission-fusion societies. The results presented in this thesis will help better

understand chimpanzee vocal communication and socio-cognitive abilities as well as further our comprehension of how complex social systems shaped the evolution of animal communication.

Keywords: vocalisations, social cognition, primates, group cohesion, social bonds

Résumé

Chez certaines espèces animales, les individus développent des liens sociaux forts et durables, qui favorisent la coopération et offrent généralement des avantages importants en termes de fitness. Au sein de ces espèces très sociales, les individus doivent être capables de coordonner et de négocier leurs relations sociales complexes, mais comment y parviennent-ils ? Une forte sociabilité favorise-t-elle l'évolution de signaux de communication spécifiques pour gérer ces relations ? Ces questions deviennent encore plus problématiques pour les espèces aux structures sociales fluides, où la cohésion entre les membres du groupe varie constamment. Le chimpanzé est une espèce idéale pour étudier ces questions, car il vit en groupes sociaux régis par une dynamique de fission-fusion élevée. Dans cette espèce, les mâles sont plus grégaires que les femelles et forment des liens très forts et stables avec des individus non apparentés du même sexe. Ces liens, qui peuvent se manifester dans différents contextes, tels que lors de l'épouillage ou de conflits, jouent un rôle crucial dans l'établissement des relations de dominance entre les mâles et ont un impact significatif sur leur succès reproductif. Cependant, comment les mâles choisissent-ils leurs partenaires sociaux et comment maintiennent-ils leurs relations avec leurs partenaires préférés ? En étudiant de manière empirique la communication vocale et la cohésion sociale des chimpanzés mâles dans divers contextes, cette thèse vise à élucider comment les mâles utilisent les vocalisations pour gérer leurs relations sociales.

J'ai d'abord exploré des contextes spécifiques où les liens sociaux sont mis à l'épreuve, c'est-à-dire lorsque la composition sociale du sous-groupe est susceptible de changer. J'ai donc étudié la production de vocalisations à courte et longue distance (i.e., 'rough grunts' et 'pant hoots') par les mâles chimpanzés lors de leur arrivée aux arbres où ils se nourrissent, un événement socialement complexe car il est particulièrement propice aux agression mais offre également des opportunités de coopération. Les résultats montrent que la communication vocale dans ce contexte semble avoir une double fonction, celle de gérer les interactions coopératives et compétitives, les mâles produisant des 'pant hoots' pour informer de manière coopérative les partenaires sociaux absents de la présence de nourriture, tandis que les 'rough grunts' semblent être produits dans le cadre d'interactions compétitives, pour éviter les agressions. Deuxièmement, j'ai étudié la production vocale de "rest hoo", une vocalisation spécifique au contexte de repos, un autre contexte pendant lequel la composition du sous-groupe est menacée en raison des futurs déplacements. Mes résultats démontrent que les "rest hoos" sont produits intentionnellement pour prolonger les périodes de repos avec les partenaires désirés, et que leur fonction serait donc de faciliter la cohésion sociale. En outre, j'ai découvert que les mâles non-dominants qui ne pratiquaient pas souvent l'épouillage produisaient des "rest hoos" plus fréquemment que les autres mâles, suggérant ainsi que la communication vocale pourrait servir de stratégie de cohésion alternative aux comportements tactiles. Enfin, dans une troisième étude, j'ai observé les associations dyadiques à court terme entre les mâles (i.e., périodes de temps pendant lesquelles les mâles restent en contact visuel) et j'ai montré que ces associations étaient principalement déterminées par les relations de dominance, car les mâles dominants étaient plus efficaces pour prolonger les associations lorsqu'ils produisaient un 'hoo' et ils étaient également plus susceptibles de mettre fin aux associations. J'ai également cherché à savoir si les mâles utilisaient des signaux vocaux (i.e., production de " hoo") ou un comportement tactile (i.e., épouillage) pour gérer ces associations et j'ai constaté que la production de 'hoo', mais pas l'épouillage, avait un impact significatif sur les associations, ce qui suggère non seulement que les mâles produisaient ces vocalisations de manière stratégique pour assurer la cohésion sociale, mais aussi

que les vocalisations pourraient permettre d'estimer les affiliations à court terme de façon plus fiable que les comportements d'épouillage.

Dans l'ensemble, ces résultats démontrent que les vocalisations ont diverses fonctions sociales, y compris la médiation de la cohésion sociale et la gestion des interactions coopératives et compétitives, et jouent donc un rôle essentiel dans les sociétés de chimpanzés. Les résultats présentés dans cette thèse aideront à mieux comprendre la communication vocale et les capacités socio-cognitives des chimpanzés, ainsi qu'à approfondir nos connaissances sur la façon dont les systèmes sociaux complexes ont façonnés l'évolution de la communication animale.

Mots-clés : vocalisations, cognition sociale, primates, cohésion de groupe, liens sociaux

Acknowledgments

There are so many people who contributed to the work presented in this thesis and who helped to make this PhD such an amazing experience.

I would like to start by thanking my supervisor, Klaus Zuberbühler, for giving me this incredible opportunity and guiding me during these last five years (almost six actually, but who is counting!). The PhD is a long and arduous road with many ups and downs but I could always feel that he did not doubt that I would succeed and his support and trust encouraged me to complete this thesis. I also thank my PhD committee: Carel van Schaik and Redouan Bshary, for agreeing to examine this thesis as well as for their insightful comments and the constructive discussion we shared at the viva. Throughout this PhD, I had the chance to meet some researchers, both in the field and back home, who I would like to thank for their invaluable advice and encouragements: Cathy Crockford, Pawel Fedurek, Thibaud Gruber, Cat Hobaiter and Simon Townsend.

In Budongo, I would have never been able to conduct my research without my incredible field assistant: Sam Adue. I don't think I can express how much I am grateful to him for sharing his knowledge of the chimps and the forest with me and for helping me with everything. No matter what project I started, whether I needed him to run ahead of the chimps to place a snake model on their path, or to stay longer in the field with me until the chimps nested, he was always supportive and brought such a positive attitude. I cannot thank him enough for his friendship and his patience (much needed to spend so many hours with me in the forest!). A huge thanks to all the other field assistants: Bosco Chandia, Geresomu Muhumuza, Monday Mbotella, Denis Lomoro, Vincent Kizza, Gideon Atayo, Robert Eguma, Steven Mugisa, for their precious help but also for all the amazing times we shared together, in and out of the forest. The Budongo Conservation Field Station was my home away from home and I would like to thank the people running it and everyone at camp for making my stay such a wonderful experience: William Aganyi, Fred Odong, Samuel Ezwa, Mary Ndobya, Sara Friday, Carol Kabikuru Rose, Monica, Fred Babwateera, Geoffrey Muhanguzi, Walter Akankwasa, Zephir Kiwedde, Moses Businge, Gophine Ericsson, James Ahebwa, Nelson Orijabo, Patrick Arua, David Rume, J-B, Jacob, David Eryenyu, Caroline Asiimwe.

Another reason why camp felt like home is that I found a second family there, with all the amazing researchers I met with whom I shared… well, everything! A warm thank you to Vesta Eleuteri (aka Muffin), Lotus Emam, Géraldine Ischer, Sophie Marshall, Charlotte Knapper, Joanna Buryn-Weitzel, Franziska Wegdell, Gal Badihi and Matthew Henderson, for the awesome time we shared together, for all the laughs, for all the Harry Potter games, and for everything else. A very emotional thank you to Maël Leroux (aka Bibouche), Eve Holden, Claire Barrault, Claire Perez, Adrienne Guignard, Clémence Bonneaud, Adrian Soldati and Marion de Vevey for their support and friendship, not only in the field, but also back at home. I feel so lucky to count them as my friends and I am so grateful for all the memorable moments we already shared and for the ones I am sure we will share in the future. An extra special thanks to Bibouche, for putting up with me squatting his couch for a whole month and keeping me motivated and happy when I needed it the most.

Back in Neuchâtel, I also met wonderful people who supported me and helped me both professionally and personally throughout my PhD. Thank you to the people I met at the very beginning of my PhD: Melissa Berthet,

Emilie Genty, Corinne Ackermann (aka Coco) and Yaëlle Bouquet, who welcomed me with open arms and guided me when I had no idea what I was doing. Thank you to the people I befriended later on: Auriane Le Floch, Raphaela Heesen, Ottilie Tilston, Maria Granell Ruiz, Anaïs Durand, Ed Halliday, Marco Zaidman, Alencar Benitez, Steve Napias, Quentin Blandenier, Clément Duckert (aka Duky), Julie Hernandez, Martina Ribalda, Athina Bondi, Noélie Métral, Julián León, Lara Narbona and Caroline Fryns. Whether we just shared some drinks and some nice conversations or whether we became very close friends, they all made my life better and I am so happy I got to know all of them. Special thanks to Melissa Berthet, who, on top of being an amazing friend, is also a remarkable scientist and always took the time to advise me. I am also especially thankful to Rapha, Marco, Anaïs, and Maria who were the most wonderful roommates and all made me feel like home. Last but not least, I would like to thank Auriane for being my favourite person in the world; I could not imagine my life without her. I would also like to thank her for her unwavering support and her invaluable advice and feedback on this thesis.

Finally, I would like to thank my friends and family for being my rock during all these years. My studies always pushed me to travel around a lot and conducting a PhD presents many challenges, but they were always there, ready to cheer me up, to encourage me and to make me feel loved. Thank you to my grandparents, my parents and my brother and sisters, whom I love more than I could say and who always believed in me and pushed me to be the best version of myself. Special thanks to my mami Moune, who has always been one of my biggest (and loudest!) supporter. I would also like to thank all my friends with whom I always have an amazing time, whether it is in Paris or Neuchâtel or even Sofia or Berlin :) Thank you for always finding time to come and share a drink with me, even though I usually only came for a couple of days with a 24 hours' notice! Special thanks to Bilgé Kimyonok for his huge support and for building me the perfect app to collect observational data in the field. A very warm thank you to Jovanah Murugan (aka Choucoulat), Judith Hendriks (aka ma bouf), Clément Vuillet, Grégoire Viegas (aka Gregounet), David Rozen-Rechels (aka Davidou), Agathe Jasson (aka Gatou), Théo Altman and Sarah Pineau, for being the best friends I could ever wish for, for always being there and supporting me long before I even started this PhD and for so many other reasons I would not have the space to list here. Lastly, I would like to thank so many other friends and family I have not specifically named but, if you are reading this, there is a pretty good chance you are one of them (especially if you are also planning on reading the rest of this thesis!), so thank you!

Table of contents

Chapter 1. General introduction

Social bonding in animals

Many species across different taxa live in social groups, an evolutionary strategy that confers some advantages such as improved access to food and mating, a reduced risk of predation or reduced parasite loads through social grooming (Chapman & Chapman, 2000; Crofoot & Wrangham, 2010; Davies et al., 2012; Grinnell, 2002; Jeschke & Tollrian, 2007) but can also be costly due to increased foraging and mating competition and higher risk of pathogen transmission (Davies et al., 2012; Krause & Ruxton, 2002; Leendertz et al., 2004; Wrangham et al., 1993). In some species, animals mitigate the cost of group-living by associating with specific group members for long periods of time. These long-term relationships between individuals, often defined as 'social bonds', are associated with a high degree of affiliative interactions between them, and the process through which these bonds are established and maintained is called 'social bonding' (Dunbar & Shultz, 2010). Originally, the term social bonding was used to describe animal monogamous relationships, as can be found in pair-living birds, for which the behavioural coordination between a male and a female is paramount to ensure the successful breeding of the offspring (Shultz & Dunbar, 2010). However, many species evolved in socioecological environments that favoured regular social interactions, which promoted the development of strong and enduring social bonds beyond the reproductive units (Massen et al., 2010; Seyfarth & Cheney, 2012). These bonds facilitate cooperation between individuals and often provide important fitness benefits (Hruschka & Silk, 2017; Silk, 2007). For instance, same-sex social bonds, which are usually calculated using the frequency or the duration of affiliative interactions, such as grooming, are associated with cooperation, increased lifespan and higher reproductive success (male bottlenose dolphins *Tursiops aduncus*, Connor et al., 2001; female spotted hyenas *Crocuta crocuta*, Smith et al., 2011; female feral horses *Equus caballus,* Cameron et al., 2009; male Barbary and Assamese macaques *Macaca assamensis* and *M. sylvanus*, Berghänel et al., 2011; Schülke et al., 2010; female baboons *Papio cynocephalus* and *P. ursinus*, Archie et al., 2014; Silk et al., 2010; male chimpanzees *Pan troglodytes verus*, Samuni et al., 2018).

Bonds between males are thought to have evolved due to the pressures generated by intragroup competition, with males forming long-term alliances to compete for dominance status and mating opportunities (Connor et al., 2001; Ostner & Schülke, 2014; Schülke et al., 2010). There are great variations in the degree to which individuals form social bonds between social groups (Seyfarth & Cheney, 2012). According to kin selection theory (Hamilton, 1964), the choice of partners should be connected to the degree of relatedness. Indeed, kin will cooperate more and form stronger bonds than non-kin due to inclusive fitness benefits (Silk, 2002; Smith, 2014). However, kin selection theory also predicts that relationships between close relatives might be more unequal than those between unrelated individuals because non-reciprocated altruistic behaviours will still provide indirect fitness benefits among kin. Generally, maternal relatives can easily recognise each other and are therefore more prone to cooperate than paternal kin. Nevertheless, some species present high male reproductive skew and age cohorts can thus be assimilated as paternal kin (Altmann, 1979). In other species, although paternal kinship cannot explain the observed pattern of cooperation, as it is the case in chimpanzees for instance (Langergraber et al., 2007), peers might still associate due to higher shared interest and familiarity (Gerber et al., 2020; Mitani et al., 2002). Furthermore, in some species, similarity in dominance ranks might play an important role in partner

choice, especially in species that frequently perform allo-grooming, such as many primate species (De Waal, 1991; Schino, 2001; Watts, 2000b).

Social bonding in primates

Most primate species live in socially complex groups, which can be challenging. Indeed, many primates live in relatively large groups and can display intricate social relationships patterns within these groups (Dunbar, 1988). Contrary to other group-living mammalian species, such as birds or ungulates, most primates live in stable groups, with little variation in the number of individuals in the group and low migration rates. This context favoured the development of complex social networks, with the social behaviours of individuals often being influenced not only by their bonds with the recipients of these behaviours but also by their relationships with third parties (Cheney et al., 1986; Cheney & Seyfarth, 1990). To navigate these complex social relationships and coordinate individual behaviour, group-living primates had to develop an efficient communication system (McComb & Semple, 2005).

Originally, social bonding in primates and its impact on individual fitness was mostly investigated in baboons. Baboons live in female philopatric societies and females form tight social bonds together, especially between kin, which are characterised by close spatial proximity, frequent grooming and coalitions (Seyfarth, 1977; Silk et al., 1999, 2012). Several studies have shown that these bonds have an important effect on female fitness, as females that form strong social bonds have greater infant survival rates and overall higher longevity than less social females (Silk et al., 2003, 2009, 2010). Social bonds in other primate species have been investigated, notably male-male bonds in macaque species, in which males form close bonds with unrelated males and preferentially support each other in agonistic coalitions (Assamese macaques, Schülke et al., 2010; bonnet macaques, *Macaca radiata* Adiseshan et al., 2011; Silk, 1994; Barbary macaques, Berghänel et al., 2011). Male-male social bonds have also been described and studied in chimpanzees, where they appear to be determinant for individual's fitness (Mitani et al., 2000; Muller & Mitani, 2005).

Social bonding in chimpanzees

To understand the importance of male social bonding in chimpanzees, it is crucial to comprehend chimpanzee social structure. Chimpanzees live in fission-fusion societies, which means that they often split into smaller groups, with temporal variations in the size and composition of these subgroups (Aureli et al., 2008; Kerth, 2010; Ramos-Fernández & Morales, 2014). Fission-fusion is a common behavioural strategy used across various animal taxa to balance the costs and benefits of group living (Krause & Ruxton, 2002; Sibly, 1983). In these systems, travel decisions are devolved from the group to the individual level (Conradt & List, 2009; Couzin et al., 2005; Stueckle & Zinner, 2008) and cohesion between group members is fluctuating constantly (Conradt & Roper, 2010; Jacobs, 2010; Kerth, 2010). The fission-fusion dynamics generate more variability in the opportunities for individuals to interact with each other, which results in a greater uncertainty about others' social relationships (Hinde, 1976; Wey et al., 2008). Compared to more cohesive social systems, fission-fusion systems generally lead to more disagreement, negotiation and coordination (Kerth, 2010) and individual behaviours and relationships have more effect on social dynamics (Sueur et al., 2011). Therefore, these systems increase group social complexity and require more decisions about proximity, which most likely put higher demands on social cognition and communication (Aureli et al., 2008; Couzin et al., 2005; King & Sueur, 2011;

Petit & Bon, 2010; Strandburg-Peshkin et al., 2018; von Rueden et al., 2015). This theory is in line with the social intelligence hypothesis (Humphrey, 1976), which stipulates that the relative brain size of a species and its cognitive abilities should be positively correlated with its social complexity (Dunbar, 1998, 2011). In agreement with this theory, species with high degrees of fission-fusion dynamics, such as bottlenose dolphins (Tsai & Mann, 2013), spider monkeys (*Ateles geoffroyi*, Aguilar-Melo et al., 2018), baboons (Kummer, 1968), bonobos (*Pan paniscus,* White & Burgman, 1990), chimpanzees (Goodall, 1986), or humans (Marlowe, 2005), have relatively larger neocortex sizes than species living in more cohesive groups (Barrett et al., 2003; Dunbar, 1998). On the other hand, some studies have found evidence supporting the ecological intelligence hypothesis (DeCasien et al., 2017; Powell et al., 2017), with primate brain size being more correlated with ecological (e.g., terrestriality, activity period, diet and home range size), rather than social variables. Nevertheless, these two hypotheses (i.e., social and ecological intelligence hypotheses) might not be opposed or exclusive and could instead be seen as complementary and would help to explain the evolution of different cognitive abilities (Rosati, 2017).

In fission-fusion societies, individuals choose which group member to associate with and can base these decisions on ecological variables. For instance, food availability plays an indirect role in these decisions by imposing a constraint on subgroup size, i.e., if the resources are scattered, optimal subgroup sizes will be small, whereas if there are large food patches, it might be more efficient for individuals to form larger groups (Asensio et al., 2009; Chapman et al., 1995; Hartwell et al., 2018; Krebs & Davies, 2009; Kummer, 1971; Lehmann et al., 2007; Sueur et al., 2011; Symington, 1990). However, studies have shown that social factors, such as social affiliations and reproductive strategies, might also have an important effect on these decisions, especially in highly social species (bottlenose dolphins, Lusseau, 2007; spider monkeys, Busia et al., 2017; Tonkean macaques, *Macaca tonkeana*, and rhesus macaques, *Macaca mulatta* Sueur et al., 2010; Northern muriquis, *Brachyteles hypoxanthus* Tokuda et al., 2012; chimpanzees, *Pan troglodytes* Mitani & Amsler, 2003).

In chimpanzees, similarly to human friendships, males often form strong and lasting social relationships between non-kin (Hruschka, 2010). The fact that relatedness only plays a limited role in partner choice can be explained in several ways. First, in the context of agonistic interactions, an individual might gain greater fitness benefits by choosing a partner based on skills rather than relatedness (Chapais, 2006; Enigk et al., 2020). Moreover, in species with long interbirth intervals, the probability for an individual to have a living identifiable sibling of the same sex with a high competitive value is quite low. Therefore, in these contexts, partner choice might be based on other factors such as familiarity and rank or age similarity (Gerber et al., 2020; Mitani et al., 2002; Rosenbaum et al., 2016).

Chimpanzee adult males remain in their natal communities throughout their lives and are very gregarious (Goodall, 1986; Mitani, 2009a, 2009b). They form highly strong and stable social bonds, which can manifest in various contexts such as party or sub-group association (Gilby & Wrangham, 2008; Pepper et al., 1999; Surbeck et al., 2017), grooming (Watts, 2000b, 2000a), cooperative hunting (Boesch, 1994; Hobaiter et al., 2017), food sharing (Mitani et al., 2002; Samuni et al., 2018), intragroup conflicts (Gilby et al., 2013; Muller & Mitani, 2005), territorial boundary patrols (Watts & Mitani, 2001) and intergroup aggressions (Samuni et al., 2021; Watts & Mitani, 2001). Furthermore, males reconcile more often after a conflict with a close bond partner (Preis et al., 2018) and they intervene during grooming bouts more often if one of the grooming partners is a close

social partner (Mielke et al., 2017). Social bonding and cooperation between males have important consequences on their fitness. For instance, males form coalitions in agonistic contexts that play a crucial role in establishing dominance relations (Gilby et al., 2013; Mitani, 2009b) and higher ranks are associated with higher fitness due to greater reproductive success (Boesch et al., 2006; Newton-Fisher et al., 2009; Wroblewski et al., 2009). Subordinates that develop strong social relationships with the alpha male, or with many other subordinates, also have higher siring success (Bray et al., 2016; Duffy et al., 2007; Feldblum et al., 2021). Additionally, cooperative mate guarding has been shown to enhance reproductive success as well (Watts, 1998). There are great individual variations in how males are successful at establishing social relationships (Muller & Mitani, 2005), although for reasons that still remain to be investigated.

Vocalisations and social bonding

Individuals in group-living species need to be able to maintain some sort of cohesion with each other and one way to do so is through vocalisations. Many of these species have evolved acoustically distinct vocalisations whose main function is to manage social cohesion (Bolt, 2020; Chaverri et al., 2013; da Cunha & Byrne, 2009). These calls, usually referred to as 'contact calls', can provide information such as the identity, the current activity, or even the desired response or the intention of the signaller (Candiotti et al., 2012; Fischer, 2008; Gruber & Zuberbühler, 2013). Intentional communication usually refers to Dennett's (1971, 1983) first-order intentionality, or imperative signalling. To identify first-order intentionality, Townsend et al. (2017) established a framework based on observable behavioural criteria: the signal must (i) be goal-directed, (ii) be recipient-directed and (iii) elicit a behavioural response from the recipient in line with the signaller's goal. Criteria for first-order intentionality have been found in signals produced by species across a wide variety of taxa, including non-mammalian species such as birds (Mocha et al., 2019; Pika & Bugnyar, 2011) or fish (Vail et al., 2013). A growing number of studies have been investigating first-order intentionality in primates, first in gestural communication (Genty et al., 2009; Leavens & Hopkins, 1998; Pika et al., 2005) and, more recently, in vocal signals (Papworth et al., 2008; Schel et al., 2013).

Studies have shown that in many primate species, notably the ones living in multi-male multi-female groups, contact calls can be preferentially directed at strong social partners (e.g., ring-tailed lemurs *Lemur catta*, Oda, 1996; squirrel monkeys *Saimiri sciureus*, Soltis et al., 2002; spider monkeys, Ramos-Fernández, 2005; rhesus macaques, Hauser & Marler, 1993; gorillas *Gorilla gorilla*, Harcourt & Stewart, 1996) and might thus be associated with affiliative relationships. Cheney & Seyfarth (2018) recently pointed out that, even though vocal communication in non-human primates have been extensively studied, the function of the calls produced still remains poorly understood. Despite the fact that vocalisations are an essential and extensive part of many primates 'social lives, vocal behaviour is rarely considered when investigating social bonding, contrary to other behaviours such as grooming, proximity and coalitionary support (e.g., Archie et al., 2014; Gilby et al., 2013; Schülke et al., 2010; Silk et al., 2010, 2013). However, some studies did find evidence that primate vocalisations are involved in social bonding. For instance, in some species, individuals exchanged more calls with preferred grooming partners and vocal signals could thus be interpreted as "grooming-at-a-distance" (Japanese macaques *Macaca fuscata*, Arlet et al., 2015; ring-tailed lemurs, Kulahci et al., 2015). In rhesus macaques, contact calls seem to play a role in reconciliation (Rendall et al., 1999), a behaviour that is usually associated with grooming (Aureli et al., 1989), and females, which spend more time grooming than males, also appear to be more vocal

than them (Greeno & Semple, 2009). Correspondingly, McComb & Semple (2005) found that the size of the vocal repertoires of non-human primate species seemed to be correlated with both their group sizes and the amount of time they spend grooming.

Vocalisations and social bonding in chimpanzees

Chimpanzees display a high degree of fission-fusion dynamics with complex affiliative networks, which could require a complex communication system. Their vocal repertoire comprises approximately 15 call types (Goodall, 1986; Slocombe & Zuberbühler, 2010), even though their calls are graded within and between call types (Marler, 1976) and some call types can thus present several variants (e.g., 'hoo' calls, Crockford et al., 2018). To maintain cohesion with distant group members, chimpanzees use a long distance call, the 'pant hoot', which they often produce in response to, or in chorus with, another individual's 'pant hoot' and these call exchanges happen more frequently between strong social partners (Eckhardt et al., 2015; Fedurek et al., 2013; Mitani & Nishida, 1993). Changes in subgroup composition mostly happen when transitioning from one activity to the next (i.e., traveling, resting or feeding); therefore, the different calls produced when starting a new activity are likely to play an important role in regulating the cohesion between individuals. When initiating traveling or resting, chimpanzees often produce acoustically distinct and context-specific vocalisations, such as 'travel hoos' or 'rest hoos' (Crockford et al., 2018). When starting to feed, chimpanzees also produce food-associated calls. The arrival at a food trees can be socially challenging as these events are regularly associated with outbreaks of aggression (Ischer et al., 2020; Muller & Mitani, 2005) but can also bring invaluable opportunities to strengthen social bonds through tolerated co-feeding or food sharing (Samuni et al., 2018; Wittig et al., 2014). Both 'hoo' vocalisations and food-associated calls could play an important role in managing social relationships but it remained to be investigated.

Hoo vocalisations

Chimpanzees produce three context-specific 'hoo' variants which are acoustically distinct (Crockford et al., 2018): 'alert hoos' are produced in an alarm context when encountering mild dangers, such as viper encounters, 'travel hoos' are produced when traveling and 'rest hoos' are produced during resting. The production of 'alert hoos' has already been studied quite extensively and these calls appear to be produced intentionally, as they seem to be directed at specific individuals and associated with visual monitoring of the audience (i.e., audience-directed) and calling only stopped when recipients were away from danger (i.e., goal-directed) (Schel et al., 2013). A playback study (Crockford et al., 2012) showed that chimpanzees appear to be able to direct these calls towards ignorant group members, suggesting that they can take into account others' state of knowledge and 'alert hoo' production also seem to be referential, with calls referring the recipients either to the signaller or the threat (Crockford et al., 2015). 'Travel hoos' also seem to be produced intentionally to initiate joint travel, as they appear to help recruit others and are preferentially directed towards allies (Gruber & Zuberbühler, 2013). Crockford et al. (2018) suggested that 'hoo' calls are all produced with the same underlying goal, i.e., to facilitate cohesion between individuals, specifically bond partners, and the three 'hoo' variants would have evolved to enable their cooperation in different contexts. However, the production and function of 'rest hoos' remained unclear.

Food-associated calls

During feeding, chimpanzees usually produce two different types of calls: long-distance 'pant hoots' and short distance 'rough grunts' (Goodall, 1986; Marler & Tenaza, 1977; Reynolds & Reynolds, 1965). 'pant hoots' are produced in a variety of contexts and have a complex acoustic structure which consists of four different units (i.e., introduction, build-up, climax and let-down) and encodes information about the identity, age and dominance rank of the caller, as well as the context of production (Fedurek et al., 2016). These calls, mostly produced by adult males, can be combined with drumming displays and travel over long distances, which originally suggested that their function was to provide information about the presence of food or the direction of travel to distant group members (Babiszewska et al., 2015; Notman & Rendall, 2005; Reynolds & Reynolds, 1965; Wrangham, 1977). However, other studies have suggested that 'pant hoots' could have more complex social function, showing that call production could be driven by social factors, such as rank or party size and composition (Clark, 1993; Clark & Wrangham, 1994; Mitani & Nishida, 1993; Wrangham et al., 2007) and could play an important role in enforcing social status as well as regulating group dynamics and male-male competition (Fedurek et al., 2014, 2016; Mitani & Nishida, 1993). Interestingly, this call also seems to be involved in social bonding, males being more prone to produce a 'pant hoot' when in proximity with affiliated individuals (Mitani & Nishida, 1993). Moreover, males often call in chorus with 'pant hoots' produced by other males (Arcadi, 1996), which also appears to play a role in social bonding (Fedurek et al., 2013; Mitani & Brandt, 1994; Mitani & Gros-Louis, 1998), and could thus be compared to human singing (Keeler et al., 2015). 'pant hoots' produced upon arrival at a feeding tree or during a feeding event are acoustically distinct from the ones produced in other contexts (Fedurek et al., 2016; Notman & Rendall, 2005). It was originally suggested that 'pant hoots' were produced in a feeding context to either inform ignorant individuals about the presence of food (Reynolds & Reynolds, 1965) or to recruit oestrous females at feeding trees to gain mating opportunities (Wrangham, 1977). Even though there was some evidence that their production could depend on the dominance rank of the individual (Clark & Wrangham, 1994), the social function of 'pant hoot' production during feeding has not been investigated yet. Indeed, most studies on vocalisations produced during feeding have been focused on 'rough grunts'.

'Rough grunts' are produced exclusively in a feeding context and can vary acoustically from low-pitched grunts to high-pitched barks with calling bouts consisting of one or several vocalisations (Goodall, 1986; Slocombe & Zuberbühler, 2006). Their acoustic structure is similar to another call, the 'pant grunt', i.e., a greeting call given when approaching or encountering a higher-ranking individual (Laporte & Zuberbühler, 2011), which therefore might suggest similarities in the cognitive processes involved in the production of these two calls. Chimpanzees produce more 'rough grunts' upon finding large quantity of food (Brosnan & De Waal, 2000; Hauser et al., 1993; Hauser & Wrangham, 1987) and the acoustic structure of the calls may encode information on the food quality (Slocombe & Zuberbühler, 2006) or even on the type of food (Slocombe & Zuberbühler, 2005). As with 'pant hoots', recent studies seem to show that social factors might play an even bigger role than ecological ones in the production of 'rough grunts'. The composition of the audience seems to influence the production of these vocalisations, such as the presence of oestrous females or higher-ranking individuals (Kalan & Boesch, 2015; Schel et al., 2013) but most studies show that males produce these calls more often towards strong social partners (Fedurek & Slocombe, 2013; Schel et al., 2013; Slocombe et al., 2010). The function of 'rough grunts'

would thus be to advertise the signaller's intention of initiating, or prolonging, a feeding bout and would help social bonding and coordinating feeding behaviour between males (Fedurek & Slocombe, 2013). A recent study also showed that these calls are often produced after agonistic interactions that occur during feeding and could then help to mediate competition in this context (Ischer et al., 2020).

Overall, both calls produced in a feeding context appear to have some role in managing social interactions during feeding but it is not yet clear whether their function would be competitive or cooperative.

Study species and site

Study species

Chimpanzees are a territorial primate species living in groups, or 'communities', which usually comprises between 20 to 150 individuals, with natal males and a larger number of females (Goodall, 1986; Muller & Mitani, 2005). Within these communities, individuals associate with each other into temporary subgroups, or 'parties', which vary in size, composition and duration and comprise between 4 to 10 individuals on average (Goodall, 1986; Mitani et al., 2002). Male chimpanzees are philopatric whereas female usually disperse from their natal groups when reaching sexual maturity, i.e., around 11 years of age (Boesch & Boesch-Achermann, 2000; Nishida et al., 2003). Females raise their offspring without paternal investment and have an interbirth interval of five to six years on average, if the offspring survives to weaning (Boesch & Boesch-Achermann, 2000; Nishida et al., 2003; Wrangham & Smuts, 1980). Females usually stay with their offspring or in same-sex parties in the core home-range of their community, whereas males are generally more gregarious (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Muller & Mitani, 2005). Male chimpanzees have a clear linear dominance hierarchy and the top high-ranking males, i.e., alpha and beta males, sire most of the offspring (Langergraber et al., 2013; Vigilant et al., 2001). Chimpanzees mostly feed on ripe fruits, but also occasionally consume insects or hunt vertebrate prey, such as small monkeys (Newton-Fisher, 1999; Nishida & Uehara, 1983; Wrangham, 1977). Their home range can vary between 5 and 30 km^2 (Chapman & Wrangham, 1993; Herbinger et al., 2001; Newton-Fisher, 2003) and individuals, mostly males, defend their territories against neighbouring communities, which can lead to violent conflicts and occasionally result in fatalities (Goodall, 1986; Muller & Mitani, 2005; Watts & Mitani, 2001; Wilson et al., 2014).

Study site

Research was conducted on the Sonso community of East African chimpanzees, *P. t. schweinfurthii*, at the Budongo Conservation Field Station (BCFS), in the Budongo Forest Reserve, located in the western Rift Valley of Uganda (latitude 1°37'N-2°00'N; longitude 31°22'– 31°46'E). The Reserve spreads across 793 km^2 including 482km^2 of continuous, medium-altitude, semi-deciduous rain forest (Eggeling, 1947), which houses an estimated population of approximately 600 wild chimpanzees (Plumptre et al., 2007). The study site was originally set up by Vernon Reynolds in 1990 as the Budongo Forest Project and comprises a system of trails which facilitates the access through the forest (Reynolds, 1992). The Sonso community has a core home-range of around 7km^2 (Newton-Fisher, 2003) and has been habituated to human presence for research purposes for more than 30 years, which allows close observations of the chimpanzees, up to 7m (Reynolds, 2005). Observations of the study community were made between January 2018 and March 2020. At the beginning of the study, the community

was composed of 75 individuals, including 37 adults (>15 years; 11 males; 26 females) and all social and kin relations between individuals are known and continuously updated (Reynolds, 2005). The subjects for this study were the 11 adult males of this community and three of them died of an epidemic in February 2019.

Thesis aim and outline

The aim of this PhD thesis was to investigate how male chimpanzees use vocalisations to manage their social relationships. In this first Chapter, I presented an overview of the ability for certain animal species to bond socially and what evolutionary advantages these social bonds can provide. I also described how vocal communication can be used to establish and maintain social bonds and I highlighted the knowledge gap present in research on chimpanzees, our closest relatives, by identifying the questions that remained to be explored. In the following chapters, I will present how I empirically investigated social bonding between male chimpanzees, more specifically examining social cohesion and the use of vocalisations in two contexts, i.e., feeding and resting, before focusing on male association patterns across contexts.

In Chapter 2, I explore the dual signalling behaviour of chimpanzees during feeding, looking at the vocal production of both context-general, long-distance 'pant hoot' and context-specific, short-distance 'rough grunt' calls by males when actively joining, or passively being joined, in food trees. I consider the effect of social (i.e., audience composition) and ecological variables (i.e., type of food encountered) on vocal production to disentangle the functions of these two calls.

Chapter 3 focuses on the production of a context-specific vocalisation, the 'rest hoo', to investigate its function and determine whether it is produced intentionally. To do so, I explore the potential goal of this call by looking at both signaller's and receiver's behaviour after call production (i.e., time spent resting) and I analyse the audience effect on call production, considering the presence of socially relevant individuals such as preferred social partners.

Chapter 4 describes male dyadic short-term association patterns and evaluates which social variables (i.e., identity of the social partner) affect the time males spend in association. I also investigate whether chimpanzees use tactile (i.e., grooming) or vocal (i.e., production of 'hoo' vocalisations) strategies to manage these associations and thus explore further the cohesive function of the 'hoo' vocalisations.

Finally, in chapter 5, I summarise the results of this thesis and present how these findings can contribute to develop our comprehension of chimpanzee vocal communication and socio-cognitive abilities and, more broadly, to further our understanding of how animal communication systems evolved to mediate complex social systems. I also consider the limitations of this study and propose some directions for future research in the field.

References

Adiseshan, A., Adiseshan, T., & Isbell, L. A. (2011). Affiliative relationships and reciprocity among adult male bonnet macaques (Macaca radiata) at Arunachala Hill, India. *American Journal of Primatology*, *73*(11), 1107–1113. https://doi.org/10.1002/ajp.20987

Aguilar-Melo, A. R., Calmé, S., Smith-Aguilar, S. E., & Ramos-Fernandez, G. (2018). Fission-fusion dynamics as a temporally and spatially flexible behavioral strategy in spider monkeys. *Behavioral Ecology and Sociobiology*, *72*(9). https://doi.org/10.1007/s00265-018-2562-y

Altmann, J. (1979). Age cohorts as paternal sibships. *Behavioral Ecology and Sociobiology*, *6*(2), 161–164. https://doi.org/10.1007/BF00292563

Arcadi, A. C. (1996). Phrase structure of wild chimpanzee pant hoots: Patterns of production and interpopulation variability. *American Journal of Primatology*, *39*(3), 159–178. https://doi.org/10.1002/(SICI)1098-2345(1996)39:3<159::AID-AJP2>3.0.CO;2-Y

Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1793), 20141261. https://doi.org/10.1098/rspb.2014.1261

Arlet, M., Jubin, R., Masataka, N., & Lemasson, A. (2015). Grooming-at-a-distance by exchanging calls in non-human primates. *Biology Letters*, *11*(10), 20150711. https://doi.org/10.1098/rsbl.2015.0711

Asensio, N., Korstjens, A. H., & Aureli, F. (2009). Fissioning minimizes ranging costs in spider monkeys: a multiple-level approach. *Behavioral Ecology and Sociobiology*, *63*(5), 649–659. https://doi.org/10.1007/s00265-008-0699-9

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R. C., Di Fiore, A., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A., Layton, R. H., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernandez, G., Strier, K. B., & Van Schaik, C. P. (2008). Fission-Fusion Dynamics: New Research Frameworks. *Current Anthropology*, *49*(4), 627–654. https://doi.org/10.1086/586708

Aureli, F., van Schaik, C. P., & Van Hooff, J. A. R. A. M. (1989). Functional Aspects of Reconciliation Among Captive Long-Tailed Macaques (Macaca fascicularis). *American Journal of Primatology*, *19*, 39–51.

Babiszewska, M., Schel, A. M., Wilke, C., & Slocombe, K. E. (2015). Social, contextual, and individual factors affecting the occurrence and acoustic structure of drumming bouts in wild chimpanzees (Pan troglodytes). *American Journal of Physical Anthropology*, *156*(1), 125–134. https://doi.org/10.1002/ajpa.22634

Barrett, L., Henzi, P., & Dunbar, R. I. M. (2003). Primate cognition: from "what now?" to "what if?" *Trends in Cognitive Sciences*, *7*(11), 494–497. https://doi.org/10.1016/j.tics.2003.09.005

Berghänel, A., Ostner, J., Schröder, U., & Schülke, O. (2011). Social bonds predict future cooperation in male Barbary macaques, Macaca sylvanus. *Animal Behaviour*, *81*(6), 1109–1116. https://doi.org/10.1016/j.anbehav.2011.02.009

Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, *48*(3), 653–667. https://doi.org/10.1006/anbe.1994.1285

Boesch, C., & Boesch-Achermann, H. (2000). *The Chimpanzees of the Taï Forest*. Oxford University Press.

Boesch, C., Kohou, G., Néné, H., & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Taï forest. *American Journal of Physical Anthropology*, *130*(1), 103–115. https://doi.org/10.1002/ajpa.20341

Bolt, L. M. (2020). Affiliative Contact Calls during Group Travel: Chirp and Wail Vocalization Use in the Male Ring-Tailed Lemur (***Lemur catta***). *Folia Primatologica*, *1*, 1–20. https://doi.org/10.1159/000508808

Bray, J., Pusey, A. E., & Gilby, I. C. (2016). Incomplete control and concessions explain mating skew in male chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1842), 20162071. https://doi.org/10.1098/rspb.2016.2071

Brosnan, S. F., & De Waal, F. B. M. (2000). Regulation of vocal output by chimpanzees finding food in the presence or absence of an audience. *Evolution of Communication*, *4*(2), 211–224.

Busia, L., Schaffner, C. M., & Aureli, F. (2017). Relationship quality affects fission decisions in wild spider monkeys (Ateles geoffroyi). *Ethology*, *123*(6–7), 405–411. https://doi.org/10.1111/eth.12609

Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences*, *106*(33), 13850–13853. https://doi.org/10.1073/pnas.0900639106

Candiotti, A., Zuberbühler, K., & Lemasson, A. (2012). Context-related call combinations in female Diana monkeys. *Animal Cognition*, *15*(3), 327–339. https://doi.org/10.1007/s10071-011-0456-8

Chapais, B. (2006). Kinship, competence and cooperation in primates. In P. M. Kappeler & C. P. Van Schaik (Eds.), *Cooperation in primates and humans: mechanisms and evolution* (pp. 47–64). Springer-Verlag.

Chapman, C. A., & Chapman, L. J. (2000). Determinants of group size in primates: The importance of travel costs. In S. Boinski & P. A. Garber (Eds.), *On the move. How and why animals travel in groups* (The Univer, pp. 24–42).

Chapman, C. A., Chapman, L. J., & Wrangham, R. W. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, *36*(1), 59–70. https://doi.org/10.1007/BF00175729

Chapman, C. A., & Wrangham, R. W. (1993). Range use of the forest chimpanzees of Kibale: Implications for the understanding of chimpanzee social organization. *American Journal of Primatology*, *31*(4), 263–273. https://doi.org/10.1002/ajp.1350310403

Chaverri, G., Gillam, E. H., & Kunz, T. H. (2013). A call-and-response system facilitates group cohesion among disc-winged bats. *Behavioral Ecology*, *24*(2), 481–487. https://doi.org/10.1093/beheco/ars188

Cheney, D. L., & Seyfarth, R. M. (1990). *How Monkeys See the World: Inside the Mind of Another Species*. Chicago University Press.

Cheney, D. L., & Seyfarth, R. M. (2018). Flexible usage and social function in primate vocalizations. *Proceedings of the National Academy of Sciences*, 201717572. https://doi.org/10.1073/pnas.1717572115

Cheney, D. L., Seyfarth, R. M., & Smuts, B. (1986). Social relationships and social cognition in nonhuman primates. *Science*, *234*(4782), 1361–1366. https://doi.org/10.1126/science.3538419

Clark, A. P. (1993). Rank differences in the production of vocalizations by wild chimpanzees as a function of social context. *American Journal of Primatology*, *31*(3), 159–179. http://dx.doi.org/10.1002/ajp.1350310302

Clark, A. P., & Wrangham, R. W. (1994). Chimpanzee Arrival pant hoots: Do Signify Food or Status? *International Journal of Pdmatology*, *15*(2). https://link.springer.com/content/pdf/10.1007%2FBF02735273.pdf

Connor, R. C., Heithaus, M. R., & Barre, L. M. (2001). Complex social structure, alliance stability and mating

access in a bottlenose dolphin 'super-alliance.' *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1464), 263–267. https://doi.org/10.1098/rspb.2000.1357

Conradt, L., & List, C. (2009). Group decisions in humans and animals: a survey. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1518), 719–742. https://doi.org/10.1098/rstb.2008.0276

Conradt, L., & Roper, T. J. (2010). Deciding group movements: Where and when to go. *Behavioural Processes*, *84*(3), 675–677. https://doi.org/10.1016/j.beproc.2010.03.005

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, *433*(7025), 513–516. https://doi.org/10.1038/nature03236

Crockford, C., Gruber, T., & Zuberbühler, K. (2018). Chimpanzee quiet hoo variants differ according to context. *Royal Society Open Science*, *5*(5), 172066. https://doi.org/10.1098/rsos.172066

Crockford, C., Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology*, *22*(2), 142–146. https://doi.org/10.1016/j.cub.2011.11.053

Crockford, C., Wittig, R. M., & Zuberbühler, K. (2015). An intentional vocalization draws others' attention: A playback experiment with wild chimpanzees. *Animal Cognition*, *18*(3), 581–591. https://doi.org/10.1007/s10071-014-0827-z

Crofoot, M. C., & Wrangham, R. W. (2010). Intergroup Aggression in Primates and Humans: The Case for a Unified Theory. In *Mind the Gap* (pp. 171–195). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-02725-3_8

da Cunha, R. G., & Byrne, R. W. (2009). The Use of Vocal Communication in Keeping the Spatial Cohesion of Groups: Intentionality and Specific Functions. In P. A. Garber, A. Estrada, J. C. Bicca-Marques, E. W. Heymann, & K. B. Strier (Eds.), *South American Primates* (Issue May 2014, pp. 341–363). Springer New York. https://doi.org/10.1007/978-0-387-78705-3_13

Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An Introduction to Behavioural Ecology* (John Wiley & Sons (ed.)). SAGE Publications Ltd. https://doi.org/10.4135/9781446211922.n13

De Waal, F. B. M. (1991). Rank distance as a central feature of rhesus monkey social organization: a sociometric analysis. *Animal Behaviour*, *41*(3), 383–395. https://doi.org/10.1016/S0003-3472(05)80839-5

DeCasien, A. R., Williams, S. A., & Higham, J. P. (2017). Primate brain size is predicted by diet but not sociality. *Nature Ecology & Evolution*, *1*(5), 0112. https://doi.org/10.1038/s41559-017-0112

Dennett, D. C. (1971). Intentional systems. *The Journal of Philosophy*, *68*(4), 87–106.

Dennett, D. C. (1983). Intentional systems in cognitive ethology: The "Panglossian paradigm" defended. *Behavioral and Brain Sciences*, *6*(03), 343. https://doi.org/10.1017/S0140525X00016393

Duffy, K. G., Wrangham, R. W., & Silk, J. B. (2007). Male chimpanzees exchange political support for mating opportunities. *Current Biology*, *17*(15), R586–R587. https://doi.org/10.1016/j.cub.2007.06.001

Dunbar, R. I. M. (1988). *Primate social systems*. Cornell University Press.

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

Dunbar, R. I. M. (2011). Evolutionary Basis of the Social Brain. In J. Decety & J. T. Cacioppo (Eds.), *The Oxford Handbook of Social Neuroscience*. Oxford University Press, Oxford. https://doi.org/10.1093/oxfordhb/9780195342161.013.0003

Dunbar, R. I. M., & Shultz, S. (2010). Bondedness and sociality. *Behaviour*, *147*(7), 775–803.

https://doi.org/10.1163/000579510X501151

Eckhardt, N., Polansky, L., & Boesch, C. (2015). Spatial cohesion of adult male chimpanzees (Pan troglodytes verus) in Taï National Park, Côte d'Ivoire. *American Journal of Primatology*, *77*(2), 125–134. https://doi.org/10.1002/ajp.22316

Eggeling, W. J. (1947). Observations on the Ecology of the Budongo Rain Forest, Uganda. *The Journal of Ecology*, *34*(1), 20. https://doi.org/10.2307/2256760

Enigk, D. K., Thompson, M. E., Machanda, Z. P., Wrangham, R. W., & Muller, M. N. (2020). Competitive ability determines coalition participation and partner selection during maturation in wild male chimpanzees (Pan troglodytes schweinfurthii). *Behavioral Ecology and Sociobiology*, *74*(7), 89. https://doi.org/10.1007/s00265-020-02872-7

Fedurek, P., Donnellan, E., & Slocombe, K. E. (2014). Social and ecological correlates of long-distance pant hoot calls in male chimpanzees. *Behavioral Ecology and Sociobiology*, *68*(8), 1345–1355. https://doi.org/10.1007/s00265-014-1745-4

Fedurek, P., Machanda, Z. P., Schel, A. M., & Slocombe, K. E. (2013). pant hoot chorusing and social bonds in male chimpanzees. *Animal Behaviour*, *86*(1), 189–196. https://doi.org/10.1016/j.anbehav.2013.05.010

Fedurek, P., Zuberbühler, K., & Dahl, C. D. (2016). Sequential information in a great ape utterance. *Scientific Reports*, *6*(1), 38226. https://doi.org/10.1038/srep38226

Feldblum, J. T., Krupenye, C., Bray, J., Pusey, A. E., & Gilby, I. C. (2021). Social bonds provide multiple pathways to reproductive success in wild male chimpanzees. *IScience*, *24*(8), 102864. https://doi.org/10.1016/j.isci.2021.102864

Fischer, J. (2008). Transmission of acquired information in nonhuman primates. In J. H. Byrne (Ed.), *Learning and memory: A comprehensive reference* (pp. 299–313). Elsevier.

Genty, E., Breuer, T., Hobaiter, C., & Byrne, R. W. (2009). Gestural communication of the gorilla (Gorilla gorilla): Repertoire, intentionality and possible origins. *Animal Cognition*, *12*(3), 527–546. https://doi.org/10.1007/s10071-009-0213-4

Gerber, L., Connor, R. C., King, S. L., Allen, S. J., Wittwer, S., Bizzozzero, M. R., Friedman, W. R., Kalberer, S., Sherwin, W. B., Wild, S., Willems, E. P., & Krützen, M. (2020). Affiliation history and age similarity predict alliance formation in adult male bottlenose dolphins. *Behavioral Ecology*, *31*(2), 361–370. https://doi.org/10.1093/beheco/arz195

Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, *67*(3), 373–381. https://doi.org/10.1007/s00265-012-1457-6

Gilby, I. C., & Wrangham, R. W. (2008). Association patterns among wild chimpanzees (Pan troglodytes schweinfurthii) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology*, *62*(11), 1831–1842. https://doi.org/10.1007/s00265-008-0612-6

Goodall, J. (1986). *The chimpanzees of Gombe: patterns of behavior*. Harvard University Press.

Greeno, N. C., & Semple, S. (2009). Sex differences in vocal communication among adult rhesus macaques. *Evolution and Human Behavior*, *30*(2), 141–145. https://doi.org/10.1016/j.evolhumbehav.2008.09.002

Grinnell, J. (2002). Modes of cooperation during territorial defense by African lions. *Human Nature*, *13*(1), 85–104.

Gruber, T., & Zuberbühler, K. (2013). Vocal Recruitment for Joint Travel in Wild Chimpanzees. *PLoS ONE*, *8*(9), e76073. https://doi.org/10.1371/journal.pone.0076073

Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, *7*(1), 1–16. https://doi.org/10.1016/0022-5193(64)90038-4

Harcourt, A. H., & Stewart, K. J. (1996). Function and meaning of wild gorilla "close" calls 2. Correlations with rank and relatedness. *Behaviour*, *133*(11–12), 827–845. https://doi.org/10.1163/156853996X00260

Hartwell, K. S., Notman, H., & Pavelka, M. S. M. (2018). Seasonal and sex differences in the fission–fusion dynamics of spider monkeys (Ateles geoffroyi yucatanensis) in Belize. *Primates*, *59*(6), 531–539. https://doi.org/10.1007/s10329-018-0685-4

Hauser, M. D., & Marler, P. (1993). Food-associated calls in rhesus macaques (Macaca mulatta): I. Socioecological factors. *Behavioral Ecology*, *4*(3), 194–205. https://doi.org/10.1093/beheco/4.3.194

Hauser, M. D., Teixidor, P., Fields, L., & Flaherty, R. (1993). Food-elicited calls in chimpanzees: effects of food quantity and divisibility. *Animal Behaviour*, *45*(4), 817–819. https://doi.org/10.1006/anbe.1993.1096

Hauser, M. D., & Wrangham, R. W. (1987). Manipulation of food calls in captive chimpanzees: A preliminary report. *Folia Primatologica*, *48*(3–4), 207–210. https://doi.org/10.1159/000156298

Herbinger, I., Boesch, C., & Rothe, H. (2001). Territory characteristics among three neighboring chimpanzee communities in the Taï National Park, Côte d'Ivoire. *International Journal of Primatology*, *22*(2), 143–167. https://doi.org/10.1023/A:1005663212997

Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man*, *11*(1), 1. https://doi.org/10.2307/2800384

Hobaiter, C., Samuni, L., Mullins, C., Akankwasa, W. J., & Zuberbühler, K. (2017). Variation in hunting behaviour in neighbouring chimpanzee communities in the Budongo forest, Uganda. *PLOS ONE*, *12*(6), e0178065. https://doi.org/10.1371/journal.pone.0178065

Hruschka, D. J. (2010). *Friendship: development, ecology, and evolution of a relationship*. University of California Press, Berkeley.

Hruschka, D. J., & Silk, J. B. (2017). Cooperative Relationships. In *Emerging Trends in the Social and Behavioral Sciences* (pp. 1–16). Wiley. https://doi.org/10.1002/9781118900772.etrds0427

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

Ischer, G., Zuberbühler, K., & Fedurek, P. (2020). The relationship between food calling and agonistic behaviour in wild chimpanzees. *Behavioural Processes*, *178*(May), 104182. https://doi.org/10.1016/j.beproc.2020.104182

Jacobs, A. (2010). Group cohesiveness during collective movements: Travelling apart together. *Behavioural Processes*, *84*(3), 678–680. https://doi.org/10.1016/j.beproc.2010.03.004

Jeschke, J. M., & Tollrian, R. (2007). Prey swarming: which predators become confused and why? *Animal Behaviour*, *74*(3), 387–393. https://doi.org/10.1016/j.anbehav.2006.08.020

Keeler, J. R., Roth, E. A., Neuser, B. L., Spitsbergen, J. M., Waters, D. J. M., & Vianney, J.-M. (2015). The neurochemistry and social flow of singing: bonding and oxytocin. *Frontiers in Human Neuroscience*, *9*(September), 1–10. https://doi.org/10.3389/fnhum.2015.00518

Kerth, G. (2010). Group decision-making in animal societies. In *Animal Behaviour: Evolution and Mechanisms*

(pp. 241–265). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-02624-9_9

King, A. J., & Sueur, C. (2011). Where Next? Group Coordination and Collective Decision Making by Primates. *International Journal of Primatology*, *32*(6), 1245–1267. https://doi.org/10.1007/s10764-011-9526-7

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.

Krebs, J. R., & Davies, N. B. (2009). *Behavioural ecology: an evolutionary approach* (J. R. Krebs & N. B. Davies (eds.)). John Wiley & Sons.

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

Kummer, H. (1968). *Social organization of Hamadryas Baboons, a field study*. University of Chicago Press.

Kummer, H. (1971). *Primate societies – group techniques of ecological adaptation*. Aldine Publishing Company.

Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences*, *104*(19), 7786–7790. https://doi.org/10.1073/pnas.0611449104

Langergraber, K. E., Mitani, J. C., Watts, D. P., & Vigilant, L. (2013). Male–female socio-spatial relationships and reproduction in wild chimpanzees. *Behavioral Ecology and Sociobiology*, *67*(6), 861–873. https://doi.org/10.1007/s00265-013-1509-6

Laporte, M. N. C., & Zuberbühler, K. (2011). The development of a greeting signal in wild chimpanzees. *Developmental Science*, *14*(5), 1220–1234. https://doi.org/10.1111/j.1467-7687.2011.01069.x

Leavens, D. A., & Hopkins, W. D. (1998). Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology*, *34*(5), 813–822. https://doi.org/10.1037/0012-1649.34.5.813

Leendertz, F. H., Ellerbrok, H., Boesch, C., Couacy-Hymann, E., Mätz-Rensing, K., Hakenbeck, R., Bergmann, C., Abaza, P., Junglen, S., Moebius, Y., Vigilant, L., Formenty, P., & Pauli, G. (2004). Anthrax kills wild chimpanzees in a tropical rainforest. *Nature*, *430*(6998), 451–452. https://doi.org/10.1038/nature02722

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case. *Evolutionary Ecology*, *21*(5), 613–634. https://doi.org/10.1007/s10682-006-9141-9

Lusseau, D. (2007). Why Are Male Social Relationships Complex in the Doubtful Sound Bottlenose Dolphin Population? *PLoS ONE*, *2*(4), e348. https://doi.org/10.1371/journal.pone.0000348

Marler, P. (1976). Social organization, communication and graded signals: The chimpanzee and the gorilla. In P. P. Bateson & R. A. Hinde (Eds.), *Growing points in ethology*. Cambridge University Press.

Marler, P., & Tenaza, R. (1977). Signaling behavior of apes with special reference to vocalizations. In *How Animals Communicate* (pp. 965–1033). Indiana University Press.

Marlowe, F. W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *14*(2), 54–67. https://doi.org/10.1002/evan.20046

Massen, J., Sterck, E., & de Vos, H. (2010). Close social associations in animals and humans: functions and mechanisms of friendship. *Behaviour*, *147*(11), 1379–1412. https://doi.org/10.1163/000579510X528224

McComb, K., & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. *Biology Letters*, *1*(4), 381–385. https://doi.org/10.1098/rsbl.2005.0366

Mielke, A., Samuni, L., Preis, A., Gogarten, J. F., Crockford, C., & Wittig, R. M. (2017). Bystanders intervene to impede grooming in Western chimpanzees and sooty mangabeys. *Royal Society Open Science*, *4*(11), 171296. https://doi.org/10.1098/rsos.171296

Mitani, J. C. (2009a). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, *77*(3), 633–640. https://doi.org/10.1016/j.anbehav.2008.11.021

Mitani, J. C. (2009b). Cooperation and competition in chimpanzees: Current understanding and future challenges. *Evolutionary Anthropology: Issues, News, and Reviews*, *18*(5), 215–227. https://doi.org/10.1002/evan.20229

Mitani, J. C., & Amsler, S. (2003). Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour*, *140*(7), 869–884. https://doi.org/10.1163/156853903770238355

Mitani, J. C., & Brandt, K. L. (1994). Social Factors Influence the Acoustic Variability in the Long-distance Calls of Male Chimpanzees. *Ethology*, *96*(3), 233–252. https://doi.org/10.1111/j.1439-0310.1994.tb01012.x

Mitani, J. C., & Gros-Louis, J. (1998). Chorusing and Call Convergence in Chimpanzees: Tests of Three Hypotheses. *Behaviour*, *135*(8), 1041–1064. https://doi.org/10.1163/156853998792913483

Mitani, J. C., Merriwether, D. A., & Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour*, *59*(4), 885–893. https://doi.org/10.1006/anbe.1999.1389

Mitani, J. C., & Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. *Animal Behaviour*, *45*(4), 735–746. https://doi.org/10.1006/anbe.1993.1088

Mitani, J. C., Watts, D. P., Pepper, J. W., & Merriwether, D. A. (2002). Demographic and social constraints on male chimpanzee behaviour. *Animal Behaviour*, *64*(5), 727–737. https://doi.org/10.1006/anbe.2002.4014

Mocha, Y. Ben, Mundry, R., & Pika, S. (2019). Joint attention skills in wild Arabian babblers (Turdoides squamiceps): A consequence of cooperative breeding? *Proceedings of the Royal Society B: Biological Sciences*, *286*(1900). https://doi.org/10.1098/rspb.2019.0147

Moore, R. (2016). Gricean Communication and Cognitive Development. *The Philosophical Quarterly*, *00*(0). https://doi.org/10.13140/RG.2.1.1875.6000

Muller, M. N., & Mitani, J. C. (2005). Conflict and Cooperation in Wild Chimpanzees. In *Advances in the Study of Behavior* (Vol. 35, pp. 275–331). https://doi.org/10.1016/S0065-3454(05)35007-8

Newton-Fisher, N. E. (1999). The diet of chimpanzees in the Budongo Forest Reserve, Uganda. *African Journal of Ecology*, *37*, 344–354. https://onlinelibrary.wiley.com/doi/full/10.1046/j.1365-2028.1999.00186.x?casa_token=Fu6D03Wj1dcAAAAA%3AbPyosUMT-mvJRE_iLiCqQa05u8EVR-5QRzZg4moemmHssmKjaMtzqkQNP43DeWNGIrHS_7VOdaTPyn4

Newton-Fisher, N. E. (2003). The home range of the Sonso community of chimpanzees from the Budongo Forest, Uganda. *African Journal of Ecology*, *41*(2), 150–156. https://doi.org/10.1046/j.1365-2028.2003.00408.x

Newton-Fisher, N. E., Thompson, M. E., Reynolds, V., Boesch, C., & Vigilant, L. (2009). Paternity and social rank in wild chimpanzees (Pan troglodytes) from the Budongo Forest, Uganda. *American Journal of Physical Anthropology*, *142*(3), 417–428. https://doi.org/10.1002/ajpa.21241

Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., Hunt, K. D., Itoh, N., Kawanaka, K., Matsumoto-Oda, A., Mitani, J. C., Nakamura, M., Norikoshi, K., Sakamaki, T., Turner, L.,

Uehara, S., & Zamma, K. (2003). Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology*, *59*(3), 99–121. https://doi.org/10.1002/ajp.10068

Nishida, T., & Uehara, S. (1983). Natural diet of chimpanzees (Pan troglodyets schweinfuthii): Long-term record from the Mahale Mountains , Tanzania. *African Study Monographs*, *3*, 109–130.

Notman, H., & Rendall, D. (2005). Contextual variation in chimpanzee pant hoots and its implications for referential communication. *Animal Behaviour*, *70*(1), 177–190. https://doi.org/10.1016/j.anbehav.2004.08.024

Oda, R. (1996). Effects of contextual and social variables on contact call production in free-ranging ringtailed lemurs (Lemur catta). *International Journal of Primatology*, *17*(2), 191–205. https://doi.org/10.1007/BF02735447

Ostner, J., & Schülke, O. (2014). The evolution of social bonds in primate males. *Behaviour*, *151*(7), 871–906. https://doi.org/10.1163/1568539X-00003191

Papworth, S., Bose, A.-S., Barker, J., Schel, A. M., & Zuberbühler, K. (2008). Male blue monkeys alarm call in response to danger experienced by others. *Biology Letters*, *4*(5), 472–475. https://doi.org/10.1098/rsbl.2008.0299

Pepper, J. W., Mitani, J. C., & Watts, D. P. (1999). General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology*, *20*(5), 613–632. https://doi.org/10.1023/A:1020760616641

Petit, O., & Bon, R. (2010). Decision-making processes: The case of collective movements. *Behavioural Processes*, *84*(3), 635–647. https://doi.org/10.1016/j.beproc.2010.04.009

Pika, S., & Bugnyar, T. (2011). The use of referential gestures in ravens (Corvus corax) in the wild. *Nature Communications*, *2*, 560. https://doi.org/10.1038/ncomms1567

Pika, S., Liebal, K., Call, J., & Tomasello, M. (2005). Gestural communication of apes. *Gesture*, *5*(1–2), 41–56. https://doi.org/10.1075/gest.5.1.05pik

Plumptre, A. J., Davenport, T. R. B., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., Ewango, C., Meirte, D., Kahindo, C., Herremans, M., Peterhans, J. K., Pilgrim, J. D., Wilson, M., Languy, M., & Moyer, D. (2007). The biodiversity of the Albertine Rift. *Biological Conservation*, *134*(2), 178–194. https://doi.org/10.1016/j.biocon.2006.08.021

Powell, L. E., Isler, K., & Barton, R. A. (2017). Re-evaluating the link between brain size and behavioural ecology in primates. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1865), 20171765. https://doi.org/10.1098/rspb.2017.1765

Preis, A., Samuni, L., Mielke, A., Deschner, T., Crockford, C., & Wittig, R. M. (2018). Urinary oxytocin levels in relation to post-conflict affiliations in wild male chimpanzees (Pan troglodytes verus). *Hormones and Behavior*, *105*(March), 28–40. https://doi.org/10.1016/j.yhbeh.2018.07.009

Ramos-Fernández, G. (2005). Vocal Communication in a Fission-Fusion Society: Do Spider Monkeys Stay in Touch With Close Associates? *International Journal of Primatology*, *26*(5), 1077–1092. https://doi.org/10.1007/s10764-005-6459-z

Ramos-Fernández, G., & Morales, J. M. (2014). Unraveling fission-fusion dynamics: how subgroup properties and dyadic interactions influence individual decisions. *Behavioral Ecology and Sociobiology*, *68*(8), 1225–

1235. https://doi.org/10.1007/s00265-014-1733-8

Rendall, D., Seyfarth, R. M., Cheney, D. L., & Owren, M. J. (1999). The meaning and function of grunt variants in baboons. *Animal Behaviour*, *57*(3), 583–592. https://doi.org/10.1006/anbe.1998.1031

Reynolds, V. (1992). Chimpanzees in the Budongo Forest, 1962–1992. *Journal of Zoology*, *228*(4), 695–699. https://doi.org/10.1111/j.1469-7998.1992.tb04470.x

Reynolds, V. (2005). *The chimpanzees of the Budongo forest: Ecology, behaviour and conservation* (Oxford Uni).

Reynolds, V., & Reynolds, R. (1965). Chimpanzees of the Budongo Forest. In *Primate behavior: field studies of monkeys and apes* (pp. 368–424). Rinehart & Winston.

Rosati, A. G. (2017). Foraging Cognition: Reviving the Ecological Intelligence Hypothesis. *Trends in Cognitive Sciences*, *21*(9), 691–702. https://doi.org/10.1016/j.tics.2017.05.011

Rosenbaum, S., Hirwa, J. P., Silk, J. B., & Stoinski, T. S. (2016). Relationships Between Adult Male and Maturing Mountain Gorillas (Gorilla beringei beringei) Persist Across Developmental Stages and Social Upheaval. *Ethology*, *122*(2), 134–150. https://doi.org/10.1111/eth.12457

Samuni, L., Crockford, C., & Wittig, R. M. (2021). Group-level cooperation in chimpanzees is shaped by strong social ties. *Nature Communications*, *12*(1), 539. https://doi.org/10.1038/s41467-020-20709-9

Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R. M., & Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1888). https://doi.org/10.1098/rspb.2018.1643

Schel, A. M., Townsend, S. W., Machanda, Z. P., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee Alarm Call Production Meets Key Criteria for Intentionality. *PLoS ONE*, *8*(10), e76674. https://doi.org/10.1371/journal.pone.0076674

Schino, G. (2001). Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour*, *62*(2), 265–271. https://doi.org/10.1006/anbe.2001.1750

Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social Bonds Enhance Reproductive Success in Male Macaques. *Current Biology*, *20*(24), 2207–2210. https://doi.org/10.1016/j.cub.2010.10.058

Scott-Phillips, T. C. (2016). Meaning in great ape communication: summarising the debate. *Animal Cognition*, *19*(1), 233–238. https://doi.org/10.1007/s10071-015-0936-3

Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, *65*(4), 671–698. https://doi.org/10.1016/0022-5193(77)90015-7

Seyfarth, R. M., & Cheney, D. L. (2012). The Evolutionary Origins of Friendship. *Annual Review of Psychology*, *63*(1), 153–177. https://doi.org/10.1146/annurev-psych-120710-100337

Shultz, S., & Dunbar, R. I. M. (2010). Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. *Biological Journal of the Linnean Society*, *100*(1), 111–123. https://doi.org/10.1111/j.1095-8312.2010.01427.x

Sibly, R. M. (1983). Optimal group size is unstable. *Animal Behaviour*, *31*(3), 947–948. https://doi.org/10.1016/S0003-3472(83)80250-4

Silk, J. B. (1994). *Social Relationships of Male Bonnet Macaques : Male Bonding in a Matrilineal Society*. *130*(3), 271–291.

Silk, J. B. (2002). Kin Selection in Primate Groups. *International Journal of Primatology*, *23*(4), 849–875.

https://doi.org/10.1023/A:1015581016205

Silk, J. B. (2007). Social Components of Fitness in Primate Groups. *Science*, *317*(5843), 1347–1351. https://doi.org/10.1126/science.1140734

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social Bonds of Female Baboons Enhance Infant Survival. *Science*, *302*(5648), 1231–1234. https://doi.org/10.1126/science.1088580

Silk, J. B., Alberts, S. C., Altmann, J., Cheney, D. L., & Seyfarth, R. M. (2012). Stability of partner choice among female baboons. *Animal Behaviour*, *83*(6), 1511–1518. https://doi.org/10.1016/j.anbehav.2012.03.028

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2009). The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1670), 3099–3104. https://doi.org/10.1098/rspb.2009.0681

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010). Strong and Consistent Social Bonds Enhance the Longevity of Female Baboons. *Current Biology*, *20*(15), 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067

Silk, J. B., Cheney, D. L., & Seyfarth, R. M. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology: Issues, News, and Reviews*, *22*(5), 213–225. https://doi.org/10.1002/evan.21367

Silk, J. B., Seyfarth, R. M., & Cheney, D. L. (1999). *The Structure of Social Relationships among Female Savanna Baboons in Moremi Reserve, Botswana*. *136*(6), 679–703.

Slocombe, K. E., & Zuberbühler, K. (2005). Functionally Referential Communication in a Chimpanzee. *Current Biology*, *15*(19), 1779–1784. https://doi.org/10.1016/j.cub.2005.08.068

Slocombe, K. E., & Zuberbühler, K. (2006). Food-associated calls in chimpanzees: responses to food types or food preferences? *Animal Behaviour*, *72*(5), 989–999. https://doi.org/10.1016/j.anbehav.2006.01.030

Slocombe, K. E., & Zuberbühler, K. (2010). Vocal communication in chimpanzees. In E. V. Lonsdorf, S. R. Ross, & T. Matsuzawa (Eds.), *The mind of the chimpanzee* (pp. 192–207). The University of Chicago Press.

Smith, J. E. (2014). Hamilton's legacy: kinship, cooperation and social tolerance in mammalian groups. *Animal Behaviour*, *92*, 291–304. https://doi.org/10.1016/j.anbehav.2014.02.029

Smith, J. E., Powning, K. S., Dawes, S. E., Estrada, J. R., Hopper, A. L., Piotrowski, S. L., & Holekamp, K. E. (2011). Greetings promote cooperation and reinforce social bonds among spotted hyaenas. *Animal Behaviour*, *81*(2), 401–415. https://doi.org/10.1016/j.anbehav.2010.11.007

Soltis, J., Bernhards, D., Donkin, H., & Newman, J. D. (2002). Squirrel monkey chuck call: vocal response to playback chucks based on acoustic structure and affiliative relationship with the caller. *American Journal of Primatology*, *57*(3), 119–130. https://doi.org/10.1002/ajp.10039

Strandburg-Peshkin, A., Papageorgiou, D., Crofoot, M. C., & Farine, D. R. (2018). Inferring influence and leadership in moving animal groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170006. https://doi.org/10.1098/rstb.2017.0006

Stueckle, S., & Zinner, D. (2008). To follow or not to follow: decision making and leadership during the morning departure in chacma baboons. *Animal Behaviour*, *75*(6), 1995–2004.

https://doi.org/10.1016/j.anbehav.2007.12.012

Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., Schaffner, C. M., Williams, L., Zinner, D., & Aureli, F. (2011). Collective decision-making and fission-fusion dynamics: a conceptual framework. *Oikos*, *120*(11), 1608–1617. https://doi.org/10.1111/j.1600-0706.2011.19685.x

Sueur, C., Petit, O., & Deneubourg, J. L. (2010). Short-term group fission processes in macaques: a social networking approach. *Journal of Experimental Biology*, *213*(8), 1338–1346. https://doi.org/10.1242/jeb.039016

Surbeck, M., Girard-Buttoz, C., Boesch, C., Crockford, C., Fruth, B., Hohmann, G., Langergraber, K. E., Zuberbühler, K., Wittig, R. M., & Mundry, R. (2017). Sex-specific association patterns in bonobos and chimpanzees reflect species differences in cooperation. *Royal Society Open Science*, *4*(5), 161081. https://doi.org/10.1098/rsos.161081

Symington, M. M. (1990). Fission-Fusion Social Organization in Ateles and Pan. *International Journal of Primatology*, *11*(1), 47–61.

Tokuda, M., Boubli, J. P., Izar, P., & Strier, K. B. (2012). Social cliques in male northern muriquis Brachyteles hypoxanthus. *Current Zoology*, *58*(2), 342–352. https://doi.org/10.1093/czoolo/58.2.342

Townsend, S. W., Koski, S. E., Byrne, R. W., Slocombe, K. E., Bickel, B., Boeckle, M., Braga Goncalves, I., Burkart, J. M., Flower, T., Gaunet, F., Glock, H. J., Gruber, T., Jansen, D. A. W. A. M., Liebal, K., Linke, A., Miklósi, Á., Moore, R., van Schaik, C. P., Stoll, S., … Manser, M. B. (2017). Exorcising Grice's ghost: an empirical approach to studying intentional communication in animals. *Biological Reviews*, *92*(3), 1427–1433. https://doi.org/10.1111/brv.12289

Tsai, Y.-J. J., & Mann, J. (2013). Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. *Marine Mammal Science*, *29*(2), 261–279. https://doi.org/10.1111/j.1748-7692.2011.00559.x

Vail, A., Manica, A., & Bshary, R. (2013). Referential gestures in fish collaborative hunting. *Nature Communications*, *4*(April), 1765. https://doi.org/10.1038/ncomms2781

Vigilant, L., Hofreiter, M., Siedel, H., & Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences*, *98*(23), 12890–12895. https://doi.org/10.1073/pnas.231320498

von Rueden, C., Gavrilets, S., & Glowacki, L. (2015). Solving the puzzle of collective action through inter-individual differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1683), 20150002. https://doi.org/10.1098/rstb.2015.0002

Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, *44*(1), 43–55. https://doi.org/10.1007/s002650050513

Watts, D. P. (2000a). Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. *International Journal of Primatology*, *21*(2), 189–210. https://doi.org/10.1023/A:1005469302911

Watts, D. P. (2000b). Grooming between male chimpanzees at Ngogo, Kibale National Park. II. Influence of male rank and possible competition for partners. *International Journal of Primatology*, *21*(2), 211–238. https://doi.org/10.1023/A:1005421419749

Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, *138*(3), 299–327. https://doi.org/10.1163/15685390152032488

Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour*, *75*(2), 333–344. https://doi.org/10.1016/j.anbehav.2007.06.020

White, F. J., & Burgman, M. A. (1990). Social organization of the pygmy chimpanzee (Pan paniscus): Multivariate analysis of intracommunity associations. *American Journal of Physical Anthropology*, *83*(2), 193–201. https://doi.org/10.1002/ajpa.1330830208

Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., Hobaiter, C., Hohmann, G., Itoh, N., Koops, K., Lloyd, J. N., Matsuzawa, T., Mitani, J. C., Mjungu, D. C., Morgan, D., Muller, M. N., Mundry, R., Nakamura, M., Pruetz, J., … Wrangham, R. W. (2014). Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature*, *513*(7518), 414–417. https://doi.org/10.1038/nature13727

Wittig, R. M., Crockford, C., Deschner, T., Langergraber, K. E., Ziegler, T. E., & Zuberbühler, K. (2014). Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1778), 20133096. https://doi.org/10.1098/rspb.2013.3096

Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe national park, Tanzania. In T. H. Clutton-Brock (Ed.), *Primate ecology: studies of feeding and ranging behavior in lemurs monkeys and apes.* (pp. 503–538). Academic Press, London.

Wrangham, R. W., Gittleman, J. L., & Chapman, C. A. (1993). Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behavioral Ecology and Sociobiology*, *32*(3), 199–209. https://doi.org/10.1007/BF00173778

Wrangham, R. W., & Smuts, B. (1980). Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility*, *Supplement*, 13–31.

Wrangham, R. W., Wilson, M. L., & Hauser, M. D. (2007). Chimpanzees (Pan troglodytes) modify grouping and vocal behaviour in response to location-specific risk. *Behaviour*, *144*(12), 1621–1653. https://doi.org/10.1163/156853907782512137

Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., & Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, Pan troglodytes schweinfurthii. *Animal Behaviour*, *77*(4), 873–885. https://doi.org/10.1016/j.anbehav.2008.12.014

Chapter 2. Male chimpanzees communicate to mediate competition and cooperation during feeding

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Manuscript published in 2022 in Animal Behaviour, 186, 41–55 (DOI: 10.1016/j.anbehav.2022.01.009).

Abstract

An ongoing debate in animal behaviour research is whether food calls function to cooperatively inform others or provide the caller with competitive advantages. When feeding, chimpanzees produce two types of calls: context-specific, close-range 'rough grunts' and context-general, long-range 'pant hoots'. We investigated this dual signalling behaviour by wild male chimpanzees who were either actively joining others or passively being joined in food trees, considering the effects of the audience composition and the type of food encountered. For arriving individuals, we found that pant hoot production was best explained by the absence of socially important individuals (i.e., social bond partners and/or high-ranking males), suggesting that callers were cooperatively informing them about food availability, probably to strengthen social relationships. In contrast, rough grunts were mostly produced by low-ranking individuals, suggesting they were part of competitive interactions to avoid aggression. For individuals already in a tree, we found that both rough grunt and pant hoot production was most common in low-ranking individuals reacting to the arrival of high-ranking males and there was no significant effect of the presence, or absence, of social bond partners. We discuss these patterns and conclude that, when chimpanzees enter a food tree, their vocal behaviour functions to mediate both cooperative and competitive interactions.

Introduction

Living in social groups is an evolutionary strategy that carries a range of advantages, such as reduced risk of predation, improved access to food and mating partners or increased protection from ectoparasites through social grooming (Chapman & Chapman, 2000; Crofoot & Wrangham, 2010; Davies et al., 2012; Grinnell, 2002; Jeschke & Tollrian, 2007). Group living also carries costs, such as higher risks of pathogen transmission and increased foraging and mating competition (Davies et al., 2012; Gruber et al., 2016; Krause & Ruxton, 2002; Leendertz et al., 2004; Wrangham et al., 1993).

Some species have evolved mechanisms to mitigate the costs of social living, by allowing individualised spatial decisions, which will inevitably lead to the formation of temporary groups (i.e., subgroups): a fission-fusion society (Conradt & Roper, 2010; Jacobs, 2010; Kerth, 2010). The term fission-fusion was first used to describe the social system of hamadryas baboons (Kummer, 1971) and refers to continuous changes in group composition, subgroup size and dispersion of subgroups (Aureli et al., 2008; Ramos-Fernández & Morales, 2014). For example, if food resources are evenly scattered, rather than clumped, travelling in large groups

becomes inefficient and leads to fission whereas large food patches can lead to fusions of subgroups (Hartwell et al., 2018; Krebs & Davies, 2009; Lehmann et al., 2007). However, changes in subgroup size are not always responses to food availability (Asensio et al., 2009; Chapman et al., 1995; Kummer, 1971; Symington, 1990) but often also reflections of social affiliations or reproduction strategies (bottlenose dolphins, Lusseau, 2007; Tonkean and rhesus macaques, Sueur et al., 2010; Northern muriquis, Tokuda et al., 2012; spider monkeys, Busia et al., 2017; chimpanzees, Mitani & Amsler, 2003). Although fission-fusion dynamics minimise competition, they also introduce variability in social interaction and uncertainty about social relations (Hinde, 1976; Wey et al., 2008). In species with high degrees of fission-fusion, subgroup composition is the result of individual decisions, in contrast to more stable groups where decision-making is a collective process (Conradt & List, 2009; Couzin et al., 2005; Ramos-Fernandez & Aureli, 2018).

According to the social intelligence hypothesis (Humphrey, 1976), the size of the brain and the cognitive abilities of a species should be positively correlated with its degree of social complexity (Dunbar, 1998, 2011). For this reason, it has been argued that living in fission-fusion societies favours the evolution of social intelligence compared to social systems with invariable group sizes (Barrett et al., 2003). Indeed, within the haplorrhine primates, fission-fusion dynamics has been reported for spider monkeys (Chapman, 1990), hamadryas baboons (Kummer, 1968), bonobos (White & Burgman, 1990), chimpanzees (Goodall, 1986) and humans (Marlowe, 2005), all of which have relatively large brains (Stephan et al., 1981). Contrastingly, other studies have found evidence that primate brain size is correlated to ecological (i.e., diet, home range size, terrestriality and activity period), rather than social, variables, thus supporting the ecological intelligence hypothesis (DeCasien et al., 2017; Powell et al., 2017). However, the social and ecological intelligence hypotheses are not necessarily exclusive and could be integrated as complementary ideas that would explain the evolution of different domains of cognition (Rosati, 2017).

In chimpanzees, changes in group composition often occur during transitions from traveling to feeding and vice versa. Arrivals at food trees can be emotionally charged events that are prone to outbreaks of severe aggression (Ischer et al., 2020; Muller & Mitani, 2005). However, the discovery of a food source also brings crucial opportunities to strengthen social bonds, for instance through tolerated co-feeding or occasional food sharing (Samuni et al., 2018; Wittig et al., 2014). In chimpanzees, male bonding has important fitness consequences as it is a basis for trust and support during various activities, such as cooperative hunting (Hobaiter et al., 2017), intergroup aggression (Herbinger et al., 2009; Wilson et al., 2014), predator defence (Boesch, 1991) and intragroup conflicts (Goodall, 1986; Mitani, 2009; Muller & Mitani, 2005). Associating with high-ranking males can therefore be beneficial (Bray et al., 2016; Duffy et al., 2007; Kaburu & Newton-Fisher, 2015). However, not all males are equally successful in establishing social bonds and often differ in their preferred partners, which may have fitness consequences (Boesch et al., 2006; Feldblum et al., 2021; Muller & Mitani, 2005; Newton-Fisher et al., 2009; Wroblewski et al., 2009). It is therefore unsurprising that chimpanzees communicate prior to and during feeding, which provides rich opportunities to determine the function and meaning of the signals involved (for a review see Clay et al., 2012; Chapman & Lefebvre, 1990; Elgar, 1986; Laidre, 2006).

Chimpanzees produce two types of calls in relation to feeding events: long-distance ‘pant hoots’ and short-distance ‘rough grunts’ (Goodall, 1986; Marler & Tenaza, 1977; Reynolds & Reynolds, 1965). Pant hoots are structurally complex calls that consist of four distinct units (introduction, build-up, climax, let-down; Fedurek et

al., 2016). These calls are mainly produced by adult males, often as choruses and in a variety of situations, although the let-down unit can be discriminated into two variants, one linked to travel and another linked to food (Fedurek et al., 2016; Notman & Rendall, 2005). Pant hoots travel over long-distances, often combined with drumming displays, suggesting that they function to inform distant group members about the presence of food or direction of travel (Babiszewska et al., 2015; Reynolds & Reynolds, 1965; Wrangham, 1977). Pant hoots also convey other information, such as the rank and identity of the caller (Fedurek et al., 2016) and call production is governed by social factors, such as rank or party size and composition (Clark, 1993; Clark & Wrangham, 1994; Mitani & Nishida, 1993; Wrangham et al., 2007). As mentioned, males often join others' pant hoots to take part in group chorusing (Arcadi, 1996), which seems to function in social bonding (Fedurek et al., 2013; Mitani & Brandt, 1994; Mitani & Gros-Louis, 1998), similar to human singing (Keeler et al., 2015).

Compared to pant hoots, chimpanzee rough grunts are much more context-specific, as they are produced exclusively in relation to feeding (Slocombe & Zuberbühler, 2005). Interestingly, rough grunts are acoustically similar to 'pant grunts', a greeting call given by lower-ranking to higher ranking individuals during approaches and other types of encounters (Laporte & Zuberbühler, 2011), suggesting similar psychological processes underlying call production. Rough grunt production is dependent on the quantity of food (Brosnan & De Waal, 2000; Hauser et al., 1993; Hauser & Wrangham, 1987) and acoustic structures vary with the perceived quality or type of food (Slocombe & Zuberbühler, 2005, 2006). As with pant hoots, social factors play a role in call production, notably the audience composition (oestrous females: Kalan & Boesch, 2015; dominance relation: Schel et al., 2013; bond partners: Fedurek & Slocombe, 2013; Schel et al., 2013; Slocombe et al., 2010).

Beyond chimpanzees, there is an ongoing debate as to whether animals are capable of cooperatively informing others or whether calling is always part of imperative or competitive interactions. Evidence for a competitive function is from data showing that food calls advertise social status or dominance rank (chimpanzees, Clark & Wrangham, 1994; pinyon jays, Dahlin et al., 2005; ravens, Heinrich & Marzluff, 1991) or even ownership and willingness to defend a resource (white-faced capuchins, Boinski & Campbell, 2010; Gros-Louis, 2004). On the other hand, food calls can also be produced by subordinates towards high-ranking individuals to avoid aggression, with possible cases of 'punishment' after failing to disclose the discovery of a food patch (spider monkeys, Chapman & Lefebvre, 1990; tufted capuchins, Di Bitetti, 2005; rhesus macaques, Hauser & Marler, 1993b).

Evidence for a cooperative function is from data showing that the structure and rate of food-associated calls can vary with food quantity (red-bellied tamarins, Caine et al., 1995; chimpanzees, Hauser et al., 1993) or quality (ravens, Bugnyar et al., 2001; bonobos, Clay & Zuberbühler, 2009; cotton-top tamarins, Elowson et al., 1991). Also, food calls are sometimes directed at preferred audiences, notably kin (rhesus macaques, Hauser & Marler, 1993a; naked mole-rats, Judd & Sherman, 1996; brown capuchins, Pollick et al., 2005), mates (chickens, Evans & Marler, 1994; bonobos, Krunkelsven et al., 1996) and bond partners (bonobos, Krunkelsven et al., 1996; chimpanzees, Slocombe et al., 2010).

Here, we revisited this cooperation/competition debate by investigating chimpanzee vocal behaviour in the feeding context. The function of both call types given during feeding remains puzzling. Indeed, pant hoots produced in a feeding context have an intimidating effect on nearby listeners and are preferably initiated by the

highest-ranking males in a party (Clark & Wrangham, 1994) while, at the same time, they might provide information about the presence of food and even attract desired partners (Reynolds & Reynolds, 1965; Wrangham, 1977). Similarly, rough grunts have been proposed to convey useful information for others about the presence and type of food (e.g., Slocombe & Zuberbühler, 2005, 2006) which may also facilitate coordinated feeding with preferred partners (e.g., Fedurek & Slocombe, 2013; Schel et al., 2013). However a recent study has shown that these calls are often produced after a history of agonistic interactions, suggesting communication for selfish reasons (Ischer et al., 2020).

As pointed out, feeding in groups is a complex social event that forces individuals to interact in close proximity and under competitive circumstances. We focused on adult males because they are more gregarious than adult females and therefore more often involved in fission-fusion decisions (Gilby and Wrangham 2008; Mitani 2009; Nishida 1983). Moreover, cooperation among males is important since, as previously mentioned, males form strong social relationships that are crucial for their fitness. Competition between males is also essential as dominance relationships are established through aggression and intimidation (Muller & Mitani, 2005). Our strategy was to dissect the feeding event into two chronologically ordered components. First, we investigated the vocal behaviour of males arriving at a food tree, while taking into account the individuals already in the tree and individuals simultaneously arriving. Second, we investigated the vocal behaviour of males already in a tree, while taking into account the identity of any newly arriving individuals and other individuals already in the tree. In both conditions, we were also interested in the impact of the absence of socially relevant individuals (i.e., high-ranking and preferred social partners) and, finally, the type of food present.

Since rough grunts are short distance calls, we expected these calls to be directed at nearby individuals, while long-distance pant-hoots would be directed at distant individuals. For the cooperative function, we predicted increased rough grunt rates in the presence of large parties and, specifically, important social partners, such as high-ranking males and association or bond partners (i.e., to initiate feeding with them). We also predicted increased pant hoot rates in small parties and in the absence of such important social partners (i.e., to inform absent individuals about the presence of food and possibly recruit them to join). For the competitive function, we predicted increased rough grunt rates in the presence of large parties and, specifically, high-ranking males (i.e., to avoid direct aggression) and increased pant hoot rates in small parties and in the absence of such individuals (i.e., to inform absent individuals about the presence of food and thus avoid possible later aggression). We also predicted that call production of both call types would be higher in low-ranking individuals. We also expected that subjects would vocalise in reaction to the newly joined (or joining) individuals or to the absence of specific individuals upon arrival; i.e., arriving subjects would vocalise towards either individuals they joined (i.e., rough grunts) or absent ones (i.e., pant hoots), whereas males already feeding would vocalise towards newly joining individuals (i.e., rough grunts).

Methods

Ethical Note

Our study was approved by the relevant local authorities in Uganda (UWA and UNCST) and complies with the ASAB/ABS guidelines for the Use of Animals in Research. Data collection was entirely observational and non-invasive.

Study site and subjects

We collected data on East African chimpanzees (*Pan troglodytes schweinfurthii*) of the Sonso community in the Budongo Forest Reserve, Uganda (latitude 1°37′–2°00′N; longitude: 31°22′–31°46′E), between January 2018 and March 2020. At the beginning of the study, the community comprised 75 individuals, 37 of which were adults (>15 years; 11 males; 26 females). In February 2019, three adult males died in an epidemic (Supplementary material Table S2.1). The group had been monitored for more than 25 years with all individuals identified and habituated to human observers with daily follows throughout the approximately 7km^2 home range (Newton-Fisher, 2003). All social and kin relations are known and continuously updated (Reynolds, 2005).

Data collection

We initially conducted full-day focal follows, usually from 07:00 to 16:30 local time, for a total observation time of 692 hours over 141 days. We followed 11 adult males but then had to exclude one male (ZD) due to low observation time (Supplementary material Table S2.1). During each follow, we continuously recorded the subject's activities with start and end times. During feeding events in trees, we recorded the 'arrival event' as the period between an individual approaching in visual range of the food tree (i.e., approximately 30m) and the moment he started feeding. For each arrival event, we recorded the tree species, the identities of all arriving individuals and all individuals already in the tree, as well as the vocal behaviour (rough grunt and pant hoot production) of all males. We excluded events during which vocalisations were produced by unidentifiable males, which happened frequently due to low visibility.

Due to a respiratory disease outbreak in 2019, three of the 10 focal animals died within a week, which destabilised the social relations between the remaining males. For this reason, we excluded the data collected in the following three months after the death of the first individual (26 February 2019 to 31 May 2019) from statistical analyses, which created two data sets (i.e., 4 January 2018 to 26 February 2019 and 1 June 2019 to 16 March 2020).

Social variables

To determine the social relations between the males, we calculated each subject's dominance rank (Elo-rating; Elo, 1978; Neumann et al., 2011) and identified his most important partners (i.e., bond partners and association partners) using long-term data collected by four trained field assistants during full-day focal follows, which also included 15 min scan samples of party compositions. We did not compute the more commonly known 'dyadic composite sociality index' (DSI; Silk et al., 2013) as we were interested in the impact of proximity and grooming separately. We opted for this strategy since a previous study had shown that proximity patterns reflected the strength of relationships whereas grooming patterns reflected the quality of relationships (Mitani, 2009). We therefore defined, for each male separately, his 'association partners' as the top three preferred proximity partners and his 'bond partners' as the top three preferred grooming partners (Bray & Gilby, 2020; Mitani & Nishida, 1993; Samuni et al., 2018, 2021).

Dominance: The rank of each adult male was established using the Elo-rating method, which has the advantage that it depicts rank relations dynamically in contrast to other methods (Elo, 1978; Neumann et al., 2011). The

behaviour used to calculate ranks was the production of pant grunt (i.e., a 'greeting' vocalisation given to higher-ranking individuals). This behaviour accurately reflects dominance relationships (Bygott, 1979) and has traditionally been used to calculate the hierarchy among chimpanzees both in the wild and captivity (Fedurek et al., 2021; Samuni et al., 2018, 2020, 2021). To have an accurate estimation of dominance ranks at the beginning of the study, we used the data collected from twelve months before the beginning of the study and then continued to collect data until the end of the study (4 January 2017 to 16 March 2020). In contrast to traditional matrix-based assessments, elo-rating is based on the Bayesian concept that rank is a dynamic variable that provides an increasingly more accurate description with each observed social interaction. Each male starts the process with a fixed score, which is continuously updated following each dyadic interaction. In particular, each time a male produces pant grunts to another male, he loses points whereas the recipient gains the same number of points. The number of points gained or lost depends on the expected outcome, which is calculated prior the interaction. Unexpected outcomes lead to more point changes than expected outcomes (Elo, 1978; Neumann et al., 2011). We calculated the Elo-ratings using the 'EloRating' R package version 0.46.11 (Neumann & Kulik, 2020). The hierarchy was stable through the two study periods (i.e., pre- and post-outbreak), enabling us to attribute one Elo-score to each male. For each male, we calculated the mean of the Elo-scores obtained at the end of the two periods (Supplementary material Table S2.1). Three individuals had consistently higher Elo-scores than the other males and were thus classified as 'high-ranking males' (Supplementary material Fig. S2.1 and Table S2.1). Elo-rating scores were standardized for statistical analyses.

Social partners: For each male dyad, we calculated both grooming-based and proximity-based dyadic sociality indices, the DSI_G and the DSI_P, to determine each male's bond and association partners, respectively. The DSI_G and DSI_P calculations were derived from the DSI introduced by Silk et al. (2013), which attributes a value of 1 to the average social bond across all dyads in the group (in our case 55 dyads; N=11 males). If a dyad has a value superior (or inferior) to 1, the dyad is considered to have a stronger (or weaker) social bond than average. To calculate the DSI_G, we used the duration of grooming interactions between the two males of the dyad (grooming given or received) recorded during the focal follows. To calculate the DSI_P, we used the occurrence of the two males of the dyad being nearest neighbours (i.e., the individual sitting in closest proximity to the focal animal) recorded in 15min scans. Since three adult males died during the outbreak, we calculated the indices for the pre- and post-outbreak periods separately. The DSI_G and the DSI_P were calculated using the 'socialindices2' R package version 0.50.0 (Neumann, 2017). For each focal male (and for each study period), the social bond partners and the association partners were the top three individuals with the highest DSI_G and DSI_P values, respectively (Supplementary material Table S2.2).

Statistical analyses

We investigated which parameters influenced the production of the two call types (i.e., pant hoot and rough grunt) depending on the role of the individual (i.e., arriving or present in the food tree) during arrival events. We were interested in whether individuals were addressing the joining (or joined) individuals or the entire party. Hence, we considered distinct variables (i.e., the number of individuals, the presence of a high-ranking male, the presence of a social bond partner and the presence of an association partner) to describe both the composition of the joining (or joined) group and the composition of the entire party.

First, we built four generalised linear mixed models (GLMMs) corresponding to the four combinations of vocalisations and roles: production of pant hoot (GLMM1) or rough grunt (GLMM2) when arriving at a food tree, and production of pant hoot (GLMM3) or rough grunt (GLMM4) when being joined (i.e., already present) in a food tree (Supplementary material Table S2.3). All GLMMs had a binomial error structure and logit link function, with the call (i.e., pant hoot for GLMM1 and 3, and rough grunt for GLMM2 and 4) production (at least one call produced / no call produced) as the response variable. The test variables were the dominance rank (Elo-rating) of the subject, the food tree species, the total number of individuals in the feeding party and the social composition (presence of a high-ranking male, a male social bond partner or a male association partner) of the entire party (all GLMMs) and of the arriving group (GLMM3 and 4) or of the group already present in the tree (GLMM1 and 2). The subject ID was entered as a random factor the in all GLMMs.

To account for the fact that the subject would sometimes produce both pant hoots and rough grunts during the same arrival events and to disentangle the functions of these two calls, we also built similar models (GLMM1b, 2b, 3b and 4b) on subsets of the data without the other call type produced (i.e., without the production of rough grunt for GLMM1b and 3b, and of pant hoot for GLMM2b and 4b).

We then used a statistical model selection and averaging approach on each of the GLMM to disentangle the effect of each variable and determine which sub-models fitted the data best. To do so, we used the *dredge* function of the 'MuMIn' R package (version 1.43.17; Barton, 2020) to generate a full sub-model set (including the null model) from each of the GLMM previously built. For each sub-model set, we used Akaike's Information Criterion values corrected for small sample size (AICc; Burnham et al., 2011) to rank the sub-models from best to worst and conducted model averaging separately, for each GLMM, across the top sub-model set, i.e., where $\Delta AICc < 2$ (Burnham & Anderson, 2004; Symonds & Moussalli, 2011). We considered variables as informative if zero was not included within their 95% confidence interval. We used the *vif* function of the 'car' R package (version 3.0-3; Fox & Weisberg, 2019) to derive variance inflation factors (VIF), which revealed no collinearity issues (largest VIF = 2.01 across all models). We calculated Cook's distances of single observations using the 'influence.ME' R package (version 0.9-9; Nieuwenhuis et al., 2012) and detected no influential cases (all values <1). Lastly, we checked model assumptions by visually checking the distribution of residuals. Additionally, Spearman rank correlation tests confirmed that the productions of both rough grunts and pant hoots by individuals arriving or being joined in the food tree, were not significantly correlated to the production of the other call ($p > 0.10$; Supplementary material Table S2.4). All GLMMs were built using the *glmer* function of the 'lme4' R package version 1.1-21 (Bates et al., 2015). All analyses were implemented in R v3.6.1 (R Core Team, 2019).

Results

General patterns

Long-term data analyses allowed us to establish the dominance rank between adult males and to determine the top three high-ranking individuals (Supplementary material Fig. S2.1 and Table S2.1) as well as the top three bond partners and association partners for each focal male (Supplementary material Table S2.2).

Across subjects (N=10 adult males), we observed N=233 arrival events, during which we recorded N=190 males joining others and N=519 males being joined in a food tree. When actively joining, subjects produced pant hoots or rough grunts in about one third of events (mean proportion of events ± SD: with pant hoots = 0.35 ± 0.14; with rough grunts = 0.36 ± 0.16; Fig. 2.1) and, when vocalising, they often produced both calls during the same events (N=31 out of 104 vocal events). When passively being joined, call rates were much lower (mean proportion of events ± SD: with pant hoots = 0.08 ± 0.04; with rough grunts = 0.14 ± 0.08; Fig. 2.1) and, when vocalising, they rarely produced both calls during the same event (N=7 out of 90 vocal events).

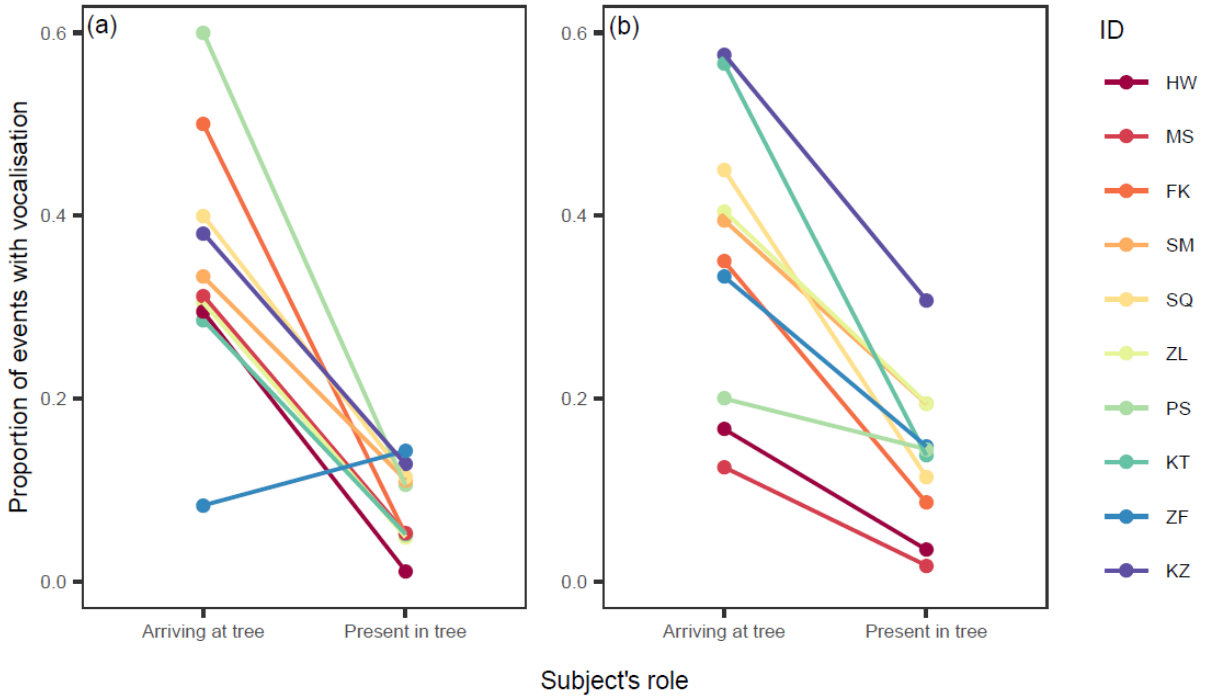

Figure 2.1. Proportion of events with a vocalisation produced by the subject depending on whether he is arriving at the food tree or already present in the tree and being joined by other individuals for (a) pant hoot and (b) rough grunt. The subjects are ordered by dominance rank (from top high-ranking to bottom low ranking).

Calling patterns when joining others

Pant hoot production was negatively related to party size and the presence of high-ranking individuals and social bond partners; i.e., higher in smaller than larger parties (β = -0.19, SE = 0.06, CI 95% = -0.31 to -0.07; Fig. 2.2a), higher when high-ranking individuals were absent (β = -1.30, SE = 0.50, CI 95% = -2.28 to -0.31; Fig. 2.2b) and higher when social bond partners were absent (β = 1.08, SE = 0.50, CI 95% = 0.10 to 2.07; Fig. 2.2c; GLMM1; Supplementary material Table S2.5).

Rough grunt production was negatively related with party size and caller rank, i.e. lower in large parties (β = -0.12, SE = 0.05, CI 95% = -0.22 to -0.03; Fig. 2.3a) and higher for low than high-ranking males (β = -0.62, SE = 0.18, CI 95% = -0.97 to -0.27; Fig. 2.3b; GLMM2; Supplementary material Table S2.5).

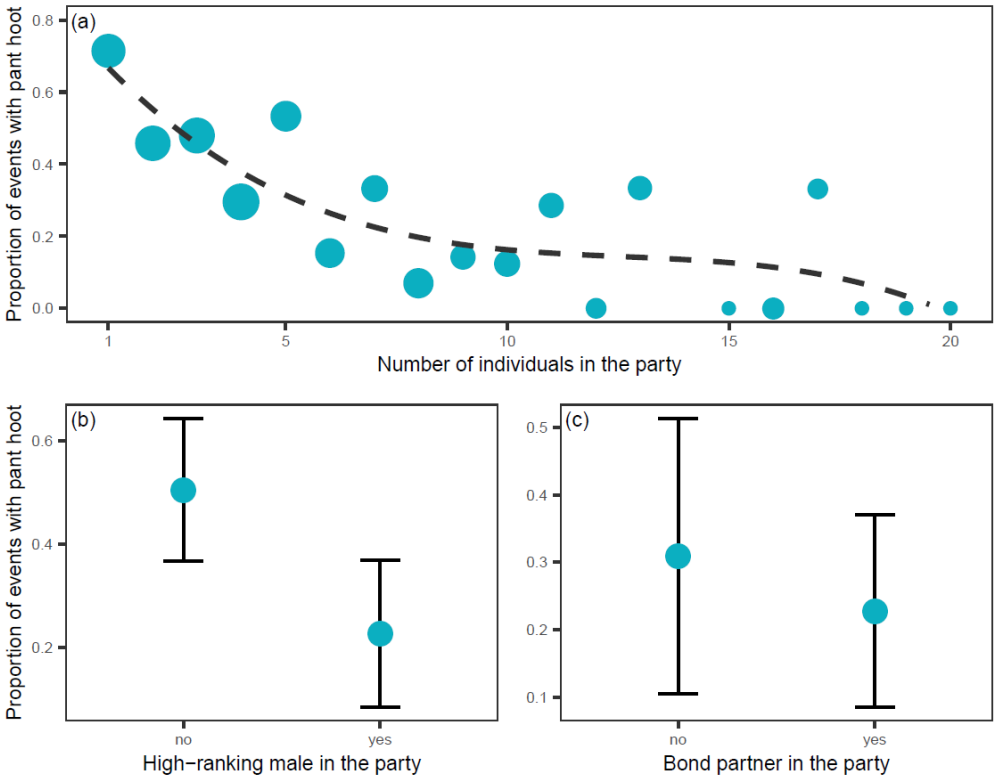

Figure 2.2. Relationship between the proportion of events with pant hoot produced by the subject arriving at the food tree and (a) the party size and (b) the presence of a high ranking male or (c) a social bond partner in the party. Larger point in plot (a) denotes larger number of observations. Points in plot (b) and (c) represent the mean proportion of events ± SD.

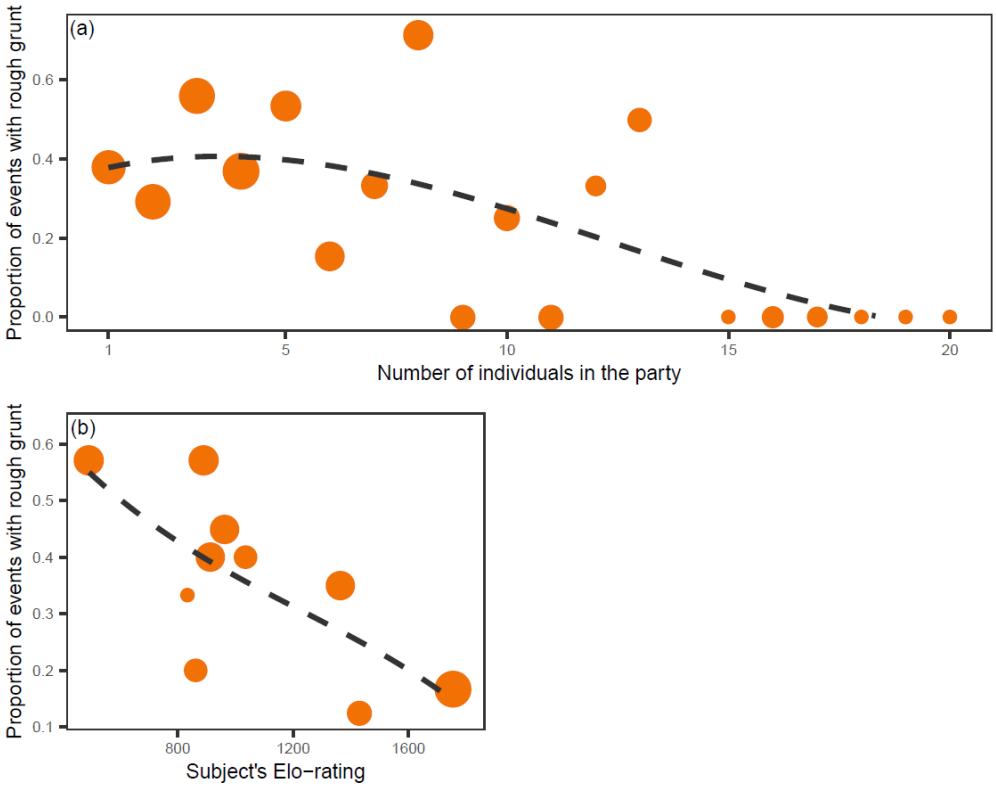

Figure 2.3. Relationship between the proportion of events with rough grunt produced by the subject arriving at the food tree and (a) the party size and (b) the dominance rank of the subject (Elo-rating). Larger point denotes larger number of observations.

Calling patterns when being joined

Pant hoot production was negatively related to party size and caller rank, and positively related to the presence of a high-ranking male in the joining group, i.e., higher in smaller than larger parties (β = -0.17, SE = 0.06, CI 95% = -0.29 to -0.05; Fig. 2.4a), higher in low-ranking callers (β = -0.52, SE = 0.22, CI 95% = -0.95 to -0.09; Fig. 2.4b) and higher when a high-ranking male joined (β = 1.26, SE = 0.40, CI 95% = 0.46 to 2.05; Fig. 2.4c; GLMM3; Supplementary material Table S2.5).

Rough grunt production, similarly to pant hoot, was also negatively related to party size and caller rank, and positively related to the presence of a high-ranking male in the joining group, i.e., higher in smaller than larger parties (β = -0.17, SE = 0.05, CI 95% = -0.26 to -0.08; Fig. 2.5a), higher in low-ranking callers (β = -0.83, SE = 0.19, CI 95% = -1.21 to -0.45; Fig. 2.5b) and higher when a high-ranking male joined (β = 1.74, SE = 0.33, CI 95% = 1.10 to 2.38; Fig. 2.5c; GLMM4; Supplementary material Table S2.5).

Overall, we did not find any significant effect of the type of food consumed (i.e., tree species) on the production of both calls.

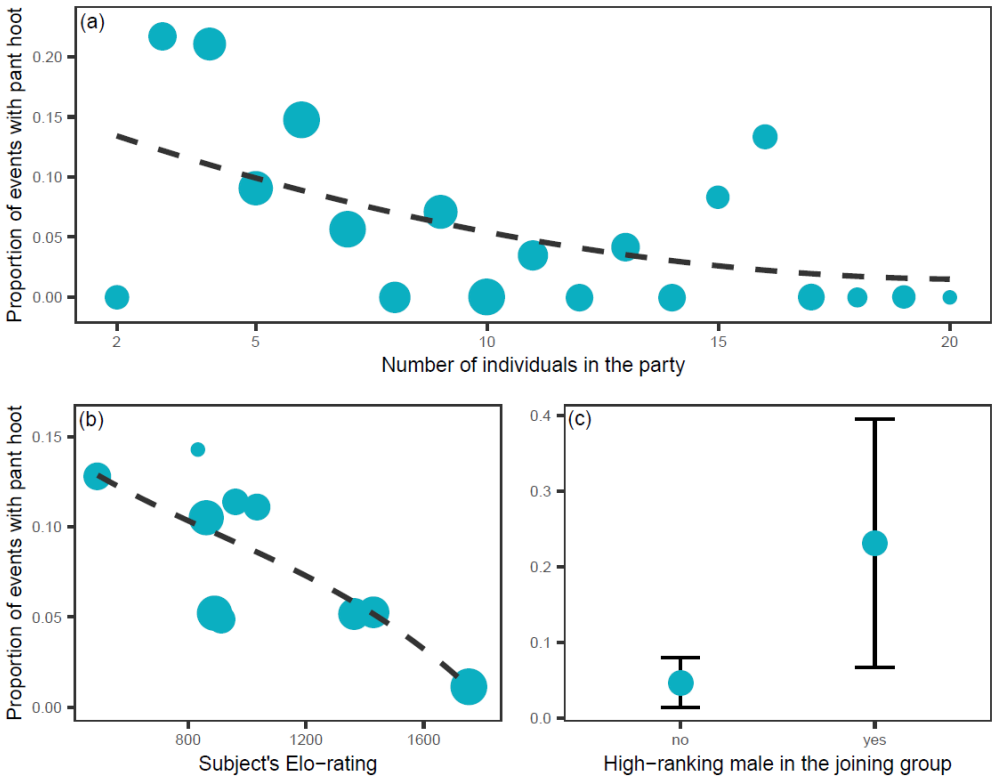

Figure 2.4. Relationship between the proportion of events with pant hoot produced by the subject being joined in the food tree and (a) the party size, (b) the dominance rank of the subject (Elo-rating) and (c) the presence of a high-ranking male in the group arriving in the food tree. Larger point in plots (a) and (b) denotes larger number of observations. Points in plot **c** represent the mean proportion of events ± SD.

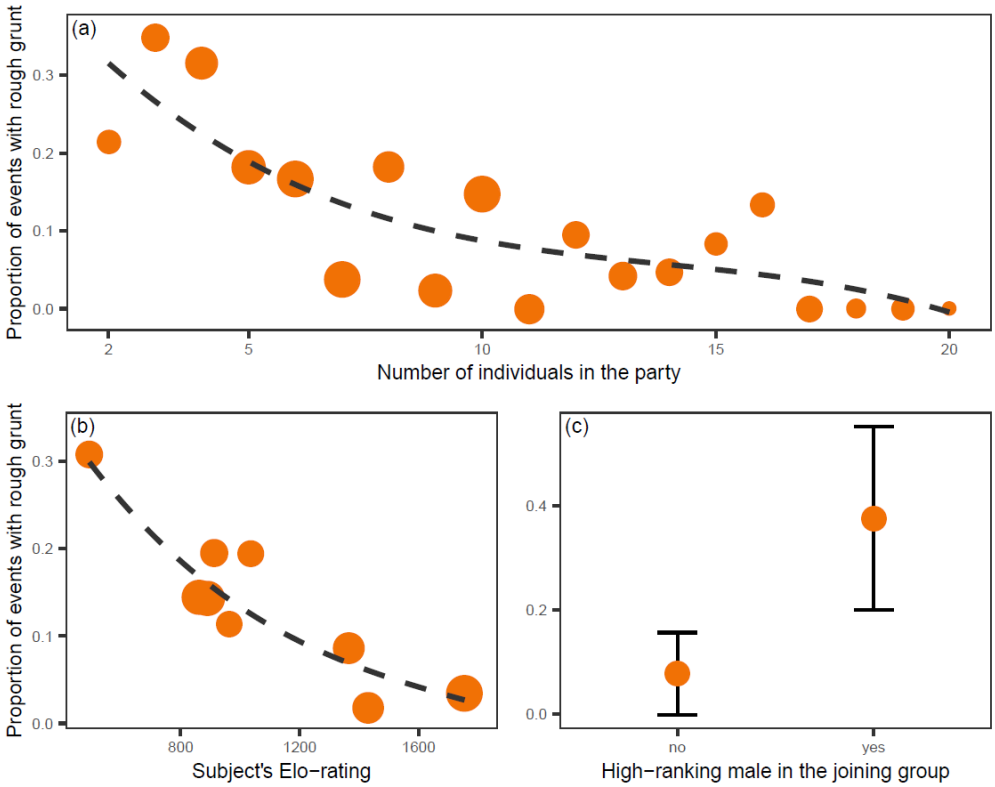

Figure 2.5. Relationship between the proportion of events with rough grunt produced by the subject being joined in the food tree and (a) the party size, (b) the dominance rank of the subject (Elo-rating) and (c) the presence of a high-ranking male in the group arriving in the food tree. Larger point in plots (a) and (b) denotes larger number of observations. Points in plot (c) represent the mean proportion of events ± SD.

To further explore the data, we reran all models for both call types produced separately (Supplementary material Table S2.6). Here, we overall found the same production patterns although some variables, i.e., presence of a preferred grooming partner in the party in the model exploring pant hoot production by arriving individuals (GLMM1b; Supplementary material Table S2.6), party size in the model exploring rough grunt production by arriving individuals (GLMM2b; Supplementary material Table S2.6) and the Elo-rating in the model exploring pant hoot production when being joined at a food tree (GLMM3b; Supplementary material Table S2.6), were no longer informative. However, results still showed a high relative importance of these variables in their models (0.82, 0.74 and 1.00, respectively; Supplementary material Table S2.6), suggesting that lack of significance was due to low sample sizes.

Discussion

There is something paradoxical about advertising the discovery of food. Rather than taking advantage of encountering a new resource, many social animals announce their discovery before starting to feed or, when already feeding, produce signals when new group members arrive. This behaviour is very prominent in chimpanzees, with individuals producing two types of calls in the feeding context, the rough grunt and the pant hoot, both when joining and when being joined in food trees. Food-calling has been observed in many species and several hypotheses have been suggested to explain the adaptive function of these vocalisations (see Clay et al., 2012 for a review). One of the most popular hypothesis is based on the assumption that callers perceive feeding as a social event and seek to inform or include others about a valuable resource suggesting that the caller will benefit from such selfless behaviour in some other way (Chapman, 1990; Dahlin et al., 2005; Heinrich &

Marzluff, 1991; Pollick et al., 2005). In primates, another supported hypothesis posits that the function of food-associated calls is to reduce foraging competition (Caine et al., 1995; Di Bitetti, 2005; Gros-Louis, 2004; Hauser & Marler, 1993b).

We monitored the vocal behaviour of ten adult male chimpanzees either when arriving or when being joined at a food tree. For both call types, we found that call production was higher in the actively joining than passively joined role. Both call rates were also higher in smaller than larger parties, regardless of whether the caller actively joins others or is passively joined.

Beyond these general patterns, there were some call-type specific effects. First, we found that arriving individuals were most likely to produce long-distance pant-hoots when socially important individuals (i.e., high-ranking males and social bond partners) were absent. Whereas males already in the tree were most likely to produce this call when high-ranking males joined and they themselves were lower ranking. We interpret these patterns as evidence for a cooperative function, i.e., calls are produced to inform distant group members about a valuable food source and, once they approach, to strengthen social relationships.

Second, for close-range rough grunts, we found that low-ranking males were generally more likely to call than high-ranking males. Arriving males were less likely to call if many others were in the tree and those in the tree were more likely to call when joined by a high-ranking male. We interpret these patterns as evidence for a greeting or appeasement function, similar to greeting calls (i.e., pant-grunts; Goodall, 1986). When producing rough grunts, males may attempt to manage socially difficult situations, i.e., co-feeding with competitors in the confined space of a tree crown, where individuals only have limited choice in terms of spatial decisions and proximity to others.

Do pant hoots recruit absent partners?

When joining a feeding party, males produced pant hoots in about a third of events. One surprising finding was that pant hoot call production by these newly arriving individuals was related to the absence of specific individuals. Our results show that subjects called more often when they were in small parties, and especially when high-ranking males and social bond partners were absent. Since pant hoots travel over long distances (>1km), it is possible that callers sought to inform absent high-ranking males and social bond partners in order to recruit them to the food tree. It has been argued that sharing information about feeding events provides opportunities to feed together or even share food, which is correlated with high levels of oxytocin and thus play a key role in social bonding (Samuni et al., 2018; Wittig et al., 2014). These social bonds are crucial to the fitness of male chimpanzees (Gilby & Wrangham, 2008; Mitani, 2009; Muller & Mitani, 2005; Nishida, 1983; Nishida & Hosaka, 1996). This interpretation is in line with previous studies that have shown that pant hoots play a role in maintaining group cohesion and regulating spatial dynamics between males (Eckhardt et al., 2015; Fedurek et al., 2014; Mitani & Nishida, 1993).

When males were already feeding in a tree, they only produced pant hoots 8% of the time when other individuals joined them. These calls were mainly produced by low-ranking males when being joined by high-ranking ones and in small parties. In the same context, the rough grunt production pattern was very similar and one hypothesis is that both these calls are produced by low-ranking individuals to avoid aggression by joining high-ranking

males (see the section below for further development of this hypothesis). On the other hand, why would these two calls (i.e., pant hoots and rough grunts) be produced with the same function? Since individuals sometimes produced both calls during the same arrival event, the two calls could be produced in combination. Indeed Leroux et al. (2021) recently showed that chimpanzees produce these calls in combination, mainly when high-ranking individuals join the feeding party. Even though their study did not specifically investigate the function of these call combinations, results suggested that the meaning of the combination seem to be related to the meaning of the two calls produced in isolation. Further research is needed to disentangle the function of the calls when produced alone or in combination.

However, in our study, when subjects were being joined in the tree, they only produced these two calls during the same events in approximately 8% of the events during which they vocalised and their patterns of production remained the same when produced in isolation. Moreover, no correlation was found between the production of these two calls (Table S2.4). These calls must therefore have distinct functions when produced alone. An hypothesis is that pant hoot production could have a different function. Indeed, if the intended recipients are in the same party (i.e., joining high-ranking males) then why use a long-distance call? We think that these calls might actually be uttered in response to pant hoots produced by arriving high-ranking males. Pant hoots are often produced in response (or in chorus) to a pant hoot initiated by another individual and these call exchanges might be socially relevant (Arcadi, 1996; Fedurek et al., 2013). So far, pant hoot chorusing has been proposed to be a low-cost bonding behaviour, adaptive to a species with a high degree of fission-fusion, and would thus play a role in maintaining social relationships (Fedurek et al., 2013; Mitani & Brandt, 1994; Mitani & Gros-Louis, 1998). We hypothesize that low-ranking individuals might chorus with high-ranking individuals' pant hoots to strengthen their relationships. Indeed, pant hoot chorusing might be important during co-feeding events since Fedurek et al. (2013) showed that male chimpanzee dyads engaged in pant hoot choruses more often on days when they spent time co-feeding. Overall, no study has yet investigated pant hoot response patterns or pant hoot choruses produced specifically in a feeding context so further research would be necessary.

Contrary to our findings, several studies have shown that pant hoots are mainly produced by high-ranking individuals and would advertise their social status (Clark & Wrangham, 1993; Fedurek et al., 2014). But these studies were investigating pant hoots produced across all contexts whereas it has since been shown that pant hoots are structurally very complex and can encode information about the identity, age, dominance rank and also the activity of the caller (Fedurek et al., 2016). Notman & Rendall (2005) even hypothesized that there could be different subtypes of pant hoots according to the context of production. Therefore, the production patterns of these pant hoot subtypes might differ and future research should consider the context of production when studying pant hoots. We also think that the recruitment effect of pant hoots produced upon arrival at food trees should be tested by observing potential recipients and their behavioural response to these calls.

Do rough grunts appease dominant competitors?

Male chimpanzees produced rough grunts more frequently when joining a feeding party (i.e., 36% of events) than when being joined in a food tree (i.e., 14% of events). Remarkably, in both situations, this behaviour was largely seen in lower-ranking males and when party size was small, suggesting that overall feeding competition was not the driving force. Instead, we hypothesize that, in small parties, individual identity was more likely to

play a role than in larger, more anonymous groups, similar to a 'dilution' effect, i.e. the idea that the chances for each specific individual to be targeted by an opponent (or predator) are inversely related to group size (Lehtonen & Jaatinen, 2016; Pappano et al., 2012). Also, victims of aggression can count on the support of allies (de Waal & Harcourt, 1992), suggesting that this is more probable when the party is large. Furthermore, males produced rough grunts more often when being joined by high-ranking males, suggesting that these calls could be directed at them, to avoid potential aggression.

We hypothesise that male chimpanzees produce rough grunts to inform others of the presence of food and therefore avoid misunderstandings or eventual aggression. The idea that animals disclose the possession of food to avoid aggression has been proposed for food calling in spider monkeys (Chapman & Lefebvre, 1990), tufted capuchin monkeys (Di Bitetti, 2005) and rhesus macaques (Hauser & Marler, 1993b) (see also Clutton-Brock & Parker, 1995). In chimpanzees, rough grunt production depends on food quantity (Brosnan & De Waal, 2000; Hauser et al., 1993; Hauser & Wrangham, 1987) and encodes information about food type and quality (Slocombe & Zuberbühler, 2005, 2006), suggesting that these calls provide information about the food source, albeit not necessarily as a cooperative attempt to inform others but as a way to avoid conflict. Although rough grunts are short-distance signals, they can still be heard beyond the immediate visual range and could thus address individuals who are not in the immediate party. This would explain why the production of rough grunts when arriving at a food tree is correlated with dominance rank but not with the presence, or absence, of high-ranking individuals, since these calls could be directed at high-ranking individuals either present in the tree (i.e., to avoid direct aggression) or absent and potentially joining (i.e., to avoid later aggression). Ischer et al. (2020) showed that rough grunt production was higher after agonistic interactions, supporting the hypothesis that the function of this call is related to aggression. However, more detailed studies investigating the relationship between calling and aggression are needed to confirm, or refute, our hypotheses. Future research should also investigate the effect of party size and would need to take into account variables such as fruit availability or tree-crown size to control for differences in competitive pressures.

Dual function of food-associated calls

In socially complex situations, chimpanzees can produce distinct calls with different functions to address different audiences. Indeed, during aggressive interactions, the victims often produce two calls, screams, to try and recruit support from bystanders, and 'waa' barks, to deter their aggressors by signalling their willingness to retaliate (Fedurek et al., 2015).

Feeding events are often associated with competitive or aggressive interactions (Muller & Mitani, 2005) but they can also present an opportunity to cooperate and strengthen social bonds (Samuni et al., 2018; Wittig et al., 2014). Here, we provide evidence that, when arriving at food trees, chimpanzees produce both pant hoots and rough grunts to achieve different social functions and help mediate both cooperative and competitive interactions. Indeed, on one hand, pant hoots seem to be directed towards socially important absent individuals (i.e., high-ranking males and social bond partners) to recruit them when arriving at a food tree, or towards arriving high-ranking males probably to chorus with them and strengthen their relationships. On the other hand, the function of rough grunts, when joining or being joined in a food tree, would be to avoid aggression, especially by higher-ranking males.

When chimpanzees arrive in a food tree, both pant hoot and rough grunts are produced towards specific individuals. The production of these calls seems to be recipient-directed and thus meets one of the key criteria for intentionality (Townsend et al., 2017). Moreover, since both calls were produced in small rather than large parties and pant hoot production was higher in absence of high-ranking males, it seems unlikely that the production of these calls would be based on arousal alone. These findings are adding to the corpus of evidence that chimpanzees have some voluntary control over their vocal production, which can be driven by intentional cognitive mechanisms (Crockford et al., 2012; Gruber & Zuberbühler, 2013; Schel et al., 2013). Investigating the recipients' behavioural response to these calls would allow us to determine if they are also produced in a goal-directed way, another key criterion for intentionality.

Previous studies presented conflicting results regarding the effect of food type on call production. Indeed, contrary to some studies (Fedurek & Slocombe, 2013; Kalan et al., 2015; Schel et al., 2013) but consistently with others (Ischer et al., 2020; Leroux et al., 2021), our results did not show any effect of this ecological variable on call production. Feeding events are complex events composed of several phases, which are associated with different social and ecological factors. Our study focused on the production of calls during arrival events, which can be socially challenging. In this context, we expect individual who vocalise to respond to this specific event and may, therefore, explain why call production was mainly driven by social variables. Future research should consider more detailed levels of context during feeding.

Our study focused on call production by adult males but females also produce pant hoots and food grunts during feeding. However, the stakes of food competition and cooperation are different for females and their calling behaviour might differ accordingly. Again, further studies investigating food-associated call production by females are necessary to develop a more comprehensive understanding of the function of these calls.

Overall, our study shows that pant hoot and rough grunt vocalisations are produced to regulate cooperative and competitive interactions upon arrival at food trees, therefore playing an important role in chimpanzee fission-fusion societies. These results underline the importance of considering both cooperation and competition, especially when studying complex social events such as feeding. As already suggested by Muller & Mitani (2005), these two processes should not be opposed and examined separately but should rather be considered as complementary since animals often cooperate to compete with conspecifics.

Acknowledgments

We are grateful to the Sonso field assistants (Sam Adue, Geresomu Muhumuza, Monday Gideon, and Chandia Bosco) and all of the staff of the Budongo Conservation Field Station for assistance with data collection in Uganda. We thank the Uganda Wildlife Authority, the Ugandan National Council for Science and Technology, and the President's office for research permissions, as well as the Royal Zoological Society of Scotland for providing core funding for Budongo Conservation Field Station. We thank Radu Slobodeanu for statistical advice and Bilgé Kimyonok for his technical support. We also thank Auriane Le Floch for comments on the manuscript.

References

Arcadi, A. C. (1996). Phrase structure of wild chimpanzee pant hoots: Patterns of production and interpopulation variability. *American Journal of Primatology*, *39*(3), 159–178. https://doi.org/10.1002/(SICI)1098-2345(1996)39:3<159::AID-AJP2>3.0.CO;2-Y

Asensio, N., Korstjens, A. H., & Aureli, F. (2009). Fissioning minimizes ranging costs in spider monkeys: a multiple-level approach. *Behavioral Ecology and Sociobiology*, *63*(5), 649–659. https://doi.org/10.1007/s00265-008-0699-9

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R. C., Di Fiore, A., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A., Layton, R. H., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernandez, G., Strier, K. B., & Van Schaik, C. P. (2008). Fission-Fusion Dynamics: New Research Frameworks. *Current Anthropology*, *49*(4), 627–654. https://doi.org/10.1086/586708

Babiszewska, M., Schel, A. M., Wilke, C., & Slocombe, K. E. (2015). Social, contextual, and individual factors affecting the occurrence and acoustic structure of drumming bouts in wild chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology*, *156*(1), 125–134. https://doi.org/10.1002/ajpa.22634

Barrett, L., Henzi, P., & Dunbar, R. I. M. (2003). Primate cognition: from "what now?" to "what if?" *Trends in Cognitive Sciences*, *7*(11), 494–497. https://doi.org/10.1016/j.tics.2003.09.005

Barton, K. (2020). *MuMIn: Multi-Model Inference* (R package version 1.43.17). https://cran.r-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Boesch, C. (1991). The Effects of Leopard Predation On Grouping Patterns in Forest Chimpanzees. *Behaviour*, *117*(3–4), 220–241. https://doi.org/10.1163/156853991X00544

Boesch, C., Kohou, G., Néné, H., & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Taï forest. *American Journal of Physical Anthropology*, *130*(1), 103–115. https://doi.org/10.1002/ajpa.20341

Boinski, S., & Campbell, A. F. (2010). The Huh Vocalization of White-faced Capuchins: a Spacing Call Disguised as a Food Call? *Ethology*, *102*(6), 826–840. https://doi.org/10.1111/j.1439-0310.1996.tb01204.x

Bray, J., & Gilby, I. C. (2020). Social relationships among adult male chimpanzees (*Pan troglodytes schweinfurthii*): variation in the strength and quality of social bonds. *Behavioral Ecology and Sociobiology*, *74*(9). https://doi.org/10.1007/s00265-020-02892-3

Bray, J., Pusey, A. E., & Gilby, I. C. (2016). Incomplete control and concessions explain mating skew in male chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1842), 20162071. https://doi.org/10.1098/rspb.2016.2071

Brosnan, S. F., & De Waal, F. B. M. (2000). Regulation of vocal output by chimpanzees finding food in the presence or absence of an audience. *Evolution of Communication*, *4*(2), 211–224.

Bugnyar, T., Kijne, M., & Kotrschal, K. (2001). Food calling in ravens: Are yells referential signals? *Animal Behaviour*, *61*(5), 949–958. https://doi.org/10.1006/anbe.2000.1668

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research*, *33*, 261–304.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in

behavioral ecology : some background , observations , and comparisons. *Behavioral Ecology and Sociobiology*, *65*(1), 23–35.

Busia, L., Schaffner, C. M., & Aureli, F. (2017). Relationship quality affects fission decisions in wild spider monkeys (*Ateles geoffroyi*). *Ethology*, *123*(6–7), 405–411. https://doi.org/10.1111/eth.12609

Bygott, J. D. (1979). Agonistic behaviour, dominance, and social structure in wild chimpanzees of the gombe national park. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (pp. 405–428).

Caine, N. G., Addington, R. L., & Windfelder, T. L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour*, *50*(1), 53–60. https://doi.org/10.1006/anbe.1995.0220

Chapman, C. A. (1990). Association patterns of spider monkeys: the influence of ecology and sex on social organization. *Behavioral Ecology and Sociobiology*, *26*(6). https://doi.org/10.1007/BF00170898

Chapman, C. A., & Chapman, L. J. (2000). Determinants of group size in primates: The importance of travel costs. In S. Boinski & P. A. Garber (Eds.), *On the move. How and why animals travel in groups* (The Univer, pp. 24–42).

Chapman, C. A., Chapman, L. J., & Wrangham, R. W. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, *36*(1), 59–70. https://doi.org/10.1007/BF00175729

Chapman, C. A., & Lefebvre, L. (1990). Manipulating foraging group size: spider monkey food calls at fruiting trees. *Animal Behaviour*, *39*(5), 891–896. https://doi.org/10.1016/S0003-3472(05)80953-4

Clark, A. P. (1993). Rank differences in the production of vocalizations by wild chimpanzees as a function of social context. *American Journal of Primatology*, *31*(3), 159–179. http://dx.doi.org/10.1002/ajp.1350310302

Clark, A. P., & Wrangham, R. W. (1993). Acoustic Analysis of Wild Chimpanzee Pant Hoots: Do Kibale Forest Chimpanzees Have an Acoustically Distinct Food Arrival Pant Hoot? *American Journal of Primatology*, *31*, 99–109. https://deepblue.lib.umich.edu/bitstream/handle/2027.42/38429/1350310203_ftp.pdf?sequence=1&isAllowed=y

Clark, A. P., & Wrangham, R. W. (1994). Chimpanzee Arrival Pant-Hoots: Do Signify Food or Status? *International Journal of Pdmatology*, *15*(2). https://link.springer.com/content/pdf/10.1007%2FBF02735273.pdf

Clay, Z., Smith, C. L., & Blumstein, D. T. (2012). Food-associated vocalizations in mammals and birds: What do these calls really mean? In *Animal Behaviour* (Vol. 83, Issue 2, pp. 323–330). Elsevier Ltd. https://doi.org/10.1016/j.anbehav.2011.12.008

Clay, Z., & Zuberbühler, K. (2009). Food-associated calling sequences in bonobos. *Animal Behaviour*, *77*(6), 1387–1396. https://doi.org/10.1016/j.anbehav.2009.02.016

Clutton-Brock, T. H., & Parker, G. A. (1995). Punishment in animal societies. *Nature*, *373*(6511), 209–216. https://doi.org/10.1038/373209a0

Conradt, L., & List, C. (2009). Group decisions in humans and animals: a survey. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1518), 719–742. https://doi.org/10.1098/rstb.2008.0276

Conradt, L., & Roper, T. J. (2010). Deciding group movements: Where and when to go. *Behavioural Processes*, *84*(3), 675–677. https://doi.org/10.1016/j.beproc.2010.03.005

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, *433*(7025), 513–516. https://doi.org/10.1038/nature03236

Crockford, C., Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology*, *22*(2), 142–146. https://doi.org/10.1016/j.cub.2011.11.053

Crofoot, M. C., & Wrangham, R. W. (2010). Intergroup Aggression in Primates and Humans: The Case for a Unified Theory. In *Mind the Gap* (pp. 171–195). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-02725-3_8

Dahlin, C. R., Balda, R. P., & Slobodchikoff, C. (2005). Food, audience and sex effects on pinyon jay (*Gymnorhinus cyanocephalus*) communication. *Behavioural Processes*, *68*(1), 25–39. https://doi.org/10.1016/j.beproc.2004.09.003

Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An Introduction to Behavioural Ecology* (John Wiley & Sons (ed.)). SAGE Publications Ltd. https://doi.org/10.4135/9781446211922.n13

DeCasien, A. R., Williams, S. A., & Higham, J. P. (2017). Primate brain size is predicted by diet but not sociality. *Nature Ecology & Evolution*, *1*(5), 0112. https://doi.org/10.1038/s41559-017-0112

de Waal, F. B. M., & Harcourt, A. (1992). Coalitions and alliances: A history of ethological research. In F. B. M. De Waal & A. Harcourt (Eds.), *Coalitions and Alliances in Humans and Other Animals* (pp. 1–27). Oxford University Press, Oxford.

Di Bitetti, M. S. (2005). Food-associated calls and audience effects in tufted capuchin monkeys, *Cebus apella nigritus*. *Animal Behaviour*, *69*(4), 911–919. https://doi.org/10.1016/j.anbehav.2004.05.021

Duffy, K. G., Wrangham, R. W., & Silk, J. B. (2007). Male chimpanzees exchange political support for mating opportunities. *Current Biology*, *17*(15), R586–R587. https://doi.org/10.1016/j.cub.2007.06.001

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

Dunbar, R. I. M. (2011). Evolutionary Basis of the Social Brain. In J. Decety & J. T. Cacioppo (Eds.), *The Oxford Handbook of Social Neuroscience*. Oxford University Press, Oxford. https://doi.org/10.1093/oxfordhb/9780195342161.013.0003

Eckhardt, N., Polansky, L., & Boesch, C. (2015). Spatial cohesion of adult male chimpanzees (*Pan troglodytes verus*) in Taï National Park, Côte d'Ivoire. *American Journal of Primatology*, *77*(2), 125–134. https://doi.org/10.1002/ajp.22316

Elgar, M. A. (1986). House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Animal Behaviour*, *34*(PART 1), 169–174. https://doi.org/10.1016/0003-3472(86)90020-5

Elo, A. E. (1978). *The rating of chess players, past and present.* Arco Pub.

Elowson, A. M., Tannenbaum, P. L., & Snowdon, C. T. (1991). Food-associated calls correlate with food preferences in cotton-top tamarins. *Animal Behaviour*, *42*(6), 931–937. https://doi.org/10.1016/S0003-3472(05)80145-9

Evans, C. S., & Marler, P. (1994). Food calling and audience effects in male chickens, *Gallus gallus*: Their relationships to food availability, courtship and social facilitation. *Animal Behaviour*, *47*(5), 1159–1170. https://doi.org/10.1006/anbe.1994.1154

Fedurek, P., Donnellan, E., & Slocombe, K. E. (2014). Social and ecological correlates of long-distance pant hoot calls in male chimpanzees. *Behavioral Ecology and Sociobiology*, *68*(8), 1345–1355.

https://doi.org/10.1007/s00265-014-1745-4

Fedurek, P., Machanda, Z. P., Schel, A. M., & Slocombe, K. E. (2013). Pant hoot chorusing and social bonds in male chimpanzees. *Animal Behaviour*, *86*(1), 189–196. https://doi.org/10.1016/j.anbehav.2013.05.010

Fedurek, P., & Slocombe, K. E. (2013). The Social Function of Food-Associated Calls in Male Chimpanzees. *American Journal of Primatology*, *75*(7), 726–739. https://doi.org/10.1002/ajp.22122

Fedurek, P., Slocombe, K. E., & Zuberbühler, K. (2015). Chimpanzees communicate to two different audiences during aggressive interactions. *Animal Behaviour*, *110*, 21–28. https://doi.org/10.1016/j.anbehav.2015.09.010

Fedurek, P., Tkaczynski, P. J., Hobaiter, C., Zuberbühler, K., Wittig, R. M., & Crockford, C. (2021). The function of chimpanzee greeting calls is modulated by their acoustic variation. *Animal Behaviour*, *174*, 279–289. https://doi.org/10.1016/j.anbehav.2021.02.002

Fedurek, P., Zuberbühler, K., & Dahl, C. D. (2016). Sequential information in a great ape utterance. *Scientific Reports*, *6*(1), 38226. https://doi.org/10.1038/srep38226

Feldblum, J. T., Krupenye, C., Bray, J., Pusey, A. E., & Gilby, I. C. (2021). Social bonds provide multiple pathways to reproductive success in wild male chimpanzees. *IScience*, *24*(8), 102864. https://doi.org/10.1016/j.isci.2021.102864

Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (Third edit). Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Gilby, I. C., & Wrangham, R. W. (2008). Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology*, *62*(11), 1831–1842. https://doi.org/10.1007/s00265-008-0612-6

Goodall, J. (1986). *The chimpanzees of Gombe: patterns of behavior*. Harvard University Press.

Grinnell, J. (2002). Modes of cooperation during territorial defense by African lions. *Human Nature*, *13*(1), 85–104.

Gros-Louis, J. (2004). The function of food-associated calls in white-faced capuchin monkeys, *Cebus capucinus*, from the perspective of the signaller. *Animal Behaviour*, *67*(3), 431–440. https://doi.org/10.1016/j.anbehav.2003.04.009

Gruber, T., & Zuberbühler, K. (2013). Vocal Recruitment for Joint Travel in Wild Chimpanzees. *PLoS ONE*, *8*(9), e76073. https://doi.org/10.1371/journal.pone.0076073

Gruber, T., Zuberbühler, K., & Neumann, C. (2016). Travel fosters tool use in wild chimpanzees. *ELife*, *5*(JULY), 1–20. https://doi.org/10.7554/eLife.16371

Hartwell, K. S., Notman, H., & Pavelka, M. S. M. (2018). Seasonal and sex differences in the fission–fusion dynamics of spider monkeys (*Ateles geoffroyi yucatanensis*) in Belize. *Primates*, *59*(6), 531–539. https://doi.org/10.1007/s10329-018-0685-4

Hauser, M. D., & Marler, P. (1993a). Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors. *Behavioral Ecology*, *4*(3), 194–205. https://doi.org/10.1093/beheco/4.3.194

Hauser, M. D., & Marler, P. (1993b). Food-associated calls in rhesus macaques (*Macaca mulatta*): II. Costs and benefits of call production and suppression. *Behavioral Ecology*, *4*(3), 206-212. https://doi.org/10.1093/beheco/4.3.206

Hauser, M. D., Teixidor, P., Fields, L., & Flaherty, R. (1993). Food-elicited calls in chimpanzees: effects of food

quantity and divisibility. *Animal Behaviour*, *45*(4), 817–819. https://doi.org/10.1006/anbe.1993.1096

Hauser, M. D., & Wrangham, R. W. (1987). Manipulation of food calls in captive chimpanzees: A preliminary report. *Folia Primatologica*, *48*(3–4), 207–210. https://doi.org/10.1159/000156298

Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology*, *28*(1), 13–21. https://doi.org/10.1007/BF00172134

Herbinger, I., Papworth, S., Boesch, C., & Zuberbühler, K. (2009). Vocal, gestural and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders: a playback study. *Animal Behaviour*, *78*(6), 1389–1396. https://doi.org/10.1016/j.anbehav.2009.09.010

Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man*, *11*(1), 1. https://doi.org/10.2307/2800384

Hobaiter, C., Samuni, L., Mullins, C., Akankwasa, W. J., & Zuberbühler, K. (2017). Variation in hunting behaviour in neighbouring chimpanzee communities in the Budongo forest, Uganda. *PLOS ONE*, *12*(6), e0178065. https://doi.org/10.1371/journal.pone.0178065

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

Ischer, G., Zuberbühler, K., & Fedurek, P. (2020). The relationship between food calling and agonistic behaviour in wild chimpanzees. *Behavioural Processes*, *178*(May), 104182. https://doi.org/10.1016/j.beproc.2020.104182

Jacobs, A. (2010). Group cohesiveness during collective movements: Travelling apart together. *Behavioural Processes*, *84*(3), 678–680. https://doi.org/10.1016/j.beproc.2010.03.004

Jeschke, J. M., & Tollrian, R. (2007). Prey swarming: which predators become confused and why? *Animal Behaviour*, *74*(3), 387–393. https://doi.org/10.1016/j.anbehav.2006.08.020

Judd, T. M., & Sherman, P. W. (1996). Naked mole-rats recruit colony mates to food sources. *Animal Behaviour*, *52*(5), 957–969. https://doi.org/10.1006/anbe.1996.0244

Kaburu, S. S. K., & Newton-Fisher, N. E. (2015). Trading or coercion? Variation in male mating strategies between two communities of East African chimpanzees. *Behavioral Ecology and Sociobiology*, *69*(6), 1039–1052. https://doi.org/10.1007/s00265-015-1917-x

Kalan, A. K., & Boesch, C. (2015). Audience effects in chimpanzee food calls and their potential for recruiting others. *Behavioral Ecology and Sociobiology*, *69*(10), 1701–1712. https://doi.org/10.1007/s00265-015-1982-1

Kalan, A. K., Mundry, R., & Boesch, C. (2015). Wild chimpanzees modify food call structure with respect to tree size for a particular fruit species. *Animal Behaviour*, *101*, 1–9. https://doi.org/10.1016/j.anbehav.2014.12.011

Keeler, J. R., Roth, E. A., Neuser, B. L., Spitsbergen, J. M., Waters, D. J. M., & Vianney, J.-M. (2015). The neurochemistry and social flow of singing: bonding and oxytocin. *Frontiers in Human Neuroscience*, *9*(September), 1–10. https://doi.org/10.3389/fnhum.2015.00518

Kerth, G. (2010). Group decision-making in animal societies. In *Animal Behaviour: Evolution and Mechanisms* (pp. 241–265). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-02624-9_9

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.

Krebs, J. R., & Davies, N. B. (2009). *Behavioural ecology: an evolutionary approach* (J. R. Krebs & N. B.

Davies (eds.)). John Wiley & Sons.

Krunkelsven, E., Dupain, J., Elsacker, L. Van, & Verheyen, R. F. (1996). Food calling by captive bonobos (*Pan paniscus*): An experiment. *International Journal of Primatology*, *17*(2), 207–217. https://doi.org/10.1007/BF02735448

Kummer, H. (1968). *Social organization of Hamadryas Baboons, a field study*. University of Chicago Press.

Kummer, H. (1971). *Primate societies – group techniques of ecological adaptation*. Aldine Publishing Company.

Laidre, M. E. (2006). Manipulation without mind-reading: Information suppression and leakage during food discovery by mandrills (*Mandrillus sphinx*). *Behaviour*, *143*(3), 365–392. https://doi.org/10.1163/156853906775897851

Laporte, M. N. C., & Zuberbühler, K. (2011). The development of a greeting signal in wild chimpanzees. *Developmental Science*, *14*(5), 1220–1234. https://doi.org/10.1111/j.1467-7687.2011.01069.x

Leendertz, F. H., Ellerbrok, H., Boesch, C., Couacy-Hymann, E., Mätz-Rensing, K., Hakenbeck, R., Bergmann, C., Abaza, P., Junglen, S., Moebius, Y., Vigilant, L., Formenty, P., & Pauli, G. (2004). Anthrax kills wild chimpanzees in a tropical rainforest. *Nature*, *430*(6998), 451–452. https://doi.org/10.1038/nature02722

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour*, *74*(6), 1617–1629. https://doi.org/10.1016/j.anbehav.2006.10.025

Lehtonen, J., & Jaatinen, K. (2016). Safety in numbers: the dilution effect and other drivers of group life in the face of danger. *Behavioral Ecology and Sociobiology*, *70*(4), 449–458. https://doi.org/10.1007/s00265-016-2075-5

Leroux, M., Bosshard, A. B., Chandia, B., Manser, A., Zuberbühler, K., & Townsend, S. W. (2021). Chimpanzees combine pant hoots with food calls into larger structures. *Animal Behaviour*, *179*, 41–50. https://doi.org/10.1016/j.anbehav.2021.06.026

Lusseau, D. (2007). Why Are Male Social Relationships Complex in the Doubtful Sound Bottlenose Dolphin Population? *PLoS ONE*, *2*(4), e348. https://doi.org/10.1371/journal.pone.0000348

Marler, P., & Tenaza, R. (1977). Signaling behavior of apes with special reference to vocalizations. In *How Animals Communicate* (pp. 965–1033). Indiana University Press.

Marlowe, F. W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *14*(2), 54–67. https://doi.org/10.1002/evan.20046

Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, *77*(3), 633–640. https://doi.org/10.1016/j.anbehav.2008.11.021

Mitani, J. C., & Amsler, S. (2003). Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour*, *140*(7), 869–884. https://doi.org/10.1163/156853903770238355

Mitani, J. C., & Brandt, K. L. (1994). Social Factors Influence the Acoustic Variability in the Long-distance Calls of Male Chimpanzees. *Ethology*, *96*(3), 233–252. https://doi.org/10.1111/j.1439-0310.1994.tb01012.x

Mitani, J. C., & Gros-Louis, J. (1998). Chorusing and Call Convergence in Chimpanzees: Tests of Three Hypotheses. *Behaviour*, *135*(8), 1041–1064. https://doi.org/10.1163/156853998792913483

Mitani, J. C., & Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. *Animal Behaviour*, *45*(4), 735–746. https://doi.org/10.1006/anbe.1993.1088

Muller, M. N., & Mitani, J. C. (2005). Conflict and Cooperation in Wild Chimpanzees. In *Advances in the Study of Behavior* (Vol. 35, pp. 275–331). https://doi.org/10.1016/S0065-3454(05)35007-8

Neumann, C. (2017). *socialindices2: social and association indices* (R package version 0.50.0). https://github.com/gobbios/socialindices/

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A., & Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour*, *82*(4), 911–921. https://doi.org/10.1016/j.anbehav.2011.07.016

Neumann, C., & Kulik, L. (2020). *EloRating: Animal dominance hierarchies by Elo rating* (R package version 0.46.11). http://cran.r-project.org/ package=EloRating

Newton-Fisher, N. E. (2003). The home range of the Sonso community of chimpanzees from the Budongo Forest, Uganda. *African Journal of Ecology*, *41*(2), 150–156. https://doi.org/10.1046/j.1365-2028.2003.00408.x

Newton-Fisher, N. E., Thompson, M. E., Reynolds, V., Boesch, C., & Vigilant, L. (2009). Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda. *American Journal of Physical Anthropology*, *142*(3), 417–428. https://doi.org/10.1002/ajpa.21241

Nieuwenhuis, R., Te Grotenhuis, H. F., & Pelzer, B. J. (2012). influence.ME: Tools for Detecting Influential Data in Mixed Effects Models. *R Journal*, *4*(2), 38–47.

Nishida, T. (1983). Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates*, *24*(3), 318–336. https://doi.org/10.1007/BF02381978

Nishida, T., & Hosaka, K. (1996). Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In *Great Ape Societies* (pp. 114–134). Cambridge University Press. https://doi.org/10.1017/CBO9780511752414.011

Notman, H., & Rendall, D. (2005). Contextual variation in chimpanzee pant hoots and its implications for referential communication. *Animal Behaviour*, *70*(1), 177–190. https://doi.org/10.1016/j.anbehav.2004.08.024

Pappano, D. J., Snyder-Mackler, N., Bergman, T. J., & Beehner, J. C. (2012). Social 'predators' within a multilevel primate society. *Animal Behaviour*, *84*(3), 653–658. https://doi.org/10.1016/j.anbehav.2012.06.021

Pollick, A. S., Gouzoules, H., & De Waal, F. B. M. (2005). Audience effects on food calls in captive brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, *70*(6), 1273–1281. https://doi.org/10.1016/j.anbehav.2005.03.007

Powell, L. E., Isler, K., & Barton, R. A. (2017). Re-evaluating the link between brain size and behavioural ecology in primates. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1865), 20171765. https://doi.org/10.1098/rspb.2017.1765

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Ramos-Fernandez, G., & Aureli, F. (2018). Fission-Fusion. In *Encyclopedia of Animal Cognition and Behavior* (Issue Humphrey 1976, pp. 1–8). Springer International Publishing. https://doi.org/10.1007/978-3-319-47829-6_1881-1

Ramos-Fernández, G., & Morales, J. M. (2014). Unraveling fission-fusion dynamics: how subgroup properties

and dyadic interactions influence individual decisions. *Behavioral Ecology and Sociobiology*, *68*(8), 1225–1235. https://doi.org/10.1007/s00265-014-1733-8

Reynolds, V. (2005). *The chimpanzees of the Budongo forest: Ecology, behaviour and conservation* (Oxford Uni).

Reynolds, V., & Reynolds, R. (1965). Chimpanzees of the Budongo Forest. In *Primate behavior: field studies of monkeys and apes* (pp. 368–424). Rinehart & Winston.

Rosati, A. G. (2017). Foraging Cognition: Reviving the Ecological Intelligence Hypothesis. *Trends in Cognitive Sciences*, *21*(9), 691–702. https://doi.org/10.1016/j.tics.2017.05.011

Samuni, L., Crockford, C., & Wittig, R. M. (2021). Group-level cooperation in chimpanzees is shaped by strong social ties. *Nature Communications*, *12*(1), 539. https://doi.org/10.1038/s41467-020-20709-9

Samuni, L., Mielke, A., Preis, A., Crockford, C., & Wittig, R. M. (2020). Intergroup Competition Enhances Chimpanzee (*Pan troglodytes verus*) In-group Cohesion. *International Journal of Primatology*, *41*(2), 342–362. https://doi.org/10.1007/s10764-019-00112-y

Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R. M., & Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1888). https://doi.org/10.1098/rspb.2018.1643

Schel, A. M., Machanda, Z. P., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour*, *86*(5), 955–965. https://doi.org/10.1016/j.anbehav.2013.08.013

Silk, J., Cheney, D. L., & Seyfarth, R. M. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology: Issues, News, and Reviews*, *22*(5), 213–225. https://doi.org/10.1002/evan.21367

Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., Squibbs, P., & Zuberbühler, K. (2010). Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behavioral Ecology and Sociobiology*, *64*(12), 1959–1966. https://doi.org/10.1007/s00265-010-1006-0

Slocombe, K. E., & Zuberbühler, K. (2005). Functionally Referential Communication in a Chimpanzee. *Current Biology*, *15*(19), 1779–1784. https://doi.org/10.1016/j.cub.2005.08.068

Slocombe, K. E., & Zuberbühler, K. (2006). Food-associated calls in chimpanzees: responses to food types or food preferences? *Animal Behaviour*, *72*(5), 989–999. https://doi.org/10.1016/j.anbehav.2006.01.030

Stephan, H., Frahm, H., & Baron, G. (1981). New and Revised Data on Volumes of Brain Structures in Insectivores and Primates. *Folia Primatologica*, *35*(1), 1–29. https://doi.org/10.1159/000155963

Sueur, C., Petit, O., & Deneubourg, J. L. (2010). Short-term group fission processes in macaques: a social networking approach. *Journal of Experimental Biology*, *213*(8), 1338–1346. https://doi.org/10.1242/jeb.039016

Symington, M. M. (1990). Fission-Fusion Social Organization in *Ateles* and *Pan*. *International Journal of Primatology*, *11*(1), 47–61.

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65,13–21.

Tokuda, M., Boubli, J. P., Izar, P., & Strier, K. B. (2012). Social cliques in male northern muriquis *Brachyteles hypoxanthus*. *Current Zoology*, *58*(2), 342–352. https://doi.org/10.1093/czoolo/58.2.342

Townsend, S. W., Koski, S. E., Byrne, R. W., Slocombe, K. E., Bickel, B., Boeckle, M., Braga Goncalves, I., Burkart, J. M., Flower, T., Gaunet, F., Glock, H. J., Gruber, T., Jansen, D. A. W. A. M., Liebal, K., Linke, A., Miklósi, Á., Moore, R., van Schaik, C. P., Stoll, S., … Manser, M. B. (2017). Exorcising Grice's ghost: an empirical approach to studying intentional communication in animals. *Biological Reviews*, *92*(3), 1427–1433. https://doi.org/10.1111/brv.12289

Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour*, *75*(2), 333–344. https://doi.org/10.1016/j.anbehav.2007.06.020

White, F. J., & Burgman, M. A. (1990). Social organization of the pygmy chimpanzee (*Pan paniscus*): Multivariate analysis of intracommunity associations. *American Journal of Physical Anthropology*, *83*(2), 193–201. https://doi.org/10.1002/ajpa.1330830208

Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., Hobaiter, C., Hohmann, G., Itoh, N., Koops, K., Lloyd, J. N., Matsuzawa, T., Mitani, J. C., Mjungu, D. C., Morgan, D., Muller, M. N., Mundry, R., Nakamura, M., Pruetz, J., … Wrangham, R. W. (2014). Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. *Nature*, *513*(7518), 414–417. https://doi.org/10.1038/nature13727

Wittig, R. M., Crockford, C., Deschner, T., Langergraber, K. E., Ziegler, T. E., & Zuberbühler, K. (2014). Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1778), 20133096. https://doi.org/10.1098/rspb.2013.3096

Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe national park, Tanzania. In T. H. Clutton-Brock (Ed.), *Primate ecology: studies of feeding and ranging behavior in lemurs monkeys and apes.* (pp. 503–538). Academic Press, London.

Wrangham, R. W., Gittleman, J. L., & Chapman, C. A. (1993). Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behavioral Ecology and Sociobiology*, *32*(3), 199–209. https://doi.org/10.1007/BF00173778

Wrangham, R. W., Wilson, M., & Hauser, M. D. (2007). Chimpanzees (*Pan troglodytes*) modify grouping and vocal behaviour in response to location-specific risk. *Behaviour*, *144*(12), 1621–1653. https://doi.org/10.1163/156853907782512137

Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., & Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour*, *77*(4), 873–885. https://doi.org/10.1016/j.anbehav.2008.12.014

Zeileis, A., & Hothorn, T. (2002). Diagnostic Checking in Regression Relationships. *R News*, *2*(3), 7–10. https://cran.r-project.org/doc/Rnews/

Supplementary material

Table S2.1. IDs of the adult male chimpanzee subjects, with their age (at the beginning of the study), total focal time, elo-rating scores and associated dominance rank.

Focal ID	Age	Focal time (hours)	Elo-rating	Dominance
HW	24	88	1755	High-ranking
MS	26	87	1431	High-ranking
FK	18	60	1365	High-ranking
SM	24	63	1035	Non-dominant
SQ	26	55	962	Non-dominant
ZL	21	66	914	Non-dominant
KT	23	83	890	Non-dominant
PS	19	87	864	Non-dominant
ZF	35	22	834	Non-dominant
KZ	22	71	493	Non-dominant
ZD*	16	10	482	Non-dominant

The subject marked with * was excluded from the analysis due to a small amount of focal time (the subject was notoriously difficult to follow). The underlined subjects died in the respiratory disease outbreak in 2019.

Table S2.2. Preferred grooming partners and preferred proximity partners, with the associated DSI_P and DSI_G values respectively, for each of the study subjects and each of the study periods.

Focal ID	Preferred grooming partners						Preferred proximity partners					
	ID1	*DSIG*	*ID2*	*DSIG*	*ID3*	*DSIG*	*ID1*	*DSIP*	*ID2*	*DSIP*	*ID3*	*DSIP*
Pre-outbreak study period (January 4th 2018 to February 26th 2019)												
FK	HW	2.51	MS	0.82	ZL	0.72	HW	1.94	PS	1.23	SM	1.12
HW	MS	7.42	ZL	3.57	SQ	2.86	KT	3.15	MS	2.96	ZL	2.74
KT	HW	2.11	MS	1.87	ZL	0.92	HW	3.15	MS	1.55	FK	1.09
KZ	ZL	1.18	PS	0.87	SM	0.81	SQ	1.39	PS	0.95	ZF	0.91
MS	HW	7.42	PS	2.71	SQ	2.06	HW	2.96	SQ	1.98	KT	1.55
PS	MS	2.71	HW	2.36	ZL	1.85	HW	1.58	FK	1.23	MS	1.15
SM	HW	1.59	ZL	1.48	PS	0.81	HW	1.93	ZD	1.27	ZL	1.15
SQ	HW	2.86	MS	2.06	PS	1.33	MS	1.98	HW	1.79	KZ	1.39
ZD	ZL	2.14	PS	1.35	SQ	1.18	ZL	1.50	SM	1.27	SQ	1.01
ZF	MS	0.83	HW	0.66	ZL	0.46	HW	1.78	SQ	0.98	KZ	0.91
ZL	HW	3.57	ZD	2.14	PS	1.85	HW	2.74	ZD	1.50	SM	1.15
Post-outbreak study period (June 1st 2019 to March 16th 2020)												
FK	HW	1.51	ZL	0.65	SM	0.62	PS	1.43	HW	1.26	SM	1.14
HW	MS	5.17	ZL	3.26	FK	1.51	ZL	3.39	KT	2.83	MS	2.62
KT	MS	1.43	HW	1.41	PS	0.52	HW	2.83	MS	1.14	PS	0.77
MS	HW	5.17	PS	2.90	KT	1.43	HW	2.62	PS	1.26	KT	1.14
PS	MS	2.90	ZL	1.85	HW	1.07	FK	1.43	MS	1.26	HW	1.14
SM	HW	1.37	FK	0.62	MS	0.44	HW	1.73	FK	1.14	ZL	0.98
ZD	ZL	1.99	PS	0.46	HW	0.02	ZL	0.94	SM	0.24	PS	0.12
ZL	HW	3.26	ZD	1.99	PS	1.85	HW	3.39	PS	1.04	SM	0.98

Table S2.3. Structure of the Generalised Linear Mixed Models (GLMMs) used in this study.

Subject's role	Call	GLMM	Response variable	Test variables	Random factor
Arriving in the food tree	Pant hoot	GLMM1	Call production (yes / no)	dominance rank + food tree species + (number of individuals, presence of a high-ranking individual, a social bond partner or an association partner) in the entire party and in the group already present in the tree	Subject ID
	Rough grunt	GLMM2			
Present in the food tree	Pant hoot	GLMM3		dominance rank + food tree species + (number of individuals, presence of a high-ranking individual, a social bond partner or an association partner) in the entire party and in the arriving group	
	Rough grunt	GLMM4			

All GLMMs have a binomial error structure and logit link function.

Table S2.4. Summary results of Spearman's rank correlation tests to explore the correlation between the productions of both calls depending on the subject's role.

Subject's role	Correlation tested	r_S	*p*
Arriving in the food tree	Pant hoot ~ Rough grunt	0.01	0.86
	Rough grunt ~ Pant hoot	0.01	0.84
Present in the food tree	Pant hoot ~ Rough grunt	0.07	0.14
	Rough grunt ~ Pant hoot	0.07	0.11

Table S2.5. Summary results of the model averaging for each variable included in the top set of sub-models (ΔAICc < 2) and for each model used in this study.

	Estimate	SE	LCI	UCI	Relative importance
GLMM1 - Probability of producing a pant hoot when joining a food tree					
Number of individuals in the feeding party	-0.19	0.06	**-0.31**	**-0.07**	1.00
Presence of a preferred grooming partner in the feeding party	1.08	0.50	**0.10**	**2.07**	1.00
Presence of a high-ranking individual in the feeding party	-1.30	0.50	**-2.28**	**-0.31**	1.00
Presence of a preferred proximity partner in the feeding party	-0.11	0.31	-1.45	0.47	0.23
Presence of a high-ranking individual in the tree	0.05	0.27	-0.91	1.53	0.21
Dominance rank (Elo-rating)	-0.03	0.10	-0.49	0.16	0.16
GLMM2 - Probability of producing a rough grunt when joining a food tree					
Number of individuals in the feeding party	-0.12	0.05	**-0.22**	**-0.03**	1.00
Dominance rank (Elo-rating)	-0.62	0.18	**-0.97**	**-0.27**	1.00
Presence of a high-ranking individual in the feeding party	0.26	0.42	-0.21	1.47	0.42
Presence of a preferred grooming partner in the tree	-0.28	0.52	-1.92	0.47	0.39
Presence of a preferred grooming partner in the feeding party	0.20	0.43	-0.38	1.81	0.27
Presence of a high-ranking individual in the tree	0.06	0.33	-1.01	1.50	0.24
Presence of a preferred proximity partner in the tree	-0.02	0.13	-1.06	0.49	0.07
GLMM3 - Probability of producing a pant hoot when being joined in a food tree					
Number of individuals in the feeding party	-0.17	0.06	**-0.29**	**-0.05**	1.00
Dominance rank (Elo-rating)	-0.52	0.22	**-0.95**	**-0.09**	1.00
Presence of a high-ranking individual in the joining group	1.26	0.40	**0.46**	**2.05**	1.00
Presence of a preferred grooming partner in the feeding party	-0.27	0.51	-1.91	0.49	0.48
Presence of a preferred proximity partner in the feeding party	0.47	0.69	-0.38	2.35	0.38
Presence of a preferred grooming partner in the joining group	-0.03	0.18	-1.20	0.70	0.12
GLMM4 - Probability of producing a rough grunt when being joined in a food tree					
Number of individuals in the feeding party	-0.17	0.05	**-0.26**	**-0.08**	1.00
Dominance rank (Elo-rating)	-0.83	0.19	**-1.21**	**-0.45**	1.00
Presence of a high-ranking individual in the joining group	1.74	0.33	**1.10**	**2.38**	1.00
Presence of a preferred grooming partner in the feeding party	0.04	0.20	-0.64	0.96	0.22
Presence of a preferred grooming partner in the joining group	-0.02	0.19	-0.90	0.68	0.21

LCI: lower 95% confidence interval; UCI: upper 95% confidence. Informative variables are in bold.

Table S2.6. Summary results of the model averaging for each variable included in the top set of sub-models (ΔAICc < 2) and for each previously presented model (Table A5) reran on a subset of the data without the other call type produced.

	Estimate	SE	LCI	UCI	Relative importance
GLMM1b - Probability of producing a pant hoot when joining a food tree					
Number of individuals in the feeding party	-0.15	0.07	**-0.28**	**-0.02**	1.00
Presence of a high-ranking individual in the feeding party	-1.12	0.51	**-2.12**	**-0.12**	1.00
Presence of a preferred grooming partner in the feeding party	0.83	0.65	-0.11	2.15	0.82
Presence of a preferred proximity partner in the feeding party	-0.20	0.44	-1.83	0.33	0.27
Presence of a preferred proximity partner in the tree	-0.04	0.19	-1.21	0.59	0.13
Dominance rank (Elo-rating)	-0.01	0.07	-0.49	0.31	0.11
GLMM2b - Probability of producing a rough grunt when joining a food tree					
Dominance rank (Elo-rating)	-0.61	0.20	**-0.99**	**-0.22**	1.00
Number of individuals in the feeding party	-0.06	0.05	-0.17	0.02	0.74
Presence of a high-ranking individual in the tree	0.05	0.20	-0.54	1.07	0.17
Presence of a preferred grooming partner in the feeding party	0.03	0.19	-0.64	1.06	0.16
GLMM3b - Probability of producing a pant hoot when being joined in a food tree					
Number of individuals in the feeding party	-0.18	0.07	**-0.31**	**-0.05**	1.00
Dominance rank (Elo-rating)	-0.43	0.23	-0.88	0.02	1.00
Presence of a high-ranking individual in the joining group	1.09	0.46	**0.19**	**1.99**	1.00
Presence of a preferred proximity partner in the feeding party	0.21	0.50	-0.61	2.10	0.28
Presence of a preferred grooming partner in the feeding party	-0.15	0.40	-1.80	0.65	0.26
Presence of a high-ranking individual in the feeding party	0.09	0.33	-0.71	1.87	0.16
Presence of a preferred grooming partner in the joining group	-0.07	0.27	-1.54	0.60	0.15
GLMM4b - Probability of producing a rough grunt when being joined in a food tree					
Number of individuals in the feeding party	-0.17	0.05	**-0.27**	**-0.08**	1.00
Dominance rank (Elo-rating)	-0.78	0.20	**-1.17**	**-0.40**	1.00
Presence of a high-ranking individual in the joining group	1.72	0.37	**0.99**	**2.44**	1.00
Presence of a preferred proximity partner in the joining group	-0.08	0.26	-1.24	0.52	0.22
Presence of a preferred grooming partner in the feeding party	0.03	0.19	-0.63	1.02	0.18
Presence of a high-ranking individual in the feeding party	-0.03	0.21	-1.15	0.79	0.17

LCI: lower 95% confidence interval; UCI: upper 95% confidence. Informative variables are in bold. GLMMs 1b, 2b, 3b and 4b correspond to previously presented models GLMMs 1, 2, 3 and 4, respectively.

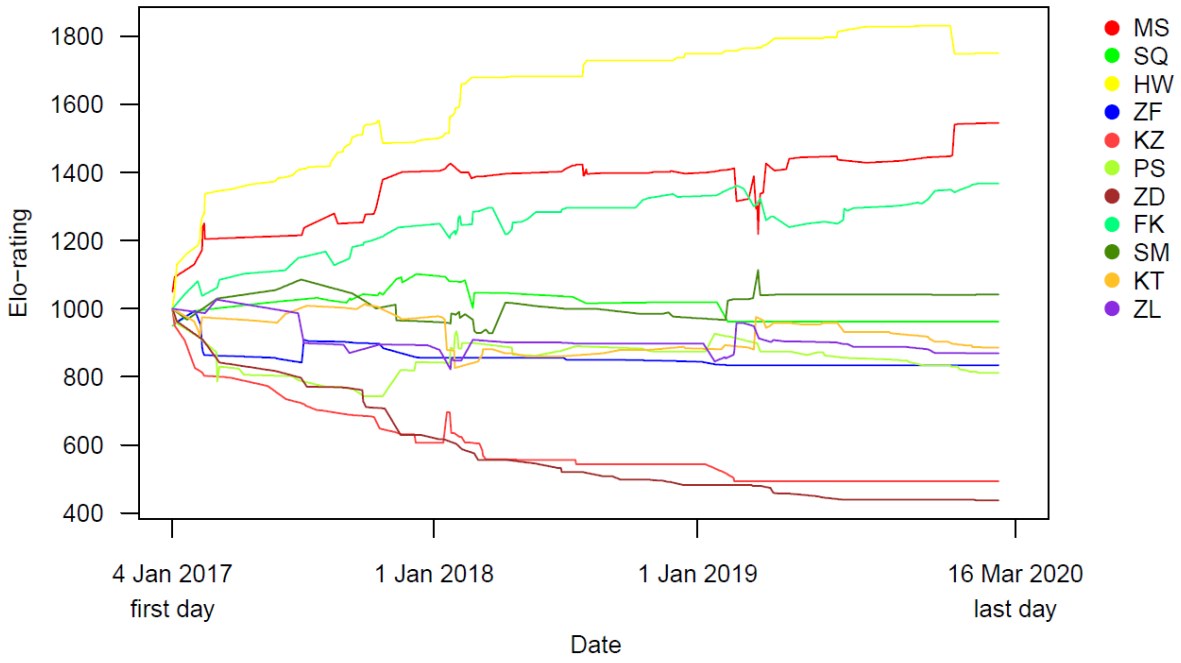

Figure S2.1. Evolution of the Elo-rating scores of the 11 adult males of the Sonso community from 12 months before the start of the study (4 January 2017) to the end of the first study period (16 March 2020).

Chapter 3. An intentional cohesion call in male chimpanzees of Budongo Forest

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Manuscript published in 2022 in Animal Cognition, 25(4), 853–866 (DOI: 10.1007/s10071-022-01597-6).

Abstract

Many social animals travel in cohesive groups but some species, including chimpanzees, form flexible fission-fusion systems where individuals have some control over group cohesion and proximity to others. Here, we explored how male chimpanzees of the Sonso community of Budongo Forest, Uganda, use communication signals during resting, a context where the likelihood of group fission is high due to forthcoming travel. We focused on a context-specific vocalisation, the 'rest hoo', to investigate its function and determine whether it is produced intentionally. We found that this call was typically given towards the end of usual silent resting bouts, i.e., the period when individuals need to decide whether to continue travelling after a brief stop-over or to start a prolonged resting bout. Subjects rested longer after producing 'rest hoos' and their resting time increased with the number of calls produced. They also rested longer if their calls were answered. Furthermore, focal subjects' resting time was prolonged after hearing others' 'rest hoos'. Subjects called more when with top proximity partners and in small parties and rested longer if a top proximity partner called. We also found an interaction effect between rank and grooming activity, with high-ranking males with a high grooming index calling less frequently than other males, suggesting that vocal communication may serve as a cohesion strategy alternative to tactile-based bonding. We discuss these different patterns and conclude that chimpanzee 'rest hoos' meet key criteria for intentional signalling. We suggest that 'rest hoos' are produced to prolong resting bouts with desired partners, which may function to increase social cohesion.

Introduction

A major challenge for group-living animals is to balance the social need for cohesion with sometimes diverging individual needs of resting, feeding or moving (Kerth 2010; Petit and Bon 2010). Fission-fusion societies are an evolutionary response to these opposing demands, enabling group members to take individual decisions depending on local food availability (Asensio et al. 2009; Chapman et al. 1995; Kummer 1971; Sueur et al. 2011; Symington 1990) and social needs, as documented in various species (bottlenose dolphins: Lusseau 2007; spider monkeys: Busia et al. 2017; chimpanzees: Mitani and Amsler 2003). In these social systems, decision-making is devolved from the collective to the private, from a small number of influential decision-makers to most group members (Conradt and List 2009; Couzin et al. 2005; Stueckle and Zinner 2008). Compared to the more standard social system, i.e., cohesive social groups, fission-fusion systems are more likely to lead to disagreement, negotiation and coordination (Kerth 2010), and this may put higher demands on social cognition and socially targeted communication (Aureli et al. 2008; Couzin et al. 2005; Strandburg-Peshkin et al. 2018). Correspondingly, and in line with the social intelligence hypothesis (Humphrey 1976), species with high degrees

of fission-fusion dynamics, such as spider monkeys (Aguilar-Melo et al. 2018), baboons (Kummer 1968), bonobos (White and Burgman 1990), chimpanzees (Goodall 1986), dolphins (Tsai and Mann 2013) or humans (Marlowe 2005), all have relatively large neocortices if compared to species living in more cohesive groups (Barrett et al. 2003; Dunbar 1998).

How do individuals adjust social cohesion? Many group-living species have evolved acoustically distinct vocalisations that function for this purpose, typically referred to as 'contact calls' (Bolt 2020; Chaverri et al. 2013; da Cunha and Byrne 2009). These calls usually provide information about the identity of the caller and, in some instances, about the caller's current activity (Candiotti et al. 2012; Fischer 2008) or desired response (Gruber and Zuberbühler 2013). In fission-fusion societies, however, patterns of cohesion are more complex and may thus require more complex communication. Chimpanzees, for instance, maintain contact with distant group members with acoustically distinct long-distance calls (i.e., 'pant-hoots') and call exchanges are more frequent between preferred social partners than other group members (Eckhardt et al. 2015; Mitani and Nishida 1993). During close-range interactions, chimpanzees use a range of other functionally distinct vocalisations, such as 'travel hoos', to coordinate departures or 'rough grunts' during feeding. These calls seem to be produced in goal-directed ways, such as to initiate travel or coordinate feeding, and are preferentially given in the presence of preferred social partners, suggesting that they possess some of the hallmarks of intentionality (Bates 1979; Fedurek and Slocombe 2013; Gruber and Zuberbühler 2013; Schel et al. 2013a).

In previous studies, it has been noted that, when resting, chimpanzees often produce a distinct vocalisation, the 'rest hoo' (Crockford et al. 2015; Gruber and Zuberbühler 2013). In this study, we were interested in investigating the function of 'rest hoo' vocalisations and determining whether such communication behaviour qualifies as intentional. Intentionality in animal communication usually refers to signals produced voluntarily by a signaller in an attempt to manipulate the recipient's behaviour (Bard 1990; Tomasello et al. 1985). While intentionality has been of interest to philosophy, empirically the concept is best investigated during natural communication acts. Here, pioneering work by Bates (1979) has proposed a definition based on key behavioural markers, i.e., a signal must be goal-directed and produced in the presence of an audience to qualify both as intentional and communicative (see Leavens et al. 2005; Leavens and Hopkins 1998). More recently, other elements of definitions have been proposed, such as the requirement that the recipient responds in line with the signaller's presumed goal, a contentious issue because recipients may be in conflict with the signaller's intention and therefore choose not to respond (see Liebal et al. 2014; Townsend et al. 2017).

The aim of this study was to investigate the function of 'rest hoo' vocalisations and whether they qualified as intentional signals. To do so, we observed a group of wild chimpanzees in Budongo Forest (Uganda) for over a year, where the demography and social relations between the individuals are known. Chimpanzees travel over considerable distances to visit food trees, interspersed by sometimes long resting periods, which account for the largest proportion of their day-time activity budgets (about 45% of time, A Bouchard, unpublished data; see also Kosheleff and Anderson 2009; Yamanashi and Hayashi 2011). Changes in cohesion and group composition are most common during activity changes, such as when transitioning between travelling and resting.

Chimpanzees can produce acoustically distinct vocalisations in these situations, notably 'rest hoos' during resting and 'travel hoos' before or during travel. A third call type that is acoustically similar is given in response

to mild dangers (i.e., 'alert hoo'). All three 'hoo' variants are close-range calls (<150m; Crockford et al. 2015, 2018) and are acoustically distinguishable, with significant variations in call durations, maximum fundamental frequencies and inter-call intervals (Crockford et al. 2018). Previous studies have suggested that 'travel' and 'alert hoos' are goal-directed and produced in presence of an audience, suggesting that they qualify as intentional signals (*sensu* Bates et al 1978). Even though 'rest hoos' have been previously mentioned in the literature, sometimes with a different name (e.g., 'extended grunt'; Goodall 1986; Laporte 2010; Mullins 2014), their function had never been investigated.

We focused on adult males due to the fact that they form stronger social bonds with each other than with females (Gilby and Wrangham 2008; Mitani 2009; Wrangham et al. 1992). Bonding in male chimpanzees is important for a variety of activities and serves as a basis for trust and support during dangerous activities, such as intergroup aggression (Herbinger et al. 2009; Wilson et al. 2014), cooperative hunting (Hobaiter et al. 2017), predator defence (Boesch 1991) and intragroup conflicts (Goodall 1986; Mitani 2009; Muller and Mitani 2005). Generally, associating with high-ranking males can also be advantageous and bring fitness benefits, such as higher reproductive success (Bray et al. 2016; Duffy et al. 2007; Feldblum et al. 2021; Kaburu and Newton-Fisher 2015).

For the aforementioned reasons, we thus expected males to care about maintaining proximity to desirable partners, i.e., preferred social partners and high-ranking males. Since group fissions are likely to happen before and after resting bouts, males are likely to be especially challenged in these situations. We tested the hypothesis that chimpanzees produced 'rest hoos' to communicate their intention to keep resting with specific individuals (i.e., that calls are goal-directed). In relation to this, we predicted that subjects should prolong resting bouts after producing 'rest hoos' and that these calls should be produced in the presence of desirable audiences, i.e., preferred social partners and high-ranking males. To test these predictions, we analysed how call production affected a signaller's resting time in different audiences. We also explored individual variation in call production, focusing on individuals' rank and grooming index. Finally, we predicted that, if 'rest hoos' were produced intentionally, the behavioural response of recipients should mainly be in line with the signaller's goal, i.e., recipients should on average prolong their resting time. We thus analysed the recipients resting time in relation to 'rest hoo' production and the signaller's identity.

Methods

Study site and subjects

Data were collected between January 2018 and March 2020 on East African chimpanzees (*Pan troglodytes schweinfurthii*) of the Sonso community in the Budongo Forest Reserve, Uganda (latitude 1°37′–2°00′N; longitude: 31°22′–31°46′E). The community has a home range of around 7 km^2 (Newton-Fisher 2003) and has been well habituated to human presence for more than 25 years. All individuals were identified and most of their social and kin relations were known (Reynolds 2005). At the beginning of the study, the community consisted of 75 individuals, including 37 adults (> 15 years, 11 males). The study subjects were the 11 adult males (although 3 of them died in an epidemic in February 2019).

Data collection

We conducted full-day (usually between 07:00 and 16:30 local time) focal follows of 11 adult male chimpanzees. One male (ZD) was excluded from analysis due to low observation time (Table 3.1). During each follow, we continuously recorded the subject's activities (feed, travel and rest) with start and end times. For each resting bout (defined as the subject stopping for at least 15s), we recorded the duration, initial party composition and time of 'rest hoo' production by the subject and by any other individual throughout the bout. For each 'hoo', we also recorded the identity of the caller and whether it elicited an immediate vocal response within the same vocal bout (i.e., within the next 5s). We excluded resting bouts during which 'rest hoos' were produced by unidentifiable individuals. We also recorded if there was a change of activity (i.e., rest, travel or feed) in the audience immediately (i.e., within 5s) before or after call production. Audio recordings of 'rest hoo' vocalisations are included in the electronic supplementary material.

Social variables

To establish the social relations between individuals, we used long-term data collected by four trained field assistants to determine each subject's dominance rank (Elo-rating), grooming index and preferred social partners (grooming and proximity partners). Similarly to Samuni et al. (2018, 2021), we did not calculate an overall sociality index but two separate indices; one based on grooming interactions (i.e., grooming partners) and another based on spatial proximity (i.e., proximity partners). Several studies have shown that relationships formed through mere spatial proximity can be different from those involving tactile grooming and, therefore, may affect individual behaviours differently (Bray and Gilby 2020; Mitani 2009; Samuni et al. 2018, 2021), including vocal behaviour (Mitani and Nishida 1993).

Data collection was during full-day focal follows to document all affiliative and agonistic interactions with every other individual in the group. Party composition (i.e., all individuals within 30m of the focal) was continuously monitored and determined every 15 min during scan sampling. Due to a respiratory disease outbreak in 2019, three of ten focal animals died, which destabilised the hierarchy and social relations between the remaining males. For this reason, we could only establish social relationships among males for the pre-outbreak period, which reduced the dataset for some analyses. Specifically, when investigating the effects of social relationships on call production or reception, we only analysed data collected until 26 February 2019 (GLM1, GLMM6, GLMM8, see below).

Dominance: The hierarchy of the different adult males was determined using the Elo-rating method (Elo 1978; Neumann et al. 2011) on 'pant grunt' data (i.e., a 'greeting' vocalisation given to higher-ranking individuals), a method that has been validated against other commonly used methods (Neumann et al. 2011). To have an accurate estimation of the dominance ranks at the beginning of the study, we used data from the twelve months before the beginning of the study followed by data collected until the end of the study period (January 4th 2017 to February 26th 2019). We calculated the Elo-ratings using the 'EloRating' R package version 0.46.11 (Neumann and Kulik 2020). The hierarchy was stable through the 2017-2019 study period, enabling us to attribute a final Elo-score to each male (i.e., the Elo-score obtained at the end of the observation period). Three males had consistently higher Elo-scores than the other males and were thus classified as 'high-ranking' (Table 3.1; Supplementary material, Fig. S3.1). Elo-rating scores were standardized for subsequent statistical analyses.

Grooming index: We determined each adult male's grooming index, which indicated how much time he spent grooming relative to the other adult males of the group. We were interested in grooming interactions, rather than the directionality of grooming, so both grooming given and received (with any individual in the group) were considered. The grooming index was calculated from the focal data as a corrected standardized grooming rate (grooming duration per observation time) using the 'socialindices2' R package version 0.50.0 (Neumann 2017) (Table 3.1).

Table 3.1. Adult male chimpanzees that participated in the study, with their age (at the beginning of the study), the total focal time, the number of 'rest hoo' calls recorded (during the focal data collection), their elo-rating scores and dominance, as well as their grooming index.

Focal ID	Age	Focal time (hours)	Number of 'rest hoos' produced	Elo-rating	Dominance	Grooming index
HW	24	88	15	1758	High-ranking	1.32897
FK	18	60	37	1361	High-ranking	-0.43526
MS	26	87	35	1316	High-ranking	1.25555
SM	24	63	26	1028	Non-dominant	-1.11299
SQ	26	55	22	962	Non-dominant	0.68209
ZL	21	66	22	958	Non-dominant	0.53392
PS	19	87	27	915	Non-dominant	-0.34498
KT	23	83	25	893	Non-dominant	-1.00136
ZF	35	22	18	834	Non-dominant	-0.3755
KZ	22	71	41	493	Non-dominant	0.97484
ZD*	16	10	0	482	Non-dominant	-1.50527

* excluded from analysis due to low focal time

Grooming and proximity partners: To determine the preferred grooming and proximity partners between all male dyads, we calculated a grooming-based and a proximity-based dyadic sociality indices for each male dyad, the DSI_G and the DSI_P (based on DSI; see Silk et al. 2013 and Supplementary material, Table S3.1). To calculate the DSI_G, we used the grooming data, defined as the duration of grooming interactions (grooming given or received) between the two males of the dyad, recorded during the focal follows. To calculate the DSI_P, we used the nearest neighbour data, defined as the individual sitting in closest proximity to the focal animal during each 15min scan, considering only data where the nearest neighbour was another adult male. The DSI_G and the DSI_P were calculated using the 'socialindices2' R package version 0.50.0 (Neumann 2017). For each focal male, the top 3 grooming partners and the top 3 proximity partners were the top three individuals who had the highest DSI_G and DSI_P values, respectively (Supplementary material, Table S3.1).

Statistical analyses

'Rest hoo' production

To establish if the subjects produced 'rest hoos' in the presence of an audience, we analysed all resting bouts (i.e. with or without 'rest hoo' production) and ran a generalized linear mixed model (GLMM1) with a binomial error structure and logit link function, with the production of 'rest hoo' vocalisation (at least one 'rest hoo' produced / no 'rest hoo' produced) as the response variable. We used the presence of a potential audience (yes/no) as the test variable and the subject ID as a random factor.

To explore which social (i.e., presence of specific individuals) and individual (i.e., rank and grooming index) parameters influenced whether the subjects produced a 'rest hoo' or not, we only analysed resting bouts with a potential audience and excluded events with 'rest hoos' produced by other individuals. We ran a generalized linear model (GLM1) with a binomial error structure and logit link function, with the production of 'rest hoo' vocalisation (at least one 'rest hoo' produced / no 'rest hoo' produced) as the response variable. Test variables were the total number of individuals present, the presence of females (yes / no), the presence of a high-ranking male (yes / no), the presence of one of the subject's top 3 grooming partners (yes / no), the presence of one of the subject's top 3 proximity partners (yes / no), as well as the interaction between the grooming index and the rank of the subject (Elo-rating). The time spent resting (in minutes) was entered as a control variable.

Since we were particularly interested to know if the presence of specific males could affect 'rest hoo' production by the subject, we analysed events when the recipient was unambiguous (i.e. when the subject was resting only with one other male). We ran a GLMM (GLMM2) with a binomial error structure and logit link function, with the production of 'rest hoo' vocalisation (at least one 'rest hoo' produced / no 'rest hoo' produced) as the response variable. Whether the resting partner was a high-ranking male (yes / no), one of the subject's top 3 grooming partners (yes / no), or top 3 proximity partners (yes / no) were the test variables. The time spent resting (in minutes) was the control variable and the subject ID was entered as a random factor.

If 'rest hoos' were produced to keep spatial proximity with specific partners, we would also expect these partners to keep resting with the subject until the end of the resting bout (i.e., until the subject departs). We thus further analysed these dyadic resting bouts between males and ran a GLMM (GLMM3) with a binomial error structure and logit link function, with the presence of the resting partner at the end of the resting bout (yes / no) as the response variable. Whether the subject produced a 'rest hoo' (at least one 'rest hoo' produced / no 'rest hoo' produced) was the test variable, the time spent resting (in minutes) was the control variable and the subject ID was entered as a random factor.

We then investigated whether subjects prolonged their resting time after producing a 'rest hoo' and whether immediate vocal response affected this resting time. If 'rest hoos' were produced randomly, the probability of this call being produced would increase with the duration of the resting bouts. Therefore, to avoid this bias, we compared the total duration of resting bouts without 'rest hoos' to the duration of resting bouts after 'rest hoo' production. To do so, we ran two other GLMMs with a gamma distribution and inverse link function, with the time spent resting (in minutes) after the subject produced his first 'rest hoo' (or total resting time for events without 'rest hoo' production) as the response variable and with the subject ID entered as a random factor. We ran GLMM4 on all resting bouts with the production of 'rest hoo' vocalisation by the subject (at least one 'rest hoo' produced / no 'rest hoo' produced) as the test variable. We ran GLMM5 on events with at least one 'rest hoo' produced by the subject and we used the immediate vocal response (at least one immediate vocal response / no vocal response) as the test variable.

We recorded some occurrences of the subject producing several 'rest hoos' during the same resting bout so we tested if the number of call produced affected the time the subject spent resting afterwards by analysing the resting bouts during which the subject produced at least one 'rest hoo'. We ran a GLMM (GLMM6) with a gamma distribution and inverse link function, with the time spent resting (in minutes) after the subject produced

a ‘rest hoo’ as the response variable and with the number of ‘rest hoo’ produced during the resting bout as the test variable. The subject ID, as well as the ID of the resting bout, were entered as random factors.

‘Rest hoo’ perception

We then investigated what happened when the subjects heard a ‘rest hoo’ produced by another male.

We first explored the recipient’s behavioural response by testing if the subject rested longer after hearing another male producing a ‘rest hoo’. We analysed the events during which the subject did not vocalise and we conducted a GLMM (GLMM7) with a gamma distribution and inverse link function, with the time spent resting (in minutes) after the first ‘rest hoo’ was heard (or total resting time for events during which the subjects did not hear any ‘rest hoo’) as the response variable. The production of ‘rest hoo’ vocalisation by another male (at least one ‘rest hoo’ produced / no ‘rest hoo’ produced) was the test variable and the subject ID was entered as a random factor.

To investigate how the identity of the caller influenced the subject’s resting behaviour, we only further analysed events during which the subject heard ‘rest hoos’ from other males. We ran a GLMM (GLMM8) with a gamma distribution and inverse link function, with the time spent resting (in minutes) after the ‘rest hoo’ was produced as the response variable. Test variables were the number of individuals present, whether the caller was a high-ranking male (yes / no), a one of the subject’s top 3 grooming partners (yes / no), or top 3 proximity partners (yes / no), as well as the interaction between the caller’s grooming index and his rank (Elo-rating). To control for the fact that several ‘rest hoos’ could be produced during the same resting bout, the remaining number of ‘rest hoo’ heard in the resting bout was the control variable and the subject ID, as well as the ID of the resting bout, were entered as random factors.

Model selection

For the GLM (GLM1) and two GLMMs (GLMM2 and 8), we used an exploratory approach, using several test variables. To disentangle the effect of each variable and determine which models fitted the data best, we used a statistical model selection approach. We first fitted several models with the test variables as fixed effects, then we selected the best model based on the lowest AICc (i.e., Akaike information criterion corrected; Burnham et al. 2011), using the *dredge* function of the ‘MuMIn’ R package version 1.43.17 (Barton 2020). Variables were considered to improve the fit of the model only if their removal from the model inflated the AICc value by more than two units (Burnham and Anderson 2004). Finally, we tested the significance of the selected models by comparing them to a corresponding null model (including control variables and, for the GLMMs, random factors), using likelihood ratio tests (LRT) (*lrtest* function of ‘lmtest’ package; Zeileis and Hothorn 2002). Only results of the selected models are presented in the results section below.

GLMMs were run using the *glmer* function of the ‘lme4’ R package version 1.1-21 (Bates et al. 2015). All analyses were implemented in R v3.6.1 (R Core Team 2019).

Results

Across subjects (N=10 adult males), we recorded N=1,494 resting bouts, N=145 during which the subject produced at least one 'rest hoo' call (9.7%) and N=147 during which another male produced at least one 'rest hoo' call (9.8%), over a study period of 141 days (690h observation). We found that resting bouts lasted 10 minutes on average (range 15s to 132min). As mentioned, for all analyses involving social variables (i.e., rank, grooming index and preferred social partners) we only considered data collected before the outbreak, which consisted of N=967 resting bouts, N=101 during which the subject produced at least one 'rest hoo' call (10.4 %) and N=97 during which another male produced at least one 'rest hoo' call (10.0%).

'Rest hoo' production

The results of the GLMM1 showed that the presence of an audience was a significant predictor of 'rest hoo' call production (GLMM1; $p < 0.001$; Supplementary material, Fig. S3.2 and Table S3.2a). When alone, focal animals produced 'rest hoos' in only 9 of 334 resting bouts (2.7%), whereas, in the presence of an audience, they produced 'rest hoo' calls in 136 of 1,066 resting bouts (12.8%).

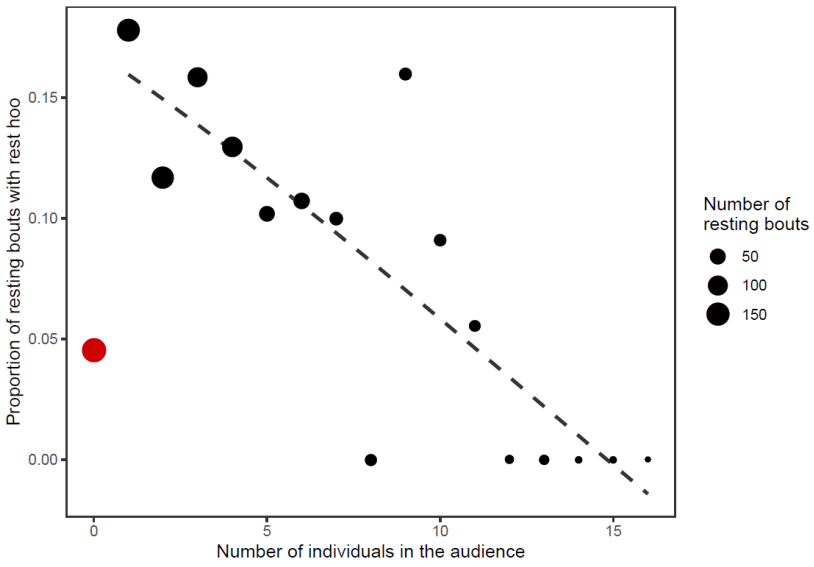

Figure 3.1. Relationship between the proportion of resting bouts with 'rest hoo' produced by the subject and the audience size (GLM1). The size of the points corresponds to the sample size (number of resting bouts recorded for each audience size). The red point represents the resting bouts when the subject was resting alone.

When further investigating data collected before the outbreak, the results of the GLM1 (Supplementary material, Table S3.2b) revealed that 'rest hoo' production could be predicted, significantly, by audience size, subjects calling more often with small rather than large audiences (p = 0,018; Fig. 3.1). It also showed that the interaction between the subject's dominance rank and grooming index was a significant predictor of 'rest hoo' production, with high-ranking males with a high grooming index calling little and other males calling much (p = 0,022; Fig. 3.2).

When investigating male dyadic resting bouts (N=83), the results of the GLMM2 (Supplementary material, Table S3.2c) showed that 'rest hoo' production could be significantly predicted by the presence of one of the subject's top 3 proximity partners rather than another male (p = 0,046; Fig. 3.3). When further investigating

these male dyadic resting bouts, the results of GLMM3 showed that the presence of the resting partner at the end of the resting bout could not be significantly predicted by the production of 'rest hoo' (p = 0.889; Supplementary material, Table S3.2d). Indeed, whether the subject produced a 'rest hoo' or not, his resting partner was present at the end of the resting bout in the majority of cases (approximately 80% of the resting bouts). One of the subject (MS) was not included in these analyses (GLMM2 and 3) since we did not have any data points with him resting alone with another male.

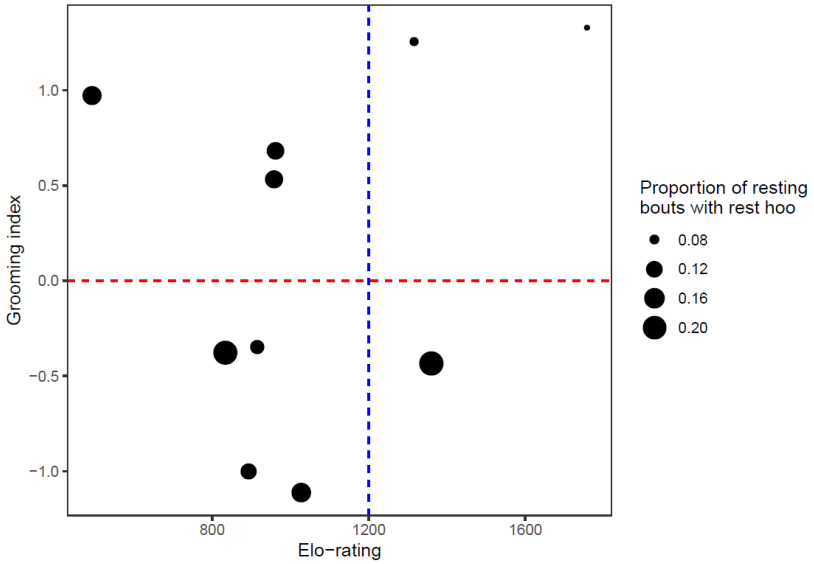

Figure 3.2. Subject's grooming index and dominance rank (Elo-rating) and his propensity to produce 'rest hoos' during resting bouts, i.e., the number of resting bouts during which he produced a 'rest hoo' over the total number of resting bouts recorded for this subject (each point corresponds to one study subject). The dashed red line indicates the mean grooming index, with individuals above the line being higher groomers. The dashed blue line indicates the separation between the top three high-ranking males (on the right of the line) and the non-dominant ones. The highest proportions of resting bouts with 'rest hoos' produced are from either non-dominant males or ones with a below-average grooming index (GLM1).

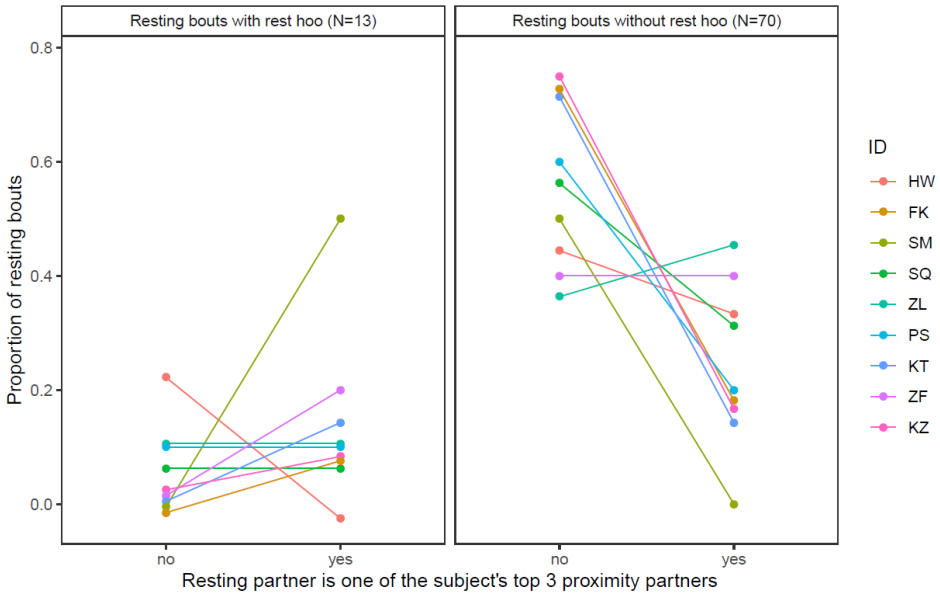

Figure 3.3. Proportion of dyadic resting bouts during which the subject produced a 'rest hoo' (left panel) or not (right panel) depending on whether the resting partner was one of the subject's top proximity partner or not, over the total number of dyadic resting bouts (N=83), for each study subject (GLMM2). The subjects are ordered by dominance rank (from top high-ranking to bottom low-ranking).

Subjects produced a 'rest hoo' after resting 9.6 min on average, which was similar to the mean duration of silent resting bouts (i.e., when no call is produced) (8.0 min; Fig. 3.4). Moreover, focal subjects rested significantly longer after producing a 'rest hoo' than without one (GLMM4; $p < 0.001$; Fig. 3.4; Supplementary material, Table S3.2e). Resting lasted longer if another male responded to the focal subject's 'rest hoo' (GLMM5; $p < 0.001$; Fig. 3.4; Supplementary material, Table S3.2f).

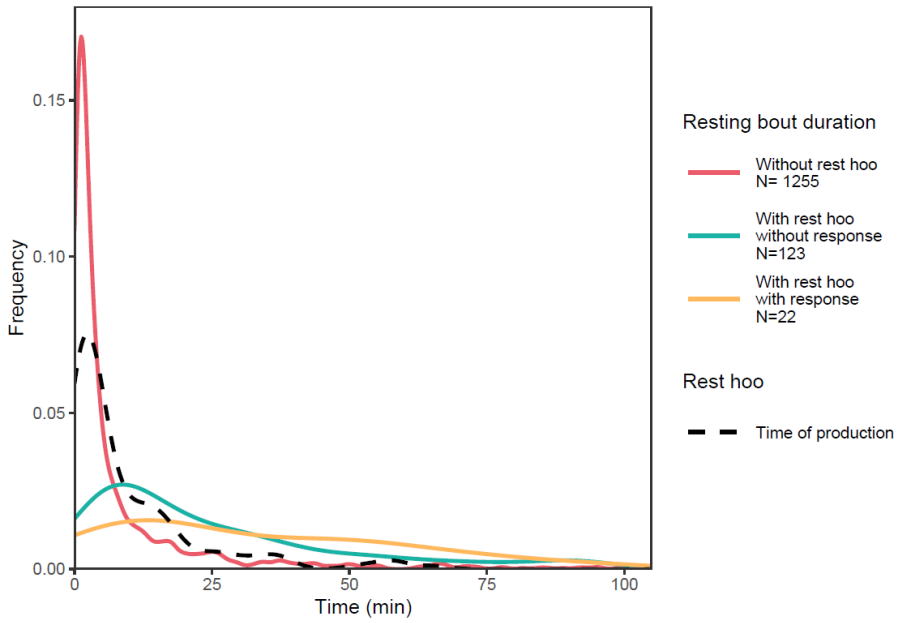

Figure 3.4. Distribution (kernel density estimates) of the time of 'rest hoo' production and of the time the subject spent resting depending on whether he produced a 'rest hoo' (GLMM4) and if this call elicited an immediate response by another individual or not (GLMM5).

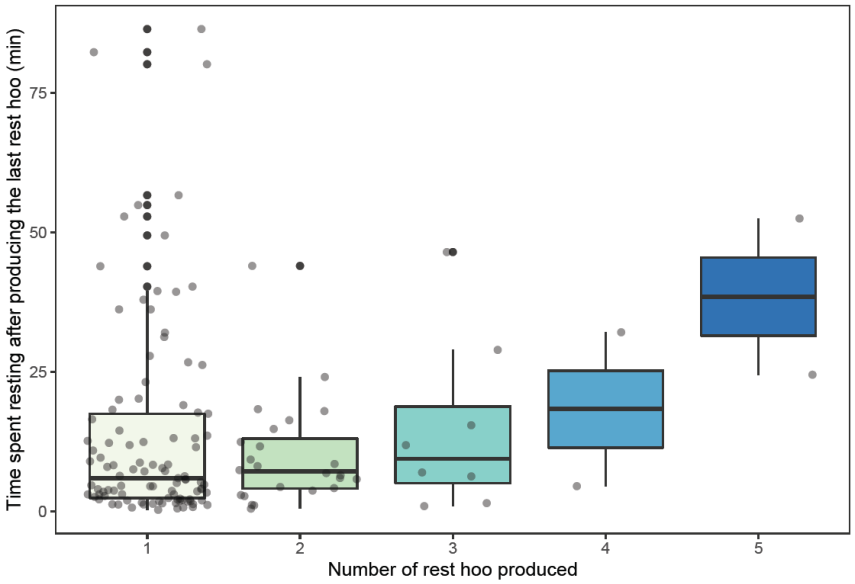

Figure 3.5. Time the subject spent resting after producing the last 'rest hoo' of the resting bout, depending on the total number of 'rest hoo' he produced during this resting bout (GLMM6).

During some resting bouts (N=36), the subject produced more than one 'rest hoo', with up to five calls produced during the same resting bout. The results of the GLMM6 showed that the time the subject spent resting after

producing a 'rest hoo' significantly increased with the number of 'rest hoo' produced ($p < 0.001$; Fig. 3.5; Supplementary material, Table S3.2g).

'Rest hoo' perception

The results of the GLMM7 showed that, when subjects heard a 'rest hoo' from another male, the subjects spent significantly more time resting afterwards than if no calls were produced or heard (GLMM7; $p < 0.001$; Fig. 3.6; Supplementary material, Table S3.2h). The results of the GLMM8 showed that subjects also rested longer if the call was produced by one of the subject's top 3 proximity partners rather than another male ($p = 0.026$; Fig. 3.7; Supplementary material, Table S3.2i).

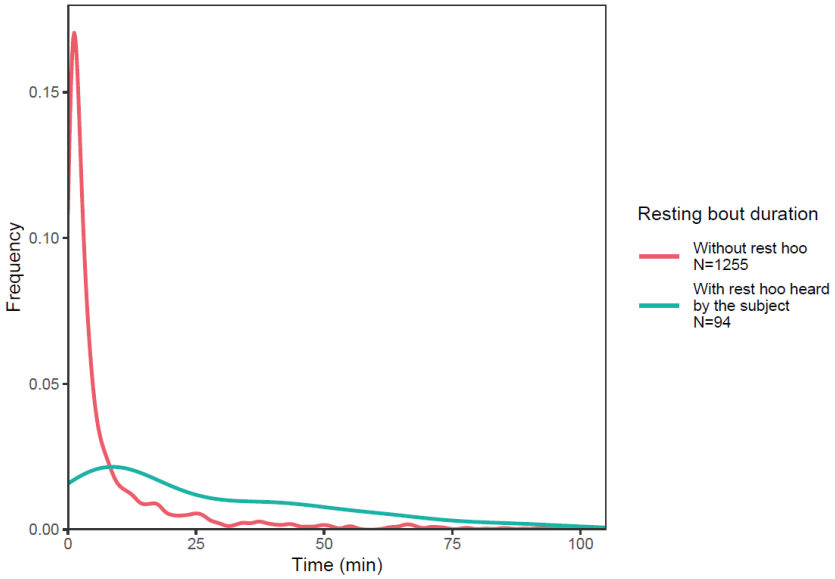

Figure 3.6. Distribution (kernel density estimates) of the time the subject spent resting depending on whether the subject heard a 'rest hoo' produced by another adult male or not (GLMM7). Only resting bouts during which the subjects did not produce a 'rest hoo' himself are displayed.

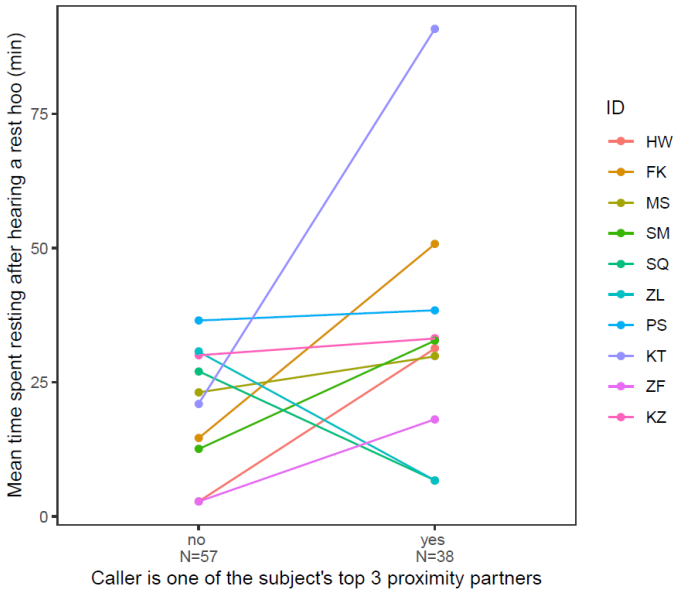

Figure 3.7. Mean time the subject spent resting after hearing a 'rest hoo' depending on whether the caller was one of the subject's top 3 proximity partners or not (GLMM8). The subjects are ordered by dominance rank (from top high-ranking to bottom low-ranking).

Finally, even though most 'rest hoos' were produced when both the caller and the recipients were resting (85.6%; 352 of 411 calls), on several occasions they were produced immediately (i.e., within the next 5s) after other individuals were trying to leave (9.0%; N=37) or in response to other group members passing by (5.4%; N=22). Here, calling had its desired effect in a considerable number of cases (40.7%; N=24), insofar as targeted individuals stopped travelling in order to join the resting caller (Supplementary material, Table S3.3).

Discussion

In this study, we were interested in exploring the context of production of 'rest hoos' by wild chimpanzee males of Budongo Forest and whether these calls had an intentional quality, i.e., whether they were emitted communicatively and with a particular goal. We found that 'rest hoos' were mainly produced when resting in small parties and towards the end of typical silent resting bouts, which have an average duration of about 8 min (Figs. 3.1 & 3.4). Calls were mainly produced if subjects were with others and were significantly predicted by whether the audience contained one of the subjects' top 3 proximity partners (Figs. 3.1 & 3.3). Also, resting bouts with 'rest hoos' were significantly longer than silent bouts, and resting time increased with the number of calls produced (Figs. 3.4, 3.5 & 3.6). Several social factors were also associated with prolonged resting bouts, notably if calls were answered by other group members (Fig. 3.2) and if the caller was one of the subject's top 3 proximity partners (Fig. 3.7). Finally, although all 10 males produced 'rest hoos', the behaviour was less common in high-ranking males with a high grooming index than in other males (Fig. 3.2). In the following sections, we discuss these results and develop our arguments supporting the claim that 'rest hoos' are produced intentionally to prolong resting with desirable partners, i.e., in a goal-directed way and in presence of a specific audience. We also speculate that this call has probably evolved as an alternative strategy to tactile-based social bonding for less popular partners (i.e., non-dominant males with a low-grooming index).

Overall, we found that the large majority of resting bouts (almost 90%) were free of 'rest hoos', suggesting that the default way of making decisions about the timing of transition from resting to another activity is by other means. Chimpanzees may use other signals, not considered in this study, to influence spatial proximity and, thus, social cohesion. Gestural, facial and multimodal signals may also play a role during resting bouts and there may be important inter-individual differences in how such signals are deployed, perhaps similar to how human infants assemble different signals into sequences during their illocutionary acts. Detailed observation of all communication channels, including follow-up behaviour, such as audience checking, would help to get a more comprehensive picture of how chimpanzees manage social distance.

Although our study focused on adult males of the Sonso community the same call is also produced by females and in other chimpanzee communities where researchers have paid specific attention (e.g., Gombe National Park, Tanzania: Goodall 1986). Therefore, future studies should investigate call production by other individuals and in other field sites, ideally using playback experiments to further investigate the behavioural responses to 'rest hoos'.

Finally, our findings also showed that social relationships can be meaningfully described in terms of spatial proximity and grooming interactions, rather than computing a generalised 'composite social index' (Silk et al. 2013). Indeed, we found that subjects called more often when in presence of a top proximity partner and rested longer after hearing a 'rest hoo' produced by a top proximity partner, whereas top grooming partners did not

seem to affect either call production or behavioural responses. As we explained above, grooming and vocalising might actually be part of alternative individual social bonding strategies and, in line with other studies (Bray and Gilby 2020; Mitani 2009; Samuni et al. 2018, 2021), we suggest that proximity and grooming should be considered separately when investigating social bonds, as they may reflect qualitative differences in relationships.

Intentional communication

Although authors differ in some key aspects, all definitions of intentional animal communication require some evidence of goal-directedness and of the signal being produced in the presence of an audience (Graham et al. 2019; Leavens et al. 2005; Townsend et al. 2017; Zuberbühler and Gomez 2018). In our study, 'rest hoos' were almost always produced in presence of an audience (Fig. 3.1), which suggests that chimpanzees have voluntary control over the production of 'rest hoos', as it has also been argued for the two other 'hoo' variants ('travel hoos': Gruber and Zuberbühler 2013; 'alert hoos': Schel et al. 2013b) and other chimpanzee vocalisations (Hopkins et al. 2007; Leavens et al. 2004; Schel et al. 2013a). Moreover, 'rest hoos' seemed to be preferentially produced in presence of one of the subject's top 3 proximity partners (Fig. 3.3). These evidence all seem to suggest that 'rest hoos' were directed towards an audience, and even towards specific individuals (i.e., top proximity partners). More crucially, similar to intentional vocalisations in human infants, chimpanzee 'rest hoos' were not produced to refer to external stimuli, but data suggest they were deployed as a way to convey the caller's apparent desire to prolong an already ongoing resting. However, we also found that in about 15% of cases, calls appeared to be given to keep others from leaving or to persuade bypassing individuals to join the resting party (which was often successful; Supplementary material, Table S3.3). Our results show that subjects rested for longer after calling than not calling (Fig. 3.4). Also, we suggest that 'rest hoo' production is part of a persuasion effort to influence recipients as, in a considerable number of cases, focal animals called multiple times during the same resting bout which was again associated with longer resting periods (Fig. 3.5). This interpretation is further supported by data showing that individual calls were sometimes immediately answered, perhaps expressions of agreement and thus shared intention, which explains why answered calls were associated with prolonged resting bouts (Fig. 3.4). Such speculations could provide interesting avenues for future research. Finally, recipients rested longer after hearing a 'rest hoo' produced by another male (Fig. 3.6), suggesting that the call elicited a behavioural response in line with the signaller's goal, i.e., to prolong resting. These findings provide strong evidence that 'rest hoos' are produced with a specific goal, i.e., to prolong an ongoing period of resting with particular male partners.

One further prediction of the intentionality hypothesis is that, following 'rest hoos', callers should be more likely to terminate resting bouts together (since callers appear to address particular recipients in the audience). However, we found that, when resting with one other male, subjects usually did not keep resting alone after their resting partners departed (only 20% of resting bouts), whether they produced a 'rest hoo' or not (GLMM3). We think this result shows that males often depart together and thus try to keep cohesion with their social partners. If males indeed produce 'rest hoos' to prolong resting with their partners then it would make sense that 'rest hoo' production would affect the duration of resting bouts but not necessarily the presence of the partner at the end of the resting bout. Indeed, subjects might want to keep cohesion with their partners even when they do not specifically wish to rest (hence, no use for 'rest hoo' vocalisations) and would thus depart and travel with them.

However, our study did not consider departing patterns (i.e., which individual stopped resting first and started traveling) and we think this should be explored further. Alternatively, it is conceivable that males only produced 'rest hoos' when cohesion was threatened, again resulting in joint resting with or without calls. We also think that, similarly to previous studies that investigated cohesion when traveling or feeding (Gruber and Zuberbühler 2013; Schel et al. 2013a), our study focused on one activity, i.e., resting, and future research should investigate overall cohesion between males and focus on association patterns across activities.

Evolution and function

In non-human primates, increases in vocal repertoire sizes are correlated with both increases in group size and time spent grooming (McComb and Semple 2005). Dunbar (1998) argued that, with increasing group size, the time required to maintain relations via grooming would reach a threshold due to time constraints (Lehmann et al. 2007). Amongst non-human primates, chimpanzees live in large groups, suggesting that this species has been under selection pressure to evolve other ways to maintain social cohesion. Recent studies in other primate species support this view and show that contact calls can be produced preferentially towards social partners, equivalent to "grooming-at-a-distance" (Japanese macaques: Arlet et al. 2015; lemurs: Kulahci et al. 2015; spider monkeys: Briseno-Jaramillo et al. 2018). Our data are in line with these findings since subjects produced 'rest hoos' preferentially in presence of one of their top 3 proximity partners (Fig. 3.3) and rested longer after hearing 'rest hoos' produced by such partners (Fig. 3.7). Even more relevant here is the fact that some individuals appear to prefer the vocal over the tactile route since callers were mainly low groomers. Whether this was due to individual differences or differences in the social position will have to be investigated with further research. Lower ranking males might also need to make more effort to maintain cohesion with other males, compared to higher-ranking ones, which would explain why they would produce more 'rest hoos'. Indeed, maintaining cohesion with higher-ranking individuals might be beneficial to form coalitions, or to have access to mates (Bray et al. 2016; Muller and Mitani 2005). This call could therefore be an alternative strategy deployed by less popular partners (i.e., all but high grooming and high-ranking individuals) as a substitute for other forms of social desirability leading to social cohesion.

Conclusions

Our results plausibly suggest that 'rest hoos' are produced intentionally to prolong resting and promote social cohesion, particularly with top proximity partners. These vocalisations might be an alternative strategy to tactile-based social bonding and, thus, bring more evidence that social cohesion and bonding through vocal communication has emerged in highly social species with large groups, due to group size and time constraints. These results bring to light an interesting relationship and interaction between tactile and vocal behaviours and suggest that future research on communication should adopt a multimodal approach (Fröhlich and van Schaik 2018; Liebal et al. 2013; Slocombe et al. 2011).

This study is currently the only in-depth study investigating the function of 'rest hoo' vocalisations, exploring the conditions in which it is produced by adult males and how this call affects the duration of resting bouts. Our results help to better understand the communication system of our closest relatives and provide interesting avenues for future research.

Acknowledgments

We are grateful to the Sonso field assistants (Sam Adue, Geresomu Muhumuza, Monday Gideon, and Chandia Bosco) and all of the staff of the Budongo Conservation Field Station for assistance with data collection in Uganda. We thank the Uganda Wildlife Authority, the Ugandan National Council for Science and Technology, and the President's Office for research permissions, as well as the Royal Zoological Society of Scotland for providing core funding for Budongo Conservation Field Station. We thank Matthieu Mulot and Radu Slobodeanu for statistical advice, Bilgé Kimyonok for technical support and Thibaud Gruber and Auriane Le Floch for discussions and comments on the manuscript.

References

Aguilar-Melo AR, Calmé S, Smith-Aguilar SE, Ramos-Fernandez G (2018) Fission-fusion dynamics as a temporally and spatially flexible behavioral strategy in spider monkeys. Behav Ecol Sociobiol 72:. https://doi.org/10.1007/s00265-018-2562-y

Arlet M, Jubin R, Masataka N, Lemasson A (2015) Grooming-at-a-distance by exchanging calls in non-human primates. Biol Lett 11:20150711. https://doi.org/10.1098/rsbl.2015.0711

Asensio N, Korstjens AH, Aureli F (2009) Fissioning minimizes ranging costs in spider monkeys: a multiple-level approach. Behav Ecol Sociobiol 63:649–659. https://doi.org/10.1007/s00265-008-0699-9

Aureli F, Schaffner CM, Boesch C, et al (2008) Fission-Fusion Dynamics: New Research Frameworks. Curr Anthropol 49:627–654. https://doi.org/10.1086/586708

Bard KA (1990) " Social tool use" by free-ranging orangutans: A Piagetian and developmental perspective on the manipulation of an animate object. In: Parker ST, Gibson KR (eds) "Language" and intelligence in monkeys and apes. Comparative developmental perspectives. Cambridge Univ. Press.

Barrett L, Henzi P, Dunbar RIM (2003) Primate cognition: from "what now?" to "what if?" Trends Cogn Sci 7:494–497. https://doi.org/10.1016/j.tics.2003.09.005

Barton K (2020) MuMIn: Multi-Model Inference

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67:. https://doi.org/10.18637/jss.v067.i01

Bates E (1979) The emergence of symbols: cognition and communication in Infancy. Academic Press, New York

Boesch C (1991) The Effects of Leopard Predation On Grouping Patterns in Forest Chimpanzees. Behaviour 117:220–241. https://doi.org/10.1163/156853991X00544

Bolt LM (2020) Affiliative Contact Calls during Group Travel: Chirp and Wail Vocalization Use in the Male Ring-Tailed Lemur (***Lemur catta***). Folia Primatol 1:1–20. https://doi.org/10.1159/000508808

Bray J, Gilby IC (2020) Social relationships among adult male chimpanzees (Pan troglodytes schweinfurthii): variation in the strength and quality of social bonds. Behav Ecol Sociobiol 74:. https://doi.org/10.1007/s00265-020-02892-3

Bray J, Pusey AE, Gilby IC (2016) Incomplete control and concessions explain mating skew in male chimpanzees. Proc R Soc B Biol Sci 283:20162071. https://doi.org/10.1098/rspb.2016.2071

Briseno-Jaramillo M, Ramos-Fernández G, Palacios-Romo TM, et al (2018) Age and social affinity effects on contact call interactions in free-ranging spider monkeys. Behav Ecol Sociobiol 72:192. https://doi.org/10.1007/s00265-018-2615-2

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociol Methods Res 261–304

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology : some background , observations , and comparisons. Behav Ecol Sociobiol 65:23–35

Busia L, Schaffner CM, Aureli F (2017) Relationship quality affects fission decisions in wild spider monkeys (Ateles geoffroyi). Ethology 123:405–411. https://doi.org/10.1111/eth.12609

Candiotti A, Zuberbühler K, Lemasson A (2012) Context-related call combinations in female Diana monkeys. Anim Cogn 15:327–339. https://doi.org/10.1007/s10071-011-0456-8

Chapman CA, Chapman LJ, Wrangham RW (1995) Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behav Ecol Sociobiol 36:59–70. https://doi.org/10.1007/BF00175729

Chaverri G, Gillam EH, Kunz TH (2013) A call-and-response system facilitates group cohesion among disc-winged bats. Behav Ecol 24:481–487. https://doi.org/10.1093/beheco/ars188

Conradt L, List C (2009) Group decisions in humans and animals: a survey. Philos Trans R Soc B Biol Sci 364:719–742. https://doi.org/10.1098/rstb.2008.0276

Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. Nature 433:513–516. https://doi.org/10.1038/nature03236

Crockford C, Gruber T, Zuberbühler K (2018) Chimpanzee quiet hoo variants differ according to context. R Soc Open Sci 5:172066. https://doi.org/10.1098/rsos.172066

Crockford C, Wittig RM, Zuberbühler K (2015) An intentional vocalization draws others' attention: A playback experiment with wild chimpanzees. Anim Cogn 18:581–591. https://doi.org/10.1007/s10071-014-0827-z

da Cunha RG, Byrne RW (2009) The Use of Vocal Communication in Keeping the Spatial Cohesion of Groups: Intentionality and Specific Functions. In: Garber PA, Estrada A, Bicca-Marques JC, et al. (eds) South American Primates. Springer New York, New York, NY, pp 341–363

Duffy KG, Wrangham RW, Silk JB (2007) Male chimpanzees exchange political support for mating opportunities. Curr Biol 17:R586–R587. https://doi.org/10.1016/j.cub.2007.06.001

Dunbar RIM (1998) The social brain hypothesis. Evol Anthropol 6:178–190. https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8

Eckhardt N, Polansky L, Boesch C (2015) Spatial cohesion of adult male chimpanzees (Pan troglodytes verus) in Taï National Park, Côte d'Ivoire. Am J Primatol 77:125–134. https://doi.org/10.1002/ajp.22316

Elo AE (1978) The rating of chess players, past and present. Arco Pub., New York, NY

Fedurek P, Slocombe KE (2013) The Social Function of Food-Associated Calls in Male Chimpanzees. Am J Primatol 75:726–739. https://doi.org/10.1002/ajp.22122

Feldblum JT, Krupenye C, Bray J, et al (2021) Social bonds provide multiple pathways to reproductive success in wild male chimpanzees. iScience 24:102864. https://doi.org/10.1016/j.isci.2021.102864

Fischer J (2008) Transmission of acquired information in nonhuman primates. In: Byrne JH (ed) Learning and memory: A comprehensive reference. Elsevier, Oxford, pp 299–313

Fröhlich M, van Schaik CP (2018) The function of primate multimodal communication. Anim Cogn 21:619–629. https://doi.org/10.1007/s10071-018-1197-8

Gilby IC, Wrangham RW (2008) Association patterns among wild chimpanzees (Pan troglodytes schweinfurthii) reflect sex differences in cooperation. Behav Ecol Sociobiol 62:1831–1842. https://doi.org/10.1007/s00265-008-0612-6

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge

Graham KE, Wilke C, Lahiff NJ, Slocombe KE (2019) Scratching beneath the surface: intentionality in great ape signal production. Philos Trans R Soc B Biol Sci 375:20180403. https://doi.org/10.1098/rstb.2018.0403

Gruber T, Zuberbühler K (2013) Vocal Recruitment for Joint Travel in Wild Chimpanzees. PLoS One 8:e76073. https://doi.org/10.1371/journal.pone.0076073

Herbinger I, Papworth S, Boesch C, Zuberbühler K (2009) Vocal, gestural and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders: a playback study. Anim Behav 78:1389–1396.

https://doi.org/10.1016/j.anbehav.2009.09.010

Hobaiter C, Samuni L, Mullins C, et al (2017) Variation in hunting behaviour in neighbouring chimpanzee communities in the Budongo forest, Uganda. PLoS One 12:e0178065. https://doi.org/10.1371/journal.pone.0178065

Hopkins WD, Taglialatela JP, Leavens DA (2007) Chimpanzees differentially produce novel vocalizations to capture the attention of a human. Anim Behav 73:281–286. https://doi.org/10.1016/j.anbehav.2006.08.004

Humphrey N (1976) The social function of intellect. In: Bateson PPG, Hinde RA (eds) Growing points in ethology. Cambridge University Press, Cambridge, pp 303–317

Kaburu SSK, Newton-Fisher NE (2015) Trading or coercion? Variation in male mating strategies between two communities of East African chimpanzees. Behav Ecol Sociobiol 69:1039–1052. https://doi.org/10.1007/s00265-015-1917-x

Kerth G (2010) Group decision-making in animal societies. In: Animal Behaviour: Evolution and Mechanisms. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 241–265

Kosheleff VP, Anderson CNK (2009) Temperature's influence on the activity budget, terrestriality, and sun exposure of chimpanzees in the Budongo Forest, Uganda. Am J Phys Anthropol 139:172–181. https://doi.org/10.1002/ajpa.20970

Kulahci IG, Rubenstein DI, Ghazanfar AA (2015) Lemurs groom-at-a-distance through vocal networks. Anim Behav 110:179–186. https://doi.org/10.1016/j.anbehav.2015.09.016

Kummer H (1971) Primate societies – group techniques of ecological adaptation. Aldine Publishing Company, Chicago

Kummer H (1968) Social organization of Hamadryas Baboons, a field study. University of Chicago Press, Chicago

Laporte MNC (2010) Pant-grunts in wild chimpanzees (Pan troglodytes schweinfurthii): the vocal development of a social signal. University of St Andrews

Leavens DA, Hopkins WD (1998) Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. Dev Psychol 34:813–822. https://doi.org/10.1037/0012-1649.34.5.813

Leavens DA, Hostetter AB, Wesley MJ, Hopkins WD (2004) Tactical use of unimodal and bimodal communication by chimpanzees, Pan troglodytes. Anim Behav 67:467–476. https://doi.org/10.1016/j.anbehav.2003.04.007

Leavens DA, Russell JL, Hopkins WD (2005) Intentionality as Measured in the Persistence and Elaboration of Communication by Chimpanzees (Pan troglodytes). Child Dev 76:291–306. https://doi.org/10.1038/jid.2014.371

Lehmann J, Korstjens AH, Dunbar RIM (2007) Group size, grooming and social cohesion in primates. Anim Behav 74:1617–1629. https://doi.org/10.1016/j.anbehav.2006.10.025

Liebal K, Waller BM, Burrows AM, Slocombe KE (2014) Intentionality. In: Primate communication: a multimodal approach. Cambridge University Press, Cambridge, pp 169–192

Liebal K, Waller BM, Burrows AM, Slocombe KE (2013) Primate communication: a multimodal approach

Lusseau D (2007) Why Are Male Social Relationships Complex in the Doubtful Sound Bottlenose Dolphin Population? PLoS One 2:e348. https://doi.org/10.1371/journal.pone.0000348

Marlowe FW (2005) Hunter-gatherers and human evolution. Evol Anthropol Issues, News, Rev 14:54–67.

https://doi.org/10.1002/evan.20046

McComb K, Semple S (2005) Coevolution of vocal communication and sociality in primates. Biol Lett 1:381–385. https://doi.org/10.1098/rsbl.2005.0366

Mitani JC (2009) Male chimpanzees form enduring and equitable social bonds. Anim Behav 77:633–640. https://doi.org/10.1016/j.anbehav.2008.11.021

Mitani JC, Amsler S (2003) Social and spatial aspects of male subgrouping in a community of wild chimpanzees. Behaviour 140:869–884. https://doi.org/10.1163/156853903770238355

Mitani JC, Nishida T (1993) Contexts and social correlates of long-distance calling by male chimpanzees. Anim Behav 45:735–746. https://doi.org/10.1006/anbe.1993.1088

Muller MN, Mitani JC (2005) Conflict and Cooperation in Wild Chimpanzees. In: Advances in the Study of Behavior. pp 275–331

Mullins C (2014) Coordination of joint activities and communication in wild chimpanzees (Pan troglodytes) of the Budongo. University of St Andrews

Neumann C (2017) socialindices2: social and association indices

Neumann C, Duboscq J, Dubuc C, et al (2011) Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. Anim Behav 82:911–921. https://doi.org/10.1016/j.anbehav.2011.07.016

Neumann C, Kulik L (2020) EloRating: Animal dominance hierarchies by Elo rating

Newton-Fisher NE (2003) The home range of the Sonso community of chimpanzees from the Budongo Forest, Uganda. Afr J Ecol 41:150–156. https://doi.org/10.1046/j.1365-2028.2003.00408.x

Petit O, Bon R (2010) Decision-making processes: The case of collective movements. Behav Processes 84:635–647. https://doi.org/10.1016/j.beproc.2010.04.009

R Core Team (2019) R: A language and environment for statistical computing

Reynolds V (2005) The chimpanzees of the Budongo forest: Ecology, behaviour and conservation, Oxford Uni

Samuni L, Crockford C, Wittig RM (2021) Group-level cooperation in chimpanzees is shaped by strong social ties. Nat Commun 12:539. https://doi.org/10.1038/s41467-020-20709-9

Samuni L, Preis A, Mielke A, et al (2018) Social bonds facilitate cooperative resource sharing in wild chimpanzees. Proc R Soc B Biol Sci 285:. https://doi.org/10.1098/rspb.2018.1643

Schel AM, Machanda ZP, Townsend SW, et al (2013a) Chimpanzee food calls are directed at specific individuals. Anim Behav 86:955–965. https://doi.org/10.1016/j.anbehav.2013.08.013

Schel AM, Townsend SW, Machanda ZP, et al (2013b) Chimpanzee Alarm Call Production Meets Key Criteria for Intentionality. PLoS One 8:e76674. https://doi.org/10.1371/journal.pone.0076674

Silk J, Cheney DL, Seyfarth RM (2013) A practical guide to the study of social relationships. Evol Anthropol Issues, News, Rev 22:213–225. https://doi.org/10.1002/evan.21367

Slocombe KE, Waller BM, Liebal K (2011) The language void: the need for multimodality in primate communication research. Anim Behav 81:919–924. https://doi.org/10.1016/j.anbehav.2011.02.002

Strandburg-Peshkin A, Papageorgiou D, Crofoot MC, Farine DR (2018) Inferring influence and leadership in moving animal groups. Philos Trans R Soc B Biol Sci 373:20170006. https://doi.org/10.1098/rstb.2017.0006

Stueckle S, Zinner D (2008) To follow or not to follow: decision making and leadership during the morning

departure in chacma baboons. Anim Behav 75:1995–2004. https://doi.org/10.1016/j.anbehav.2007.12.012

Sueur C, King AJ, Conradt L, et al (2011) Collective decision-making and fission-fusion dynamics: a conceptual framework. Oikos 120:1608–1617. https://doi.org/10.1111/j.1600-0706.2011.19685.x

Symington MM (1990) Fission-Fusion Social Organization in Ateles and Pan. Int J Primatol 11:47–61

Tomasello M, George BL, Kruger AC, et al (1985) The development of gestural communication in young chimpanzees. J Hum Evol 14:175–186. https://doi.org/10.1016/S0047-2484(85)80005-1

Townsend SW, Koski SE, Byrne RW, et al (2017) Exorcising Grice's ghost: an empirical approach to studying intentional communication in animals. Biol Rev 92:1427–1433. https://doi.org/10.1111/brv.12289

Tsai Y-JJ, Mann J (2013) Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. Mar Mammal Sci 29:261–279. https://doi.org/10.1111/j.1748-7692.2011.00559.x

White FJ, Burgman MA (1990) Social organization of the pygmy chimpanzee (Pan paniscus): Multivariate analysis of intracommunity associations. Am J Phys Anthropol 83:193–201. https://doi.org/10.1002/ajpa.1330830208

Wilson ML, Boesch C, Fruth B, et al (2014) Lethal aggression in Pan is better explained by adaptive strategies than human impacts. Nature 513:414–417. https://doi.org/10.1038/nature13727

Wrangham RW, Clark AP, Isabirye-Basuta G (1992) Female social relationships and social organization of Kibale Forest chimpanzees. In: Nishida T, McGrew WC, Marler P, et al. (eds) Topics in primatology. Vol. 1: Human Origins. University ofTokyo Press, Tokyo, pp 81–98

Yamanashi Y, Hayashi M (2011) Assessing the effects of cognitive experiments on the welfare of captive chimpanzees (Pan troglodytes) by direct comparison of activity budget between wild and captive chimpanzees. Am J Primatol 73:1231–1238. https://doi.org/10.1002/ajp.20995

Zeileis A, Hothorn T (2002) Diagnostic Checking in Regression Relationships. R News 2:7–10

Zuberbühler K, Gomez J-C (2018) Primate Intentional Communication. In: The International Encyclopedia of Anthropology. John Wiley & Sons, Ltd, Oxford, UK, pp 1–10

Supplementary material

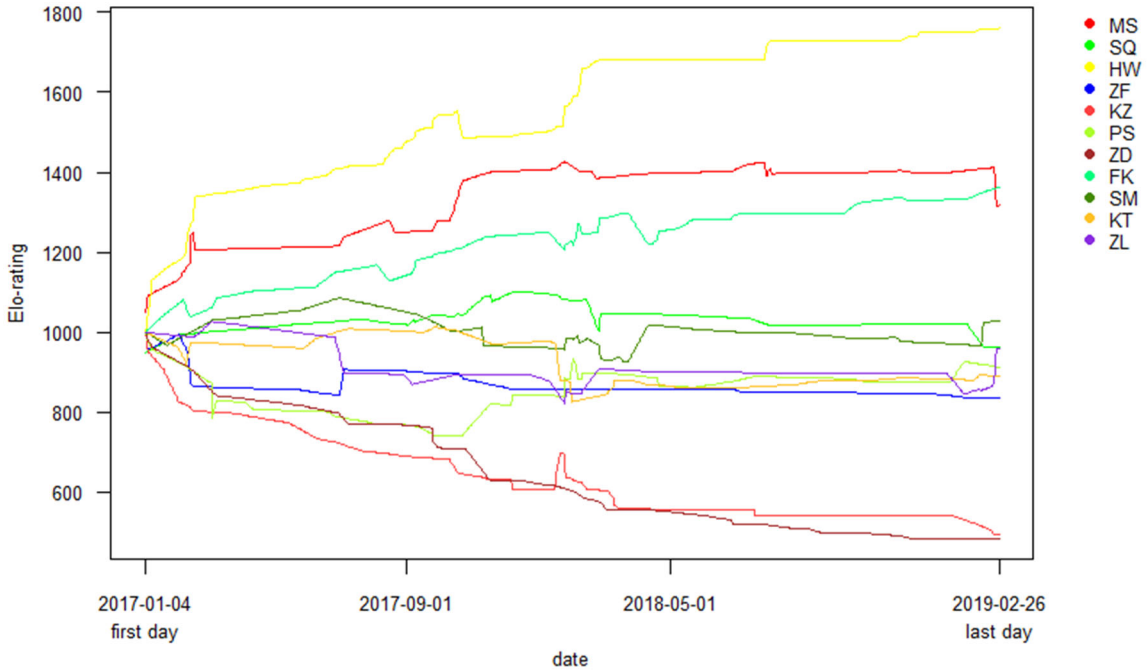

Figure S3.1. Evolution of the Elo-rating scores of the 11 adult males of the Sonso community from 12 months before the start of the study (January 4th 2017) to the end of the first study period (February 26th 2019). In contrast to traditional matrix-based assessments, elo-rating conceptualises rank as a dynamic variable that changes with each social interaction. Each male starts the process with a fixed score, which is continuously updated following each dyadic interaction. In particular, each time a male produces pant grunts to another male, he loses points whereas the recipient gains the same number of points. The number of points gained or lost depends on the expected outcome, which is calculated prior the interaction. Unexpected outcomes lead to more point changes than expected outcomes (Elo 1978; Neumann et al. 2011).

Table S3.1. Top 3 grooming partners and top 3 proximity partners, with the associated DSI_P and DSI_G values respectively, for each of the study subjects. The DSI_P and DSI_G calculations were derived from the DSI introduced by Silk et al. (2013) which attributes a value of 1 to the average social bond across all dyads in the group (in our case 55 dyads; N=11 males). If a dyad has a value superior (or inferior) to 1, the dyad is considered to have a stronger (or weaker) social bond than average. However, in this study, we did not use the value of the group mean (1) to compare DSI, but we established each subject's preferred partners by selecting the three highest DSI values (both for DSI_G and DSI_P) for each subject. We chose this method to account for the fact that some individuals are intrinsically more social than others, i.e., a very social male will have most of its DSIs above 1 whereas an asocial male will have most of his DSIs below one.

Focal ID	Top 3 grooming partners						Top 3 proximity partners					
	ID1	DSI_G	*ID2*	DSI_G	*ID3*	DSI_G	*ID1*	DSI_P	*ID2*	DSI_P	*ID3*	DSI_P
FK	HW	2.506	MS	0.82049	ZL	0.72276	HW	1.93591	PS	1.23312	SM	1.11567
HW	MS	7.41631	ZL	3.56719	SQ	2.86252	KT	3.14544	MS	2.96374	ZL	2.74109
KT	HW	2.10979	MS	1.8699	ZL	0.91899	HW	3.14544	MS	1.54579	FK	1.08609
KZ	ZL	1.18471	PS	0.87028	SM	0.80654	SQ	1.38666	PS	0.94672	ZF	0.90951
MS	HW	7.41631	PS	2.71263	SQ	2.05929	HW	2.96374	SQ	1.97565	KT	1.54579
PS	MS	2.71263	HW	2.36197	ZL	1.8472	HW	1.57758	FK	1.23312	MS	1.1528
SM	HW	1.58801	ZL	1.47764	PS	0.80995	HW	1.93149	ZD	1.26756	ZL	1.15455
SQ	HW	2.86252	MS	2.05929	PS	1.3291	MS	1.97565	HW	1.78858	KZ	1.38666
ZD	ZL	2.14204	PS	1.34719	SQ	1.1774	ZL	1.4993	SM	1.26756	SQ	1.01107
ZF	MS	0.82979	HW	0.66267	ZL	0.4642	HW	1.78382	SQ	0.98214	KZ	0.90951
ZL	HW	3.56719	ZD	2.14204	PS	1.8472	HW	2.74109	ZD	1.4993	SM	1.15455

Table S3.2. Coefficients and significance of the variables entered in

(a) the GLMM with a Binomial distribution to analyse whether the presence of an audience affected 'rest hoo' production (GLMM1).

(b) the GLM with a Binomial distribution to analyse which parameters influenced hoo production by the focal adult males during resting bouts (GLM1). A model selection approach was used with this model.

(c) the GLMM with a Binomial distribution to analyse which social parameters influenced hoo production by the focal adult males during male dyadic resting bouts (GLMM2). A model selection approach was used with this model.

(d) the GLMM with a Binomial distribution to analyse whether the production of 'rest hoo' by the subject affected the presence of the resting partner at the end of male dyadic resting bouts (GLMM3).

(e) the GLMM with a Gamma distribution to analyse whether the production of 'rest hoo' by the subject affected the time he spent resting (GLMM4).

(f) the GLMM with a Gamma distribution to analyse whether immediate vocal responses to 'rest hoo' produced by the subject affected the time he spent resting (GLMM5).

(g) the GLMM with a Gamma distribution to analyse whether the number of 'rest hoo' produced by the subject affected the time he spent resting (GLMM6).

(h) the GLMM with a Gamma distribution to analyse whether the reception of 'rest hoo' (i.e., produced by other individuals) affected the time the subject spent resting (GLMM7).

(i) the GLMM with a Gamma distribution to analyse which parameters influence the time the focal individual spent resting after hearing a rest hoo vocalisation produced by another adult male (GLMM8). A model selection approach was used with this model.

(a) GLMM 1 - Probability of the focal individual calling depending on the presence of an audience

Variables	Estimate	SE	Z	*p*
Presence of an audience (Yes)	1.67	0.35	4.76	<0.001

Random effect: Subject ID (Variance=0.01, SD=0.10)

(b) *GLM1 - Probability of the focal individual calling* (Best fitting model*: AICc = 487)

Variables	Estimate	SE	Z	*p*
Duration of the resting event	0.04	0.01	7.70	<0.001
Number of individuals in the audience	-0.11	0.05	-2.37	0.018
Grooming index	-0.24	0.15	-1.60	0.110
Dominance rank (Elo-rating)	0.28	0.21	1.33	0.183
Grooming index * Dominance rank	-0.46	0.20	-2.28	0.022

Full model: Duration of the resting event + number of individuals in the audience + presence of a female (yes / no) + presence of a high-ranking male (yes / no) + presence of a top 3 grooming partner (yes / no) + presence of a top 3 proximity partner (yes / no) + grooming index * dominance rank

* χ^2 tests for the log-likelihood ratios, best fitting model–null model, $\chi^2 = 15.69$, $p = 0.003$

(c) *GLMM 2 - Probability of the focal individual calling when resting in male dyads* (Best fitting model*: AICc = 74)

Variables	Estimate	SE	Z	*p*
Resting partner is a top 3 proximity partner (Yes)	1.25	0.63	2.00	0.046

Full model: Duration of the resting event + resting partner is a high-ranking male (yes / no) + resting partner is a top 3 grooming partner (yes / no) + resting partner is a top 3 proximity partner (yes / no)

* χ^2 tests for the log-likelihood ratios, best fitting model–null model, $\chi^2 = 0.12$, $p < 0.001$; Random effect: Subject ID (Variance=0.00, SD=0.00)

(d) GLMM3 - *Presence of the resting partner at the end of male dyadic resting bouts*

Variables	Estimate	SE	Z	*p*
Production of 'rest hoo' (Yes)	-0.12	0.85	-0.14	0.889
Resting time after producing a 'rest hoo'	-0.03	0.02	-2.10	0.035

(e) GLMM 4 - Resting time depending on 'rest hoo' production

Variables	Estimate	SE	Z	*p*
Production of 'rest hoo' (Yes)	-0.07	0.01	-9.39	<0.001

Random effect: Subject ID (Variance=0.00, SD=0.02)

(f) GLMM 5 - Resting time depending on immediate vocal response

Variables	Estimate	SE	Z	*p*
Immediate vocal response (Yes)	-0.017	0.003	-6.53	<0.001

Random effect: Subject ID (Variance=0.00, SD=0.02)

(g) GLMM 6 - Resting time depending on the number of 'rest hoo' produced

Variables	Estimate	SE	Z	*p*
Number of 'rest hoo' produced	0.006	0.002	3.59	<0.001

Random effects: Subject ID (Variance=0.00, SD=0.00) and Resting bout ID (Variance=0.01, SD=0.10)

(h) GLMM 7 - Resting time depending on 'rest hoo' reception

Variables	Estimate	SE	Z	*p*
Immediate vocal response (Yes)	-0.075	0.008	-9.64	<0.001

Random effect: Subject ID (Variance=0.00, SD=0.00)

(i) GLMM8 - *Resting time after hearing a rest hoo* (Best fitting model*: AICc = 800)

Variables	Estimate	SE	Z	*p*
Remaining number of hoos in the resting bout	-0.007	0.002	-4.38	<0.001
Caller is a top 3 proximity partner (yes)	-0.019	0.008	-2.23	0.026

Full model: remaining number of hoos in the resting bout + number of individuals present + caller is a high-ranking male (yes / no) + caller is a top 3 grooming partner (yes / no) + caller is a top 3 proximity partner (yes / no) + caller's sociability * caller's rank

* χ^2 tests for the log-likelihood ratios, best fitting model–null model, $\chi^2 = 4.42$, $p = 0.035$; Random effects: Subject ID (Variance=0.00, SD=0.00) and Resting bout ID (Variance=0.00, SD=0.00)

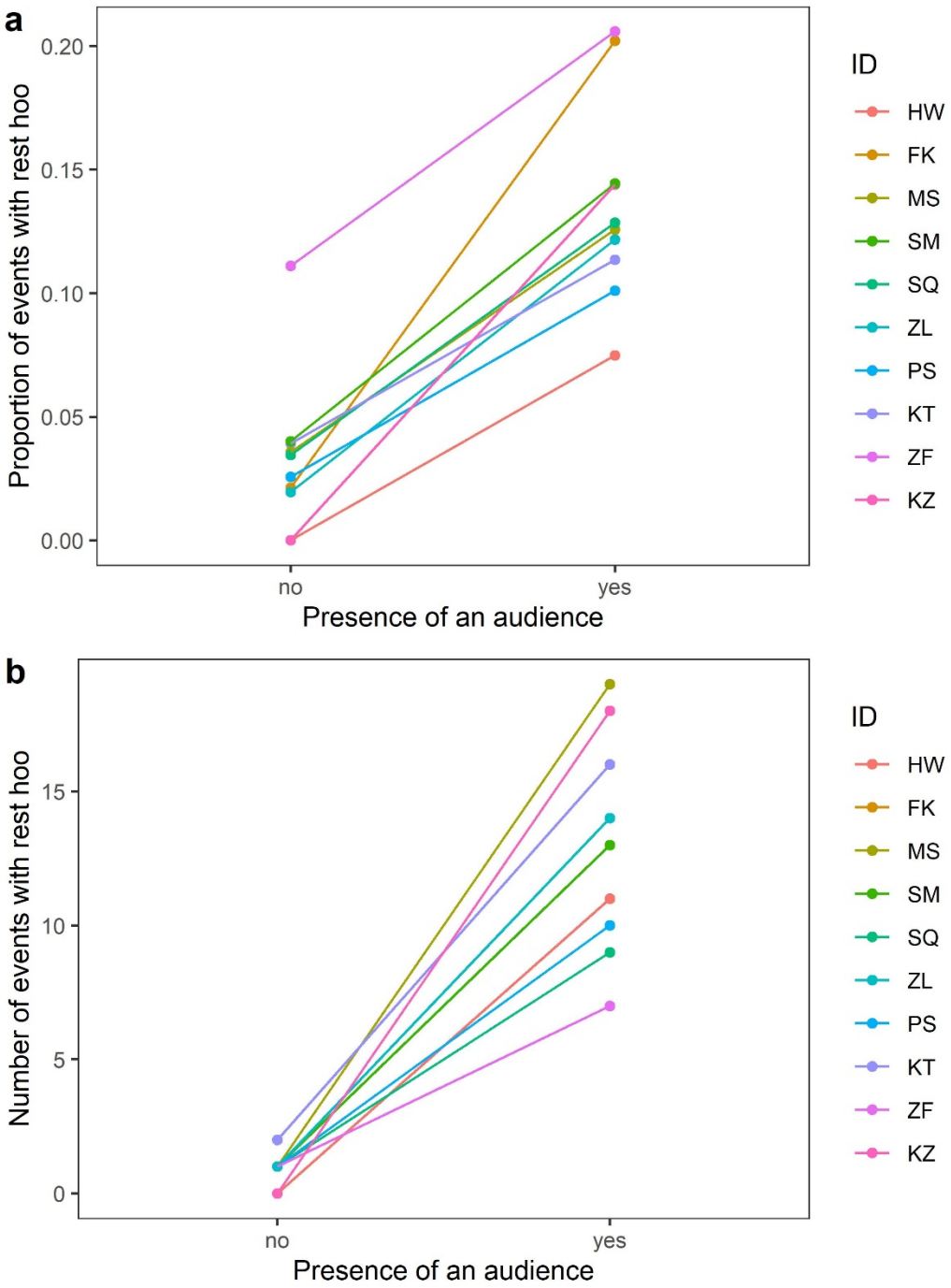

Figure S3.2. a Proportion and **b** raw numbers of events with at least one rest hoo produced by the focal individual depending on the presence of a potential audience for each study subject (GLMM1). The subjects are ordered by dominance rank (from top high-ranking to bottom low-ranking).

Table S3.3. Behaviour of the recipients immediately (i.e., within 5s) before and after the subject produced a 'rest hoo'. We recorded the number of events when there was no change in the activity of the audience (i.e., everyone was resting), when at least one individual in the audience started traveling or when individuals were passing by, before the subject produced a 'rest hoo'. For the last two categories, we also recorded whether the traveling individual kept traveling or joined the subject resting after he produced the 'rest hoo'.

Receiver's behaviour **before** call production	Receiver's behaviour **after** call production	Number of events	
Rests		352	
Initiates travel	starts resting	10	37
	keeps traveling	27	
Travels	starts resting	14	22
	keeps traveling	8	
TOTAL		411	

Chapter 4. Vocal communication is a better predictor of male dyadic associations in chimpanzees than grooming

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Manuscript in preparation, to be submitted after the submission of the thesis

Abstract

Male chimpanzees form long-term relationships with other males, which have a demonstrated impact on biological fitness. However, due to the fission-fusion social system, males often spend time apart, intersected by short-term associations with different partners. Here, we investigated the vocal and tactile strategies males used to manage short-term dyadic associations. We found that males preferably groomed higher-ranking partners or partners who groomed them, while grooming interactions themselves did not directly affect association times. Instead, 'hoo' vocalisations prolonged the duration of associations and callers were less likely to terminate an association. We also found that high-ranking males were more likely to terminate dyadic associations. Generally, 'hoos' were more often given by lower-ranking males and males that were groomed, although 'hoos' were more effective in prolonging associations if given by high-ranking males or by both partners. Overall, we found that short-term dyadic associations were mainly determined by rank relations, but also that 'hoo' calls played a regulatory function in determining their duration, suggesting the males used them strategically to manage social cohesion. Finally, association patterns were strongly influenced by 'hoo' vocalisations but not grooming, suggesting that vocalisations may be a more accurate predictor of short-term affiliations.

Introduction

Fission-fusion are a widely-used behavioural strategy across taxa to optimise the costs and benefits of group living (Sibly 1983; Krause and Ruxton 2002), which refers to temporal variations in the size and composition of subgroups and spatial cohesion between members. However, the resulting continuous change in subgroup composition creates coordination problems for group members who can no longer depend on collective travel decisions (Couzin et al. 2005; Stueckle and Zinner 2008; Conradt and List 2009; Sueur et al. 2010a). In fission – fusion societies, spatial cohesion between group members is in near-constant flux (Kerth 2010; Conradt and Roper 2010; Jacobs 2010), while travel decisions are shifted from the group to the individual level, two factors that presumably increase the cognitive load on individuals (Aureli et al. 2008).

This fission-fusion dynamics increases variability in opportunities for individuals to interact as well as uncertainty about the social relationships between others (Hinde 1976; Wey et al. 2008). Generally, in fission-fusion societies, individual behaviours and relationship quality have greater influences on social dynamics than in more cohesive social systems (Watts 2005; Sueur et al. 2011). Fission-fusion systems increase the social complexity in a group and demand more decisions about proximity, which most likely requires more complex

computations (Petit and Bon 2010; King and Sueur 2011; von Rueden et al. 2015). Species that practice fission-fusion grouping are thus pertinent for theories of cognitive evolution, particularly the social intelligence hypothesis, which stipulates that relative brain size (and associated cognitive abilities) should be positively correlated with social complexity (Humphrey 1976; Dunbar 1998). In line with this prediction, species with high degrees of fission-fusion dynamics, such as elephants, dolphins, and chimpanzees, generally have a relatively larger neocortex sizes than species living in stable groups (Dunbar 1998; Barrett et al. 2003).

But how do individuals living in fission-fusion systems decide with whom to associate? Food availability plays an indirect role in association decisions by constraining subgroup size (Kummer 1971; Symington 1990; Chapman et al. 1995; Asensio et al. 2009). However, social factors might also affect decisions, especially in species where individual relationships play an important role (bottlenose dolphins, Lusseau 2007; Tonkean and rhesus macaques Sueur et al. 2010b; Northern muriquis, Tokuda et al. 2012; spider monkeys, Busia et al. 2017; chimpanzees, Mitani and Amsler 2003). In some social species, individuals can form strong and enduring same-sex social bonds (Van Schaik and Van Hooff 1994; Massen et al. 2010; Seyfarth and Cheney 2012), which are visible by elevated levels of affiliative interactions and cooperation. There is mounting evidence in different species that social bonds confer strong fitness benefits, such as increased lifespan or higher reproductive success (spotted hyenas, Smith et al. 2011; bottlenose dolphins, Frère et al. 2010; baboons, Silk et al. 2009; chimpanzees, Samuni et al. 2018).

The focus of this study is on social bonds between male chimpanzees (see the Methods section for a definition of the long-term social bonds), which are thought to have evolved due to the pressures generated by intragroup competition, with males forming long-term alliances to compete for mating opportunities and dominance status (Connor et al. 2001; Schülke et al. 2010; Ostner and Schülke 2014). In chimpanzees, adult males remain in their natal communities throughout their lives and form some of the strongest and most stable relationships with non-kin observed in mammals (Mitani 2009a; Hruschka 2010). These social bonds are the basis for various, often dangerous, cooperative activities, such as coalitionary intragroup aggression (Muller and Mitani 2005; Gilby et al. 2013), cooperative hunting (Boesch 1994), food sharing (Samuni et al. 2018), predator defence (Boesch 1991), boundary patrols and intergroup conflicts (Watts and Mitani 2001; Samuni et al. 2021). Coalitions during agonistic events play a crucial role in establishing dominance relations (Mitani 2009b; Gilby et al. 2013) and high-ranking males have higher fitness due to higher reproductive success (Boesch et al. 2006; Wroblewski et al. 2009; Newton-Fisher et al. 2009). For instance, subordinates who form strong social bonds with the alpha male or with many other subordinates have higher siring success (Duffy et al. 2007; Bray et al. 2016; Feldblum et al. 2021), and there are considerable individual differences in how successful males are at establishing social relationships (Muller and Mitani 2005), although for reasons yet to be discovered.

How do chimpanzees manage to maintain proximity with social partners? Vocal signals play a key role, mainly by impacting on the movement patterns of other individuals, such as in relation to traveling (Gruber and Zuberbühler 2013), feeding (Fedurek and Slocombe 2013), or when out of sight (Mitani and Nishida 1993; Eckhardt et al. 2015). For instance, the long-distance ‘pant hoot’ is individually distinct, can be heard for hundreds of meters and seem to play an important role in regulating group dynamics (Fedurek et al. 2014; Desai et al. 2021). Another important vocalisation, which has received less attention, is the short-distance 'hoo' call. There appear to be three structural variants of this call produced in three distinct contexts (Crockford et al.

2018): before and during travel ('travel hoo'), during resting ('rest hoo'), and when encountering a threat ('alert hoo'). The common underlying function of these calls appears to be to manage group cohesion in different situations (Crockford et al. 2018). 'Alert hoos' trigger the strongest recipient responses, typically causing careful approach towards the caller (Crockford et al. 2012, 2015, 2017; Schel et al. 2013). 'Alert hoos' are usually given to disconcerting external events, such as encountering a snake or a dead duiker, suggesting the calls carry referential content. 'Travel' and 'rest hoos' are also context-specific but mainly inform about the caller's behavioural intention, i.e., to initiate travel or to continue resting, and these calls appeared to be addressed to preferred social partners (Gruber and Zuberbühler 2013; Bouchard and Zuberbühler 2022a).

Previous studies have investigated the social coordination of chimpanzees in a few specific contexts, notably danger (Crockford et al. 2012), traveling (Gruber and Zuberbühler 2013; Fröhlich et al. 2016), foraging (Fedurek and Slocombe 2013; Kalan and Boesch 2015; Bouchard and Zuberbühler 2022b) and resting (Bouchard and Zuberbühler 2022a). The aim of this study was to investigate the use of vocal signals and tactile behaviour in male chimpanzees across contexts during dyadic short-term associations. Males often associate with each other (i.e., they stay in each other's visual range) for long periods of time during the day, but no study has explored how males maintain or dissolve these associations. Our hypothesis was that males differed in their desirability as association partners and that this predicted which males would seek to prolong an association. In terms of behavioural mechanisms, we hypothesised that 'hoo' vocalisations and grooming played key roles. This was due to prior research which showed that both 'hoo' calls (Gruber and Zuberbühler 2013; Bouchard and Zuberbühler 2022a) and grooming (a common social bonding mechanism in primates, Muller and Mitani 2005; Fedurek and Dunbar 2009; Mitani 2009b) facilitated social cohesion, i.e., spatial proximity between individuals. Specifically, we predicted that, when with a desirable partner (i.e., high-ranking or closely bonded partner), males would be more active in using vocal and tactile behaviours to maintain and prolong the association compared to when with a less desirable partner (i.e., low-ranking or non-closely bonded partner). Less desirable males, in turn, would be required to make more efforts to maintain associations, i.e., by producing 'hoo' vocalisations and grooming more frequently.

Methods

Study site and subjects

We collected data from East African chimpanzees (*Pan troglodytes schweinfurthii*) of the Sonso community at the Budongo Conservation Field Station in Budongo Forest Reserve, Uganda (latitude 1°37′–2°00′N; longitude: 31°22′–31°46′E) between January 2018 and February 2019. This community has a core home range of approximately 7 km^2 (Newton-Fisher 2003) and has been well habituated to human presence for more than 25 years. At the beginning of the study, the community consisted of 75 established individuals, including 37 adults (> 15 years, 11 males). All individuals were named and most of their social and kin relations described (Reynolds 2005). Permission to conduct this research was granted by the Ugandan Wildlife Authority as well as the Ugandan National Council for Science and Technology.

Data collection

We conducted full-day (usually between 7 am and 4:30 pm) focal follows of 11 adult males. We recorded the subject's activities (i.e., travel, feed or rest) with start and end times and we documented party composition (i.e., all individuals within 30m of the focal) continuously. These data allowed us to establish male dyadic association events, defined as the period during which two adult males (i.e., our focal subject and another male) spent uninterrupted time together (i.e., within visual range, <30m away) for more than 30 minutes, including at least one joint travel activity and one joint resting activity. For each of these events, we recorded the duration of the event and the identity of the partner. When we could clearly establish which partner departed and terminated the association (e.g., both partners were resting and one of them got up and left), we also recorded the identity of the departing individual and attributed a unique ID to this departure event. We also recorded every grooming interaction between the subject and his association partner (i.e., grooming given or received by the subject) and every 'hoo' (i.e., 'travel hoo' or 'rest hoo') produced by the subject or his partner, with the time at which they occurred, and attributed them a unique ID. When the focal subject was associating with several males at the same time, we attributed a unique Event ID to all the associations that overlapped. We had to exclude two males from the analyses due to low observation time and insufficient sample size of dyadic association events (Supplementary material Table S4.1).

Social variables

Most studies investigating chimpanzee social bonds measure bonds by establishing dyadic indices based on grooming behaviour and proximity (or association) data, either calculating separate indices (Mitani and Nishida 1993; Mitani 2009a; Bray and Gilby 2020; Samuni et al. 2021) or one composite social index (Silk et al. 2013a; Feldblum et al. 2021; Heesen et al. 2021). Previous studies have shown that relationships formed through grooming and those formed through spatial proximity may reflect different types of social bonds and thus affect individual behaviours in a different way (Mitani and Nishida 1993; Mitani 2009a; Bray and Gilby 2020; Samuni et al. 2021). For this reason, we decided to calculate two separate dyadic indices to measure long-term social bonds between males, one based on grooming interactions and one based on spatial proximity, to determine, for each subject, his preferred long-term grooming and proximity partners, respectively.

To establish the dominance status and the grooming index of subjects, as well as their preferred grooming and proximity partners, we used the long-term data collected by four trained field assistants (Sam Adue, Geresomu Muhumuza, Monday Gideon and Chandia Bosco). They conducted full-day focal follows of randomly chosen individuals on a daily basis to record affiliative and agonistic behaviours, as well as 15 minutes scan sampling to record the party composition.

Dominance status

We used the Elo-rating method (Elo 1978; Neumann et al. 2011) to establish the hierarchy between the different adult males of the group, which we calculated using 'pant grunt' data (i.e., greeting vocalisation given to higher-ranking individuals). We used the data collected from twelve months before the study started until the end of the study period (from January 4th 2017 to February 26th 2019) to have an accurate estimate of the hierarchy at the beginning of the study (Supplementary material Fig. S4.1). The Elo-ratings were calculated using the

'EloRating' package version 0.46.11 (Neumann and Kulik 2020). The hierarchy was stable throughout the study period, which enabled us to attribute one Elo-score to each male (i.e., the Elo-score obtained at the end of the observation period; Supplementary material Table S4.1 and Fig. S4.1). Elo- rating scores were standardized for statistical analyses.

Sociability

The sociability of all subjects was established by calculating a standardized grooming rate from the focal data (using interaction durations and total focal observation time). This provided an overall grooming index value for the study period for each subject, which indicated how much a subject was prone to grooming, compared to the rest of the group, with values higher than the group mean representing "high groomers", whereas males with lower values were designated as "low groomers" (Supplementary material Table S4.1). The grooming index was calculated using the 'socialindices2' package version 0.50.0 (Neumann 2017).

Preferred grooming and proximity partners

To determine each male's preferred grooming and proximity partners, we calculated, for each adult male dyad, a grooming-based and a proximity-based dyadic indices, the DSI_G and the DSI_P. The DSI_G and the DSI_P calculations were derived from the DSI introduced by Silk et al. (2013) which attributes a value of 1 to the average social bond across all dyads in the group (in our case 55 dyads; N=11 males). The DSI_G was calculated using the duration of grooming interactions between each male dyad, recorded during the focal follows. The DSI_P was calculated using the occurrence of nearest neighbour data (i.e., identity of the individual in closest proximity to the focal subject within the party, i.e., <30m away) recorded during the 15min scan samplings. Both indices took into account the total observation time of each focal individual and were calculated using the 'socialindices2' package version 0.50.0 (Neumann 2017). We established each subject's preferred long-term partners by selecting the three highest DSI values (both for the DSI_G and the DSI_P) for each subject (Supplementary material Table S4.2).

Statistical analyses

We first investigated which variables affected the time subjects spent in dyadic association with other males by analysing all dyadic association events. We built a linear mixed model (LMM1) with a Gaussian error structure and identity link function, with the duration of the dyadic association event (in minutes) as the response variable, which was transformed to log + 1 to comply with model assumptions. The subject ID, the partner ID and the Event ID were entered as random factors. The test variables were the production of 'hoo' by the subject or his partner (at least one 'hoo' produced / no 'hoo' produced), the interaction between the grooming index and the dominance rank (Elo-rating) of the subject, the difference in grooming index and in Elo-rating between the subject and his partner, the DSI_G and the DSI_P of the dyad and whether the subject groomed (yes / no) or was groomed (yes / no) by his partner.

We then investigated the subject's propensity to terminate a dyadic association event. We thus analysed all the dyadic association events for which we could determine the identity of the individual who departed and ran a generalized linear mixed model (GLMM2) with a binomial error structure and logit link function, with the

identity of the individual terminating the association (subject / partner) as the response variable and the subject ID, the partner ID and the Departure ID as random factors. The test variables were the production of 'hoo' by the subject (at least one 'hoo' produced / no 'hoo' produced), the number of 'hoo' produced by the subject, the interaction between the grooming index and the dominance rank (Elo-rating) of the subject, the difference in grooming index and in Elo-rating between the subject and his partner, the DSI_G and the DSI_P of the dyad and whether the subject groomed (yes / no) or was groomed (yes / no) by his partner.

To investigate which variables influenced 'hoo' production by the subject, we ran another GLMM (GLMM3) with a binomial error structure and logit link function on all dyadic association events, with the production of 'hoo' by the subject (at least one 'hoo' produced / no 'hoo' produced) as the response variable and the subject ID, the partner ID and the Event ID as random factors. The test variables were the interaction between the grooming index and the dominance rank (Elo-rating) of the subject, the difference in grooming index and in Elo-rating between the subject and his partner, the DSI_G and the DSI_P of the dyad, and whether the subject groomed (yes / no) or was groomed (yes / no) by his partner. The time spent in association (in minutes) was entered as a control variable.

To investigate which variables influenced the grooming behaviour of the subject, we ran another GLMM (GLMM4) with a binomial error structure and logit link function on all dyadic association events, with the subject's grooming behaviour (subject groomed / did not groom his partner) as the response variable and the subject ID, the partner ID and the Event ID as random factors. The test variables were the interaction between the grooming index and the dominance rank (Elo-rating) of the subject, the difference in grooming index and in Elo-rating between the subject and his partner, the DSI_G and the DSI_P of the dyad, whether the subject produced a 'hoo' (yes / no), whether his partner produced a 'hoo' (yes / no) and the time spent in association (in minutes).

Finally, since 'hoo' production seemed to prolong the time spent in association (see results of GLMM1 and 3), we would expect 'hoo' vocalisations to be produced during the beginning of association events. We thus performed a one-sample Kolmogorov-Smirnov test to compare the distribution of the relative time of 'hoo' production (i.e., time of production during the association event / total duration of the event) to a uniform distribution to determine if 'hoos' were produced randomly or significantly more during the first half of association events. We further investigated how long males spent in association after 'hoo' production by analysing dyadic association events during which at least one 'hoo' was produced, either by the subject or his partner. We ran another LMM (LMM5) with a Gaussian error structure and identity link function, with the time spent in association after the last 'hoo' produced (in minutes) as the response variable, which was transformed to log + 1 to comply with model assumptions. The subject ID, the partner ID and the ID of the last call were entered as random factors. The test variables were whether only one individual or both partners produced a 'hoo' (one individual / both), the number of 'hoo' produced, the interaction between the grooming index and the dominance rank (Elo-rating) of the caller (of the last 'hoo' produced), the difference in grooming index and in Elo-rating between the caller (of the last 'hoo' produced) and his partner, the DSI_G and the DSI_P of the dyad, whether the caller (of the last 'hoo' produced) groomed (yes / no) or was groomed (yes / no) by his partner and whether any female was present when the last call was produced (yes / no).

To disentangle the effect of both call variants (i.e., 'travel hoo' and 'rest hoo'), we also built similar models (LMM1b, GLMM2b, 3b, 4b and LMM5b) on a subset of the data with association events during which no 'travel hoo' was produced, thus only considering 'rest hoo' production. Due to low sample sizes, we could not run the same models considering only 'travel hoo' production (i.e., without 'rest hoo' produced).

We ran all GLMMs using the *lmer* (for LMMs) and *glmer* (for GLMMs) functions of the 'lme4' R package version 1.1-21 (Bates et al. 2015) and used a statistical model selection approach to establish which models fitted best the data (see Supplementary material Table S4.3 for the structure of the full models). First, we used the *dredge* function of the 'MuMIn' R package (version 1.43.17 ; Barton 2020) to fit several models with the test variables as fixed effects and we selected the best one based on the lowest AICc (i.e., Akaike information criterion corrected, Burnham et al. 2011). Variables were considered to improve the fit of the model only if their removal from the model increased the AICc value by more than two units (Burnham and Anderson 2004) and they were considered as informative if zero was not included within their 95% confidence interval. Then, we calculated variance inflation factors (VIF) using the *vif* function of the 'car' R package (version 3.0-3; Fox and Weisberg 2019), which revealed no collinearity issues (largest VIF = 2.25 across all models). Only results of the selected models are presented in the results section below.

All analyses were implemented in R v3.6.1 (R Core Team 2019).

Results

Across males (N=9), we recorded N=344 dyadic association events, lasting 99.6 minutes on average (SD ±72.0), which included N=151 events (43.9%) during which at least one of the two partners produced a 'hoo' and N=67 (19.5%) events during which we observed a grooming interaction. We recorded N=40 association events during which both partners produced 'hoo' vocalisations and, in 40.0% (N=16) of these events, one of the male produced a 'hoo' in immediate response to his partner (i.e., <5 sec afterwards).

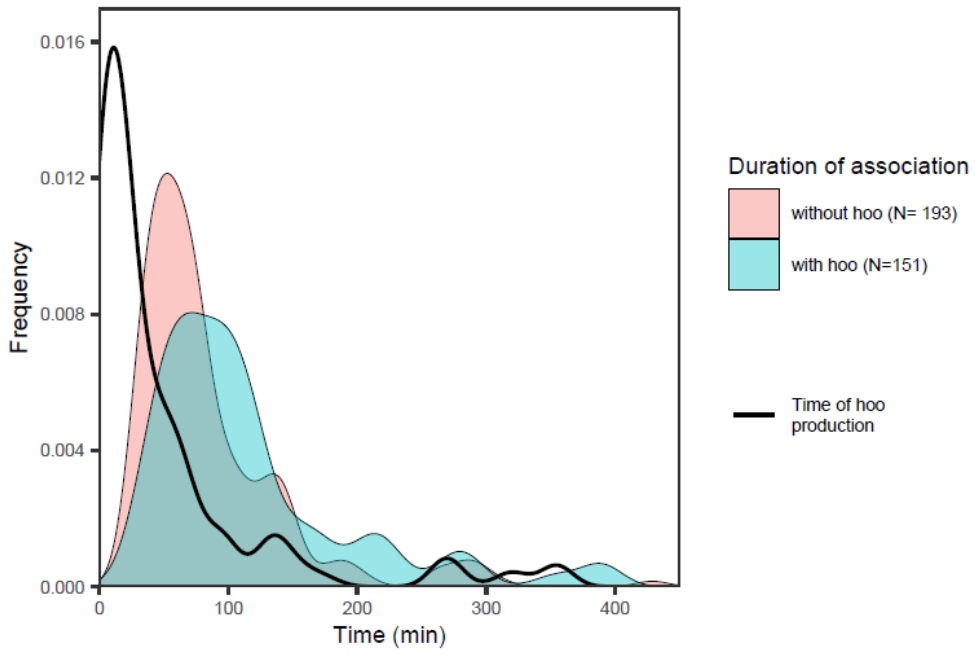

Figure 4.1. Distribution (kernel density estimates) of the time of 'hoo' production and of the time the subject spent in dyadic association with another male, depending on whether he, or the partner, produced a 'hoo'.

Time spent in association was positively correlated with the production of 'hoo'; i.e., longer when one of the partners produced a 'hoo' (β = 0.28, SE = 0.05, CI 95% = 0.19 to 0.37; Fig. 4.1; LMM1, best fitting model: AICc = 336; Table 4.1).

Table 4.1. Summary results of the models resulting from the model selection process.

	Estimate	SE	LCI	UCI
LMM1 - Duration of dyadic association events				
(Best fitting model: AICc = 336)				
Production of 'hoo' (Yes)	0.28	0.05	**0.19**	**0.37**
GLMM2 - Probability of the subject terminating the association				
(Best fitting model: AICc = 132)				
Production of 'hoo' (Yes)	-22.26	4.24	**-30.57**	**-13.96**
Number of 'hoo' produced	0.78	1.31	-1.79	3.34
Subject's elo-rating	17.12	3.06	**11.12**	**23.12**
Rank difference between the subject and his partner	1.89	1.36	-0.76	4.55
GLMM3 - Probability of the subject producing a 'hoo'				
(Best fitting model: AICc = 266)				
Duration of dyadic association event	0.003	0.001	**0.002**	**0.004**
The partner groomed the subject (Yes)	7.766	2.761	**2.355**	**13.177**
Subject's elo-rating	-5.517	2.005	**-9.447**	**-1.587**
GLMM4 - Probability of the subject grooming his partner				
(Best fitting model: AICc = 146)				
The partner groomed the subject (Yes)	6.41	1.52	**3.42**	**9.40**
Rank difference between the subject and his partner	-1.30	0.53	**-2.34**	**-0.26**
LMM5 - Time spent in association after the last 'hoo' produced				
(Best fitting model: AICc = 383)				
Both individuals produced a 'hoo' (Yes)	0.48	0.19	**0.10**	**0.85**
Caller's elo-rating	0.23	0.10	**0.03**	**0.43**

LCI: lower 95% confidence interval; UCI: upper 95% confidence. Informative variables are in bold.

We then investigated who terminated association events and found that the probability of a subject terminating an event was lower if he produced a 'hoo' (β = -22.26, SE = 4.24, CI 95% = -30.57 to -13.96; Fig. 4.2a). Conversely, the probability increased with the dominance rank of the subject (β = 17.12, SE = 3.06, CI 95% = 11.12 to 23.12; Fig. 4.2b; GLMM2, best fitting model: AICc = 132; Table 4.1).

We also found that the subject had a higher probability of producing a 'hoo' during the association event if he was groomed by his partner during the same event (β = 7.766, SE = 2.761, CI 95% = 2.355 to 13.177; Fig. 4.3a) and the probability decreased with the rank of the subject; i.e., the higher ranking the subject was, the less likely he was to produce a 'hoo' (β = -5.517, SE = 2.005, CI 95% = -9.447 to -1.587; Fig. 4.3b; GLMM3, best fitting model: AICc = 266; Table S4.1). The results of this model also showed that the probability of the subject producing a 'hoo' increased with the duration of the association (β = 0.003, SE = 0.001, CI 95% = 0.002 to 0.004), thus confirming the results of LMM1 showing that association time depended on 'hoo' production.

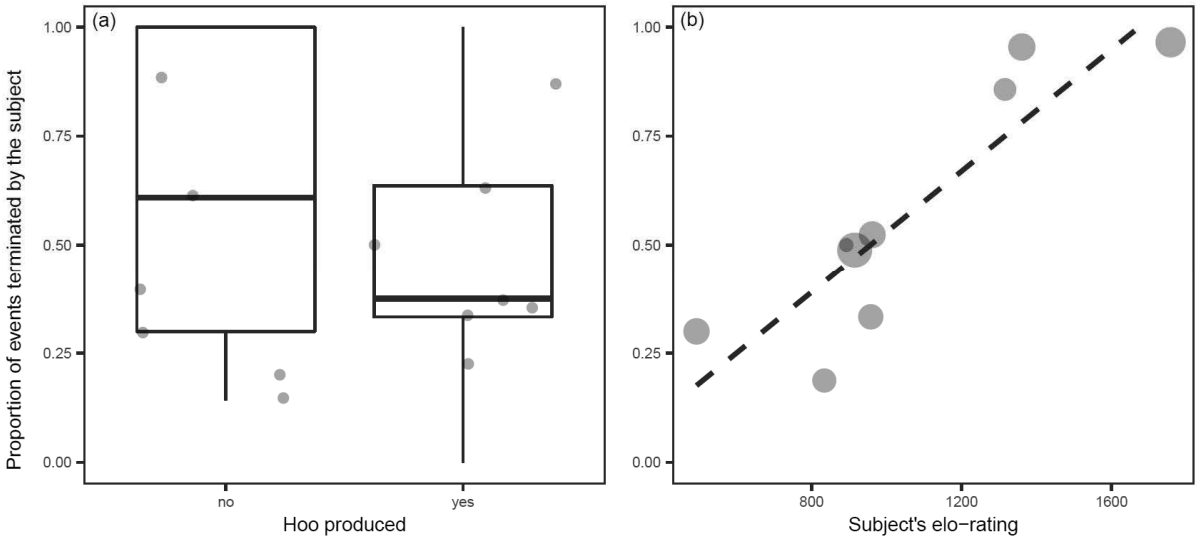

Figure 4.2. Proportion of events at the end of which the subjects terminated the association depending on **a** if the subject produced a 'hoo' or not and **b** his dominance rank.

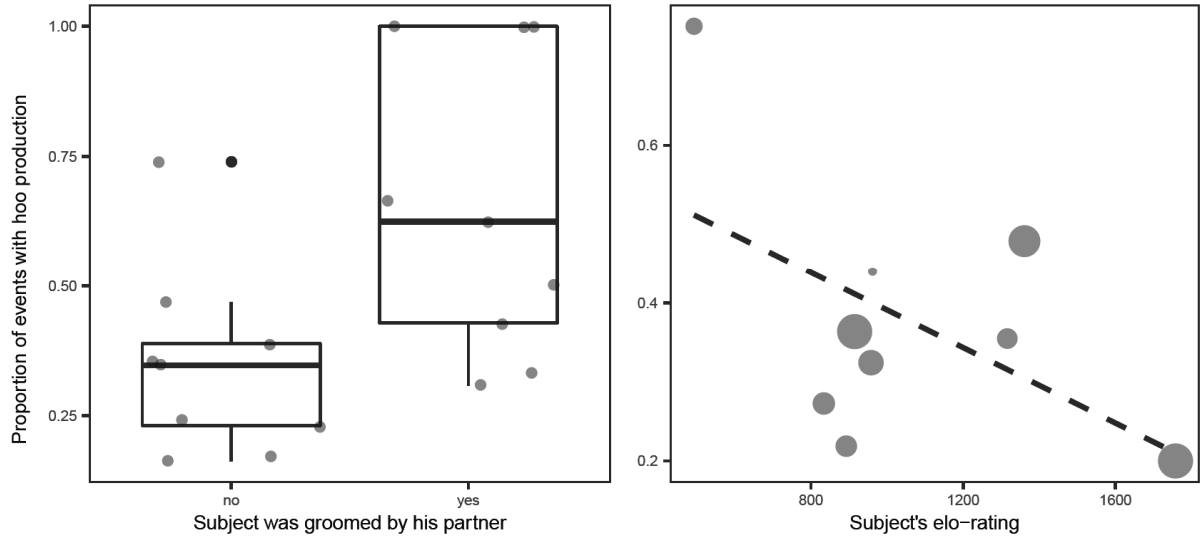

Figure 4.3. Proportion of events with 'hoo' produced by the subject depending on **a** whether his partner groomed him or not and **b** the subject's dominance rank.

When investigating the subject's grooming behaviour during dyadic associations, we found that the subject had a higher probability of grooming his association partner if this partner groomed him (β = 6.41, SE = 1.52, CI 95% = 3.42 to 9.40; Fig. 4.4a) and the probability decreased with the difference in rank between the partners; i.e., the higher ranking the subject was, compared to his partner, the less likely he was to groom his partner (β = -1.30, SE = 0.53, CI 95% = -2.34 to -0.26; Fig. 4.4b; GLMM4, best fitting model: AICc = 146; Table 4.1).

Finally, 'hoos' were mostly produced during the first half of association events (Kolmogorov-Smirnov test: $P < 0.001$), or after 50.7 min of association on average (SD ±76.1), with association events lasting 118.0 min on average (SD ±80.3) when at least one partner produced a 'hoo', whereas silent association events lasted 85.6 min on average (SD ±61.4). We also found that the remaining time spent in association after the last 'hoo' was produced lasted longer if both partners produced a 'hoo' (β = 0.48, SE = 0.19, CI 95% = 0.10 to 0.85; Fig. 4.5a), and this time also increased with the last caller's dominance rank; i.e., the association time lasted longer if the

last caller was a high ranking male (β = 0.23, SE = 0.10, CI 95% = 0.03 to 0.43; Fig. 4.5b; LMM5, best fitting model: AICc = 383; Table 4.1).

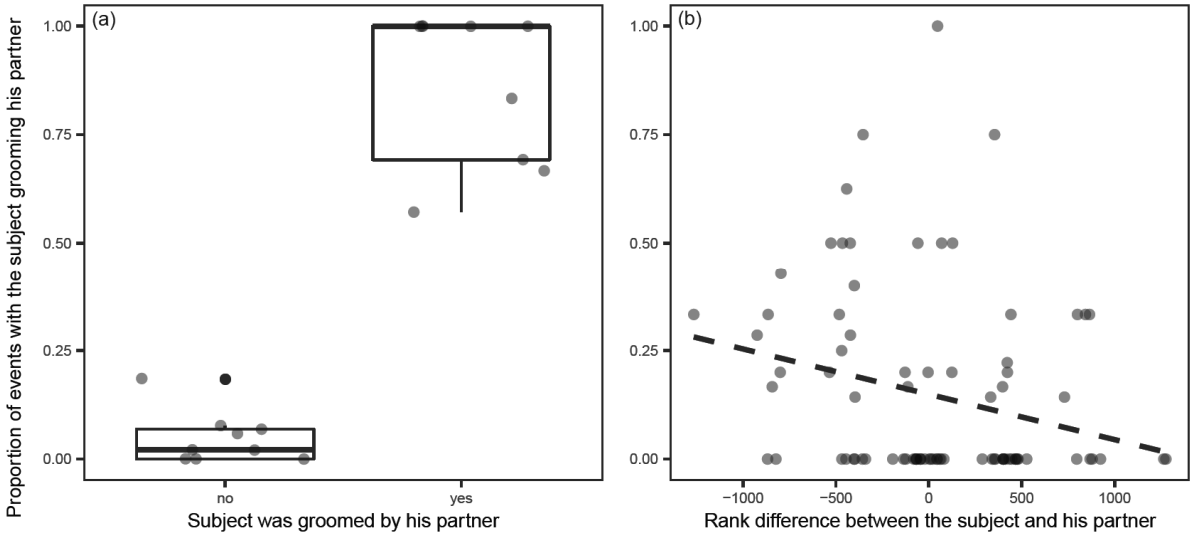

Figure 4.4. Proportion of events with the subject grooming his association partner depending on **a** whether his partner groomed him and **b** the difference in rank between him and his partner.

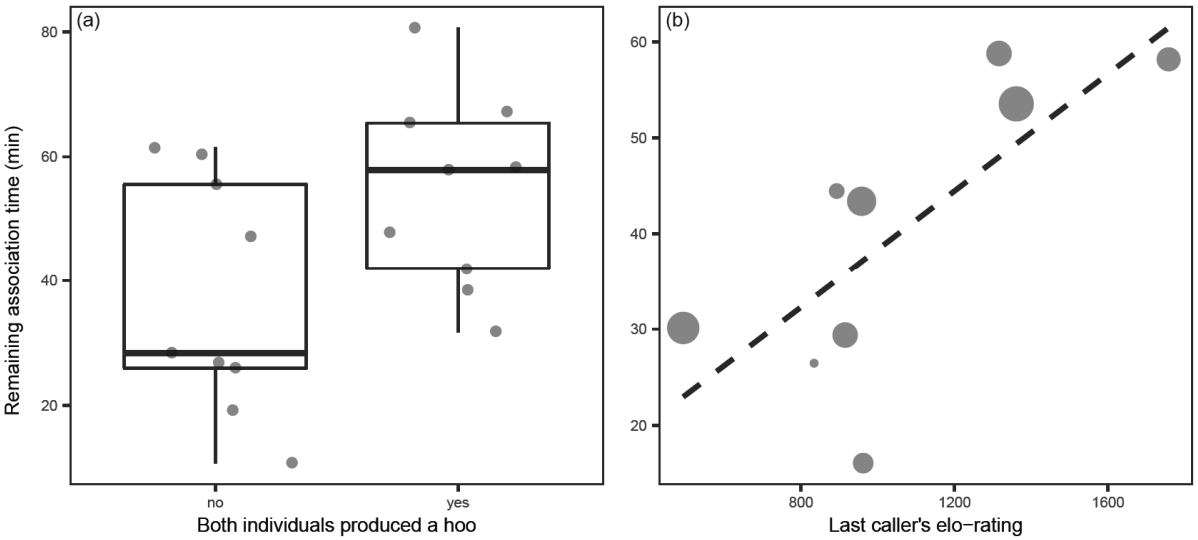

Figure 4.5. Remaining time the partners spent in association after the last 'hoo' was produced depending on **a** whether both individuals called or not and **b** the last caller's dominance rank.

We obtained similar results when running the same models on a subset of the data excluding events with 'travel hoo' production (Supplementary material Table S4.4). In this set of analyses, the time spent in association after the last 'rest hoo' produced was no longer significantly affected by whether both individuals produced a 'rest hoo' (LMM5b; Supplementary material Table S4.4). Moreover, the production of 'travel hoos' was significantly correlated with the production of 'rest hoos' (chi-square test: χ_1^2 = 5.83, P = 0.016).

Discussion

In this study, we describe some of the mechanisms underlying dyadic associations in male chimpanzees throughout their daily routines. We investigated which factors could predict whether two males continue to associate in subgroups together or split apart in different subgroups, focusing on a tactile behaviour, i.e., grooming, and a close-distance vocal behaviour, i.e. 'hoo' vocalisations. We found that 'hoo' vocalisations (i.e., 'travel hoo' or 'rest hoo') were produced during nearly half of all associations, which generally prolonged these events, additionally augmented by the caller's rank and if both partners called. Males produced 'hoo' vocalisations more often when they were low-ranking or when being groomed by their partner and, when they did, they were less likely to terminate the association. We also found that high-ranking males were more prone to terminate associations than low-ranking ones. Finally, we observed grooming interactions in approximately 20% of all association events and found that males groomed their partners more often when their partners were higher-ranking and when their partners groomed them during the same association event.

Hoo vocalisations

Previous studies have shown that 'travel hoos' and 'rest hoos' appear to be intentionally produced to initiate traveling and prolong resting with preferred social partners (Gruber and Zuberbühler 2013; Bouchard and Zuberbühler 2022a). Our results confirm that 'hoo' vocalisations promote cohesion across contexts and point to some of the underlying mechanisms of call production. Indeed, we found that 'hoos' were mostly produced during the first half of association events (after approximately 51 min) and before the end of typical silent association events (lasting around 86 min), which would suggest that 'hoos' are not randomly produced. Moreover, we found that association time increased if both partners called (26.5% of events with 'hoo' produced) and, in many cases (40% of these events), partners seemed to immediately reply to each other's calls. These results suggest that 'hoo' vocalisations do not simply indicate the signaller's motivation to rest or travel independently of the actions of others but might indeed be produced to affect others' and even to seek a mutual commitment to stay together.

When analysing the effect of 'rest hoo' production separately (i.e., excluding events with 'travel hoos') on the dyadic association patterns, we obtained similar results, thus confirming the cohesion function of this call. 'Travel hoo' vocalisations were produced less frequently, preventing us to analyse them separately, although this would be a worthy topic for further research. Interestingly, the large majority (N=21; 65.6%) of 'travel hoos' were produced during association events when 'rest hoos' were also produced, with a significant correlation between 'travel hoos' and 'rest hoos', possibly reflecting the same underlying motivation by the caller, despite changing context.

Grooming

Contrary to our predictions, whether partners groomed or not during an association event did not seem to affect the duration of this event. However, when investigating the grooming interactions that happened during the association events, we found that subjects groomed their partners more often if they were being groomed by their partners or if these partners were higher ranking than them. These results could depict two different patterns: one of mutual grooming (i.e., the subject grooms his partner if the partner grooms him) and one of unidirectional

grooming, which is mainly directed at desirable social partners (i.e., higher-ranking males). Even though grooming is often used as a measure of long-term social bonds in chimpanzees, unidirectional grooming and mutual grooming do not have the same payoffs and might not play the same role in social bonding. Fedurek and Dunbar (2009) showed that the function of mutual grooming could be to create and maintain social bonds, as mutual grooming was correlated with other affiliative behaviours, such as tolerance and proximity. However, these results have been challenged by Machanda et al. (2014) and Allanic et al. (2020), who found more support for the immediate investment hypothesis, which stipulates that mutual grooming would signal willingness to invest in prolonging the grooming bout. Although Machanda et al. (2014) found little support for the social bonding function of mutual grooming, they found that unidirectional grooming was preferentially directed at preferred long-term association partners and might thus play a role in maintaining social bonds. Our results support the fact that mutual and unidirectional grooming should be considered separately in future studies, as to disentangle their role in social bonding.

Social bonds

Surprisingly, we did not find any evidence that males stayed longer or made any effort (i.e., 'hoo' production) to stay longer with preferred social partners (i.e., proximity and grooming partners). These results highlight the fact that the social indices commonly used when investigating chimpanzee relationships might not always be relevant, especially when studying short-term social dynamics. Indeed, these indices, which are very often calculated using proximity and grooming data, either separately or combined (e.g., Bray & Gilby, 2020; Samuni et al., 2018, 2021; Schel, Machanda, et al., 2013; Webb et al., 2017), are calculated over long periods of time and do not allow to observe the evolution and variations of the social relationships, contrary to the Elo-rating method used to calculate the hierarchy between individuals (Elo, 1978; Neumann et al., 2011). Therefore, these indices might not reflect the present state of mind of the subject and, depending on the behaviours being studied, might not be psychologically relevant. Moreover, grooming interactions during the associations did not seem particularly directed at preferred grooming partners. This could be explained by the fact that males might use different grooming strategies depending on their partners. For instance, preferred grooming partners might engage in reciprocated or mutual grooming, whereas males might be more prone to groom unidirectionally high-ranking individuals, as a social tool to maintain the association. Again, this highlights the necessity to explore how these different grooming patterns might affect male social relationships.

Similarly to other primate species, grooming and support during agonistic interactions are two widely recognised indicators of social bonds in chimpanzees (Muller and Mitani 2005; Mitani 2009a; Fedurek and Dunbar 2009). However, as previously suggested, these two behaviours are costly and can only occur in specific contexts (i.e., resting and agonistic interactions, respectively), whereas vocal signals are contextually more flexible and represent a less costly way to strengthen social bonds (Slocombe et al. 2010; Fedurek et al. 2013). Indeed, vocal signals can be produced in a variety of contexts, such as traveling and feeding, and they do not necessitate the signaller to be in close proximity with its recipient. In this study, results showed that most 'hoos' were produced during resting (i.e., 'rest hoos'), a context during which males potentially could groom each other. Yet, vocal signals remained a better predictor of short-term affiliation than grooming, even in this context, which suggests that vocalisations might not only be used as a default option when grooming is not available. Moreover, males were more likely to produce a 'hoo' when they were groomed by their partners during the same event, which

would indicate that grooming could affect a male's intention to prolong his short-term association with his partner. However, 'hoo' production, and not direct grooming interactions (given or received), seemed to affect male association patterns. Hence, we propose that indices based on grooming behaviours might not be the best predictor of short-term social goals. We suggest, instead, that the production of specific vocal signals, such as 'hoo' vocalisations, might be a better indicator of short-term affiliative relationships. These results are in line with a previous study, which showed that, on a short-term basis, specific vocal exchanges (i.e., pant hoot chorusing) but not grooming were correlated with other affiliative behaviours, such as tolerated co-feeding and coalitions (Fedurek et al. 2013). However, it is not always possible to determine the intended recipient of a vocalisation and it might thus be more relevant to consider vocal exchanges, such as pant-hoot chorusing (Fedurek et al. 2013). Other vocal signals, such as 'hoo' vocalisations, can also elicit immediate vocal responses (Gruber and Zuberbühler 2013; Bouchard and Zuberbühler 2022a) and could also offer interesting avenues for future research.

Dominance rank

Another key finding of our study is that high-ranking males seemed to be driving the association patterns, as they terminated the associations more often and, when they produced 'hoo' vocalisations, they were more successful in prolonging the association than lower-ranking ones. Males also seemed to make more effort to stay with higher-ranking males as they produced 'hoo' vocalisations more often when associating with them. Overall, it seems that high-ranking males were the most desirable partners. Associating with higher-ranking males, and especially the alpha male, can bring many fitness advantages to subordinates, such as preferential access to mates and better siring success (Duffy et al. 2007; Feldblum et al. 2021). Therefore, males might choose to associate with specific partners strategically, as to manage their relationships with other males. The way chimpanzees form and maintain alliances, with the use of certain behaviours, such as grooming or meat sharing, has been described as political (De Waal 1982; Watts 2002; Mitani 2006). For instance, males seem to exchange coalitionary support of the alpha male for selective access to mating, which was characterised as a political tactic (Duffy et al. 2007). Even though our study did not take into account coalitionary support, proximity is clearly a necessary precondition for any political benefits. Therefore, the way males associate with each other and how they maintain these associations (e.g., production of 'hoo' vocalisations) might constitute an important part of their political strategies.

Conclusion and limitations

Overall, our results seem to support the fact that male chimpanzee social relationships strongly affect their spatial dynamics, with dominance rank being a key driver of association patterns. Moreover, males seem to use vocal communication strategically to achieve their short-time social goals and facilitate cohesion with desired partners. However, our study cannot exclude that other factors, such as the distribution of food patches or the presence of oestrous females, could also influence these patterns and further investigations are needed to disentangle other possible effects. Nonetheless, if males just spent long periods of time feeding together, these events were not taken into account since we only considered association events including resting and traveling activities. Finally, even though female chimpanzees are less gregarious than males, male-female and female-female relationships, like male-male relationships, can manifest as enduring social bonds or short-term

affiliations (Langergraber et al. 2009, 2013). We did not examine the impact of 'hoo' vocalisations on the male-female or female-female relationships here but this would be interesting to explore in future studies.

Acknowledgments

We are grateful to the Sonso field assistants (Sam Adue, Geresomu Muhumuza, Monday Gideon, and Chandia Bosco) and all of the staff of the Budongo Conservation Field Station for assistance with data collection in Uganda. We thank the Uganda Wildlife Authority, the Ugandan National Council for Science and Technology, and the President's office for research permissions, as well as the Royal Zoological Society of Scotland for providing core funding for Budongo Conservation Field Station. We thank Bilgé Kimyonok for technical support and Adrian Soldati and Auriane Le Floch for comments on the manuscript.

References

Allanic M, Hayashi M, Matsuzawa T (2020) Investigating the Function of Mutual Grooming in Captive Bonobos (***Pan paniscus***) and Chimpanzees (***Pan troglodytes***). Folia Primatol 91:481–494. https://doi.org/10.1159/000506308

Asensio N, Korstjens AH, Aureli F (2009) Fissioning minimizes ranging costs in spider monkeys: a multiple-level approach. Behav Ecol Sociobiol 63:649–659. https://doi.org/10.1007/s00265-008-0699-9

Aureli F, Schaffner CM, Boesch C, et al (2008) Fission-Fusion Dynamics: New Research Frameworks. Curr Anthropol 49:627–654. https://doi.org/10.1086/586708

Babiszewska M, Schel AM, Wilke C, Slocombe KE (2015) Social, contextual, and individual factors affecting the occurrence and acoustic structure of drumming bouts in wild chimpanzees (Pan troglodytes). Am J Phys Anthropol 156:125–134. https://doi.org/10.1002/ajpa.22634

Barrett L, Henzi P, Dunbar RIM (2003) Primate cognition: from "what now?" to "what if?" Trends Cogn Sci 7:494–497. https://doi.org/10.1016/j.tics.2003.09.005

Barton K (2020) MuMIn: Multi-Model Inference

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67:. https://doi.org/10.18637/jss.v067.i01

Boesch C (1994) Cooperative hunting in wild chimpanzees. Anim Behav 48:653–667. https://doi.org/10.1006/anbe.1994.1285

Boesch C (1991) The Effects of Leopard Predation On Grouping Patterns in Forest Chimpanzees. Behaviour 117:220–241. https://doi.org/10.1163/156853991X00544

Boesch C, Kohou G, Néné H, Vigilant L (2006) Male competition and paternity in wild chimpanzees of the Taï forest. Am J Phys Anthropol 130:103–115. https://doi.org/10.1002/ajpa.20341

Bouchard A, Zuberbühler K (2022a) An intentional cohesion call in male chimpanzees of Budongo Forest. Anim Cogn. https://doi.org/10.1007/s10071-022-01597-6

Bouchard A, Zuberbühler K (2022b) Male chimpanzees communicate to mediate competition and cooperation during feeding. Anim Behav 186:41–55. https://doi.org/10.1016/j.anbehav.2022.01.009

Bray J, Gilby IC (2020) Social relationships among adult male chimpanzees (Pan troglodytes schweinfurthii): variation in the strength and quality of social bonds. Behav Ecol Sociobiol 74:112. https://doi.org/10.1007/s00265-020-02892-3

Bray J, Pusey AE, Gilby IC (2016) Incomplete control and concessions explain mating skew in male chimpanzees. Proc R Soc B Biol Sci 283:20162071. https://doi.org/10.1098/rspb.2016.2071

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociol Methods Res 261–304

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology : some background , observations , and comparisons. Behav Ecol Sociobiol 65:23–35

Busia L, Schaffner CM, Aureli F (2017) Relationship quality affects fission decisions in wild spider monkeys (Ateles geoffroyi). Ethology 123:405–411. https://doi.org/10.1111/eth.12609

Chapman CA, Chapman LJ, Wrangham RW (1995) Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behav Ecol Sociobiol 36:59–70. https://doi.org/10.1007/BF00175729

Clark AP (1993) Rank differences in the production of vocalizations by wild chimpanzees as a function of social

context. Am J Primatol 31:159–179

Clark AP, Wrangham RW (1994) Chimpanzee Arrival Pant-Hoots: Do Signify Food or Status? Int J Primatology 15(2)

Clark HH (2006) Social Actions , Social Commitments. In: Enfield NJ, Levinson SC (eds) Roots of Human Sociality: Culture, Cognition and Interaction. Berg, Oxford, England, pp 126–150

Clark HH (1996) Using Language. Cambridge University Press, Cambridge, UK

Connor RC, Heithaus MR, Barre LM (2001) Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance.' Proc R Soc London Ser B Biol Sci 268:263–267. https://doi.org/10.1098/rspb.2000.1357

Conradt L, List C (2009) Group decisions in humans and animals: a survey. Philos Trans R Soc B Biol Sci 364:719–742. https://doi.org/10.1098/rstb.2008.0276

Conradt L, Roper TJ (2010) Deciding group movements: Where and when to go. Behav Processes 84:675–677. https://doi.org/10.1016/j.beproc.2010.03.005

Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. Nature 433:513–516. https://doi.org/10.1038/nature03236

Crockford C, Gruber T, Zuberbühler K (2018) Chimpanzee quiet hoo variants differ according to context. R Soc Open Sci 5:172066. https://doi.org/10.1098/rsos.172066

Crockford C, Wittig RM, Mundry R, Zuberbühler K (2012) Wild chimpanzees inform ignorant group members of danger. Curr Biol 22:142–146. https://doi.org/10.1016/j.cub.2011.11.053

Crockford C, Wittig RM, Zuberbühler K (2015) An intentional vocalization draws others' attention: A playback experiment with wild chimpanzees. Anim Cogn 18:581–591. https://doi.org/10.1007/s10071-014-0827-z

Crockford C, Wittig RM, Zuberbühler K (2017) Vocalizing in chimpanzees is influenced by social-cognitive processes. Sci Adv 3:e1701742. https://doi.org/10.1126/sciadv.1701742

De Waal FBM (1982) Chimpanzee Politics: Power and Sex among Apes. Harper & Row, New York, NY

Desai NP, Fedurek P, Slocombe KE, et al (2021) Chimpanzee pant-hoots encode information about individual but not group differences

Duffy KG, Wrangham RW, Silk JB (2007) Male chimpanzees exchange political support for mating opportunities. Curr Biol 17:R586–R587. https://doi.org/10.1016/j.cub.2007.06.001

Dunbar RIM (1998) The social brain hypothesis. Evol Anthropol 6:178–190. https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8

Eckhardt N, Polansky L, Boesch C (2015) Spatial cohesion of adult male chimpanzees (Pan troglodytes verus) in Taï National Park, Côte d'Ivoire. Am J Primatol 77:125–134. https://doi.org/10.1002/ajp.22316

Elo AE (1978) The rating of chess players, past and present. Arco Pub., New York, NY

Fedurek P, Donnellan E, Slocombe KE (2014) Social and ecological correlates of long-distance pant hoot calls in male chimpanzees. Behav Ecol Sociobiol 68:1345–1355. https://doi.org/10.1007/s00265-014-1745-4

Fedurek P, Dunbar RIM (2009) What Does Mutual Grooming Tell Us About Why Chimpanzees Groom? Ethology 115:566–575. https://doi.org/10.1111/j.1439-0310.2009.01637.x

Fedurek P, Machanda ZP, Schel AM, Slocombe KE (2013) Pant hoot chorusing and social bonds in male chimpanzees. Anim Behav 86:189–196. https://doi.org/10.1016/j.anbehav.2013.05.010

Fedurek P, Slocombe KE (2013) The Social Function of Food-Associated Calls in Male Chimpanzees. Am J

Primatol 75:726–739. https://doi.org/10.1002/ajp.22122

Fedurek P, Zuberbühler K, Dahl CD (2016) Sequential information in a great ape utterance. Sci Rep 6:38226. https://doi.org/10.1038/srep38226

Feldblum JT, Krupenye C, Bray J, et al (2021) Social bonds provide multiple pathways to reproductive success in wild male chimpanzees. iScience 24:102864. https://doi.org/10.1016/j.isci.2021.102864

Fox J, Weisberg S (2019) An R Companion to Applied Regression, Third edit. Sage, Thousand Oaks, CA

Frère CH, Krutzen M, Mann J, et al (2010) Social and genetic interactions drive fitness variation in a free-living dolphin population. Proc Natl Acad Sci 107:19949–19954. https://doi.org/10.1073/pnas.1007997107

Fröhlich M, Wittig RM, Pika S (2016) Should I stay or should I go? Initiation of joint travel in mother–infant dyads of two chimpanzee communities in the wild. Anim Cogn 19:483–500. https://doi.org/10.1007/s10071-015-0948-z

Genty E, Heesen R, Guéry J-P, et al (2020) How apes get into and out of joint actions. Interact Stud Soc Behav Commun Biol Artif Syst 21:353–386. https://doi.org/10.1075/is.18048.gen

Gilby IC, Brent LJN, Wroblewski EE, et al (2013) Fitness benefits of coalitionary aggression in male chimpanzees. Behav Ecol Sociobiol 67:373–381. https://doi.org/10.1007/s00265-012-1457-6

Gruber T, Zuberbühler K (2013) Vocal Recruitment for Joint Travel in Wild Chimpanzees. PLoS One 8:e76073. https://doi.org/10.1371/journal.pone.0076073

Heesen R, Bangerter A, Zuberbühler K, et al (2021) Assessing joint commitment as a process in great apes. iScience 24:102872. https://doi.org/10.1016/j.isci.2021.102872

Heesen R, Bangerter A, Zuberbühler K, et al (2020) Bonobos engage in joint commitment. Sci Adv 6:. https://doi.org/10.1126/sciadv.abd1306

Hinde RA (1976) Interactions, Relationships and Social Structure. Man 11:1. https://doi.org/10.2307/2800384

Hruschka DJ (2010) Friendship: development, ecology, and evolution of a relationship. University of California Press, Berkeley

Humphrey N (1976) The social function of intellect. In: Bateson PPG, Hinde RA (eds) Growing points in ethology. Cambridge University Press, Cambridge, pp 303–317

Jacobs A (2010) Group cohesiveness during collective movements: Travelling apart together. Behav Processes 84:678–680. https://doi.org/10.1016/j.beproc.2010.03.004

Kalan AK, Boesch C (2015) Audience effects in chimpanzee food calls and their potential for recruiting others. Behav Ecol Sociobiol 69:1701–1712. https://doi.org/10.1007/s00265-015-1982-1

Kerth G (2010) Group decision-making in animal societies. In: Animal Behaviour: Evolution and Mechanisms. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 241–265

King AJ, Sueur C (2011) Where Next? Group Coordination and Collective Decision Making by Primates. Int J Primatol 32:1245–1267. https://doi.org/10.1007/s10764-011-9526-7

Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, Oxford, UK

Kummer H (1971) Primate societies – group techniques of ecological adaptation. Aldine Publishing Company, Chicago

Langergraber KE, Mitani JC, Vigilant L (2009) Kinship and social bonds in female chimpanzees (Pan troglodytes). Am J Primatol 71:840–851. https://doi.org/10.1002/ajp.20711

Langergraber KE, Mitani JC, Watts DP, Vigilant L (2013) Male–female socio-spatial relationships and

reproduction in wild chimpanzees. Behav Ecol Sociobiol 67:861–873. https://doi.org/10.1007/s00265-013-1509-6

Lusseau D (2007) Why Are Male Social Relationships Complex in the Doubtful Sound Bottlenose Dolphin Population? PLoS One 2:e348. https://doi.org/10.1371/journal.pone.0000348

Machanda ZP, Gilby IC, Wrangham RW (2014) Mutual grooming among adult male chimpanzees: the immediate investment hypothesis. Anim Behav 87:165–174. https://doi.org/10.1016/j.anbehav.2013.10.028

Massen J, Sterck E, de Vos H (2010) Close social associations in animals and humans: functions and mechanisms of friendship. Behaviour 147:1379–1412. https://doi.org/10.1163/000579510X528224

Mitani JC (2009a) Male chimpanzees form enduring and equitable social bonds. Anim Behav 77:633–640. https://doi.org/10.1016/j.anbehav.2008.11.021

Mitani JC (2009b) Cooperation and competition in chimpanzees: Current understanding and future challenges. Evol Anthropol Issues, News, Rev 18:215–227. https://doi.org/10.1002/evan.20229

Mitani JC (2006) Reciprocal exchange in chimpanzees and other primates. In: Cooperation in Primates and Humans. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 107–119

Mitani JC, Amsler S (2003) Social and spatial aspects of male subgrouping in a community of wild chimpanzees. Behaviour 140:869–884. https://doi.org/10.1163/156853903770238355

Mitani JC, Nishida T (1993) Contexts and social correlates of long-distance calling by male chimpanzees. Anim Behav 45:735–746. https://doi.org/10.1006/anbe.1993.1088

Muller MN, Mitani JC (2005) Conflict and Cooperation in Wild Chimpanzees. In: Advances in the Study of Behavior. pp 275–331

Neumann C (2017) socialindices2: social and association indices

Neumann C, Duboscq J, Dubuc C, et al (2011) Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. Anim Behav 82:911–921. https://doi.org/10.1016/j.anbehav.2011.07.016

Neumann C, Kulik L (2020) EloRating: Animal dominance hierarchies by Elo rating

Newton-Fisher NE (2003) The home range of the Sonso community of chimpanzees from the Budongo Forest, Uganda. Afr J Ecol 41:150–156. https://doi.org/10.1046/j.1365-2028.2003.00408.x

Newton-Fisher NE, Thompson ME, Reynolds V, et al (2009) Paternity and social rank in wild chimpanzees (Pan troglodytes) from the Budongo Forest, Uganda. Am J Phys Anthropol 142:417–428. https://doi.org/10.1002/ajpa.21241

Notman H, Rendall D (2005) Contextual variation in chimpanzee pant hoots and its implications for referential communication. Anim Behav 70:177–190. https://doi.org/10.1016/j.anbehav.2004.08.024

Ostner J, Schülke O (2014) The evolution of social bonds in primate males. Behaviour 151:871–906. https://doi.org/10.1163/1568539X-00003191

Petit O, Bon R (2010) Decision-making processes: The case of collective movements. Behav Processes 84:635–647. https://doi.org/10.1016/j.beproc.2010.04.009

R Core Team (2019) R: A language and environment for statistical computing

Reynolds V (2005) The chimpanzees of the Budongo forest: Ecology, behaviour and conservation, Oxford Uni

Reynolds V, Reynolds R (1965) Chimpanzees of the Budongo Forest. In: Primate behavior: field studies of

monkeys and apes. Rinehart & Winston, New York, pp 368–424

Samuni L, Crockford C, Wittig RM (2021) Group-level cooperation in chimpanzees is shaped by strong social ties. Nat Commun 12:539. https://doi.org/10.1038/s41467-020-20709-9

Samuni L, Preis A, Mielke A, et al (2018) Social bonds facilitate cooperative resource sharing in wild chimpanzees. Proc R Soc B Biol Sci 285:. https://doi.org/10.1098/rspb.2018.1643

Schel AM, Townsend SW, Machanda ZP, et al (2013) Chimpanzee Alarm Call Production Meets Key Criteria for Intentionality. PLoS One 8:e76674. https://doi.org/10.1371/journal.pone.0076674

Schülke O, Bhagavatula J, Vigilant L, Ostner J (2010) Social Bonds Enhance Reproductive Success in Male Macaques. Curr Biol 20:2207–2210. https://doi.org/10.1016/j.cub.2010.10.058

Seyfarth RM, Cheney DL (2012) The Evolutionary Origins of Friendship. Annu Rev Psychol 63:153–177. https://doi.org/10.1146/annurev-psych-120710-100337

Sibly RM (1983) Optimal group size is unstable. Anim Behav 31:947–948. https://doi.org/10.1016/S0003-3472(83)80250-4

Silk JB, Beehner JC, Bergman TJ, et al (2009) The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proc R Soc B Biol Sci 276:3099–3104. https://doi.org/10.1098/rspb.2009.0681

Silk JB, Brosnan SF, Henrich J, et al (2013a) Chimpanzees share food for many reasons: The role of kinship, reciprocity, social bonds and harassment on food transfers. Anim Behav 85:941–947. https://doi.org/10.1016/j.anbehav.2013.02.014

Silk JB, Cheney DL, Seyfarth RM (2013b) A practical guide to the study of social relationships. Evol Anthropol Issues, News, Rev 22:213–225. https://doi.org/10.1002/evan.21367

Slocombe KE, Kaller T, Turman L, et al (2010) Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. Behav Ecol Sociobiol 64:1959–1966. https://doi.org/10.1007/s00265-010-1006-0

Smith JE, Powning KS, Dawes SE, et al (2011) Greetings promote cooperation and reinforce social bonds among spotted hyaenas. Anim Behav 81:401–415. https://doi.org/10.1016/j.anbehav.2010.11.007

Stueckle S, Zinner D (2008) To follow or not to follow: decision making and leadership during the morning departure in chacma baboons. Anim Behav 75:1995–2004. https://doi.org/10.1016/j.anbehav.2007.12.012

Sueur C, Deneubourg J-L, Petit O (2010a) Sequence of quorums during collective decision making in macaques. Behav Ecol Sociobiol 64:1875–1885. https://doi.org/10.1007/s00265-010-0999-8

Sueur C, King AJ, Conradt L, et al (2011) Collective decision-making and fission-fusion dynamics: a conceptual framework. Oikos 120:1608–1617. https://doi.org/10.1111/j.1600-0706.2011.19685.x

Sueur C, Petit O, Deneubourg JL (2010b) Short-term group fission processes in macaques: a social networking approach. J Exp Biol 213:1338–1346. https://doi.org/10.1242/jeb.039016

Symington MM (1990) Fission-Fusion Social Organization in Ateles and Pan. Int J Primatol 11:47–61

Tokuda M, Boubli JP, Izar P, Strier KB (2012) Social cliques in male northern muriquis Brachyteles hypoxanthus. Curr Zool 58:342–352. https://doi.org/10.1093/czoolo/58.2.342

Van Schaik CP, Van Hooff JARAM (1994) Male Bonds: Afilliative Relationships Among Nonhuman Primate Males. Behaviour 130:309–337. https://doi.org/10.1163/156853994X00587

von Rueden C, Gavrilets S, Glowacki L (2015) Solving the puzzle of collective action through inter-individual

differences. Philos Trans R Soc B Biol Sci 370:20150002. https://doi.org/10.1098/rstb.2015.0002

Watts DP (2005) Sexual segregation in non-human primates. In: Ruckstuhl K, Neuhaus P (eds) Sexual Segregation in Vertebrates. Cambridge University Press, Cambridge, pp 327–347

Watts DP (2002) Reciprocity and interchange in the social relationships of wild male chimpanzees. Behaviour 139:343–370. https://doi.org/10.1163/156853902760102708

Watts DP, Mitani JC (2001) Boundary patrols and intergroup encounters in wild chimpanzees. Behaviour 138:299–327. https://doi.org/10.1163/15685390152032488

Wey T, Blumstein DT, Shen W, Jordán F (2008) Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim Behav 75:333–344. https://doi.org/10.1016/j.anbehav.2007.06.020

Wrangham RW (1977) Feeding behaviour of chimpanzees in Gombe national park, Tanzania. In: Clutton-Brock TH (ed) Primate ecology: studies of feeding and ranging behavior in lemurs monkeys and apes. Academic Press, London, pp 503–538

Wrangham RW, Wilson ML, Hauser MD (2007) Chimpanzees (Pan troglodytes) modify grouping and vocal behaviour in response to location-specific risk. Behaviour 144:1621–1653. https://doi.org/10.1163/156853907782512137

Wroblewski EE, Murray CM, Keele BF, et al (2009) Male dominance rank and reproductive success in chimpanzees, Pan troglodytes schweinfurthii. Anim Behav 77:873–885. https://doi.org/10.1016/j.anbehav.2008.12.014

Supplementary material

Table S4.1. IDs of the adult male chimpanzee subjects, with their age (at the beginning of the study), the total focal time, the number of dyadic association events recorded, their elo-rating scores, their grooming index and associated sociability. The subjects marked with * were excluded from the analyses due to small amounts of focal time.

Focal ID	Age	Focal time (hours)	Number of association events	Elo-rating	Grooming index
HW	24	48	55	1758	1.32897
FK	18	37	48	1361	-0.43526
MS	26	46	31	1316	1.25555
SM*	24	12	3	1028	-1.11299
SQ	26	55	25	962	0.68209
ZL	21	33	37	958	0.53392
PS	19	64	55	915	-0.34498
KT	23	37	32	893	-1.00136
ZF	35	22	33	834	-0.3755
KZ	22	71	28	493	0.97484
ZD*	16	5	0	482	-1.50527

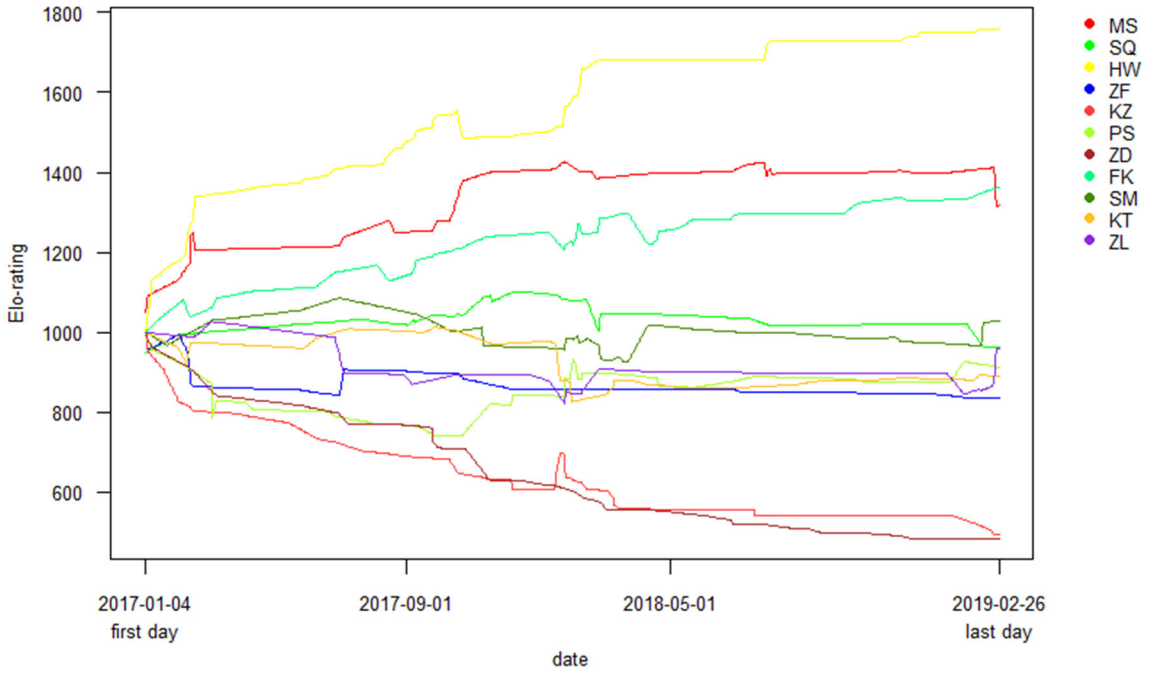

Figure S4.1. Evolution of the Elo-rating scores of the 11 adult males of the Sonso community from 12 months before the start of the study (January 4th 2017) to the end of the first study period (February 26th 2019). In contrast to traditional matrix-based assessments, elo-rating conceptualises rank as a dynamic variable that changes with each social interaction. Each male starts the process with a fixed score, which is continuously updated following each dyadic interaction. In particular, each time a male produces pant grunts to another male, he loses points whereas the recipient gains the same number of points. The number of points gained or lost depends on the expected outcome, which is calculated prior the interaction. Unexpected outcomes lead to more point changes than expected outcomes (Elo 1978; Neumann et al. 2011).

Table S4.2. DSI_G and DSI_P values for each male dyad.

ID1	ID2	DSIg	DSIp
FK	HW	2.51	1.94
FK	KT	0.03	1.09
FK	KZ	0.30	0.88
FK	MS	0.82	0.63
FK	PS	0.00	1.23
FK	SM	0.18	1.12
FK	SQ	0.03	1.11
FK	ZD	0.05	0.59
FK	ZF	0.61	0.71
FK	ZL	0.72	0.89
HW	KT	2.11	3.15
HW	KZ	1.18	0.81
HW	MS	7.42	2.96
HW	PS	2.36	1.58
HW	SM	1.59	1.93
HW	SQ	2.86	1.79
HW	ZD	0.00	0.15
HW	ZF	0.66	1.78
HW	ZL	3.57	2.74
KT	KZ	0.36	0.39
KT	MS	1.87	1.55
KT	PS	0.02	0.91
KT	SM	0.00	0.34
KT	SQ	0.31	0.61
KT	ZD	0.04	0.51
KT	ZF	0.03	0.70
KT	ZL	0.92	1.20
KZ	MS	0.59	0.66
KZ	PS	0.87	0.95
KZ	SM	0.81	0.89
KZ	SQ	0.45	1.39
KZ	ZD	0.00	0.32
KZ	ZF	0.00	0.91
KZ	ZL	1.18	0.73
MS	PS	2.71	1.15
MS	SM	0.27	0.70
MS	SQ	2.06	1.98
MS	ZD	0.01	0.07
MS	ZF	0.83	0.54
MS	ZL	0.84	0.60
PS	SM	0.81	1.49
PS	SQ	1.33	0.98
PS	ZD	1.35	1.17
PS	ZF	0.33	0.67
PS	ZL	1.85	0.84
SM	SQ	0.20	0.88
SM	ZD	0.11	1.27
SM	ZF	0.49	0.75
SM	ZL	1.48	1.15
SQ	ZD	1.18	1.01
SQ	ZF	0.28	0.98
SQ	ZL	1.59	0.93
ZD	ZF	0.00	0.42
ZD	ZL	2.14	1.50
ZF	ZL	0.46	0.68

Table S4.3. Structure of the full models used in this study.

Model	Response Variable	Test Variables	Random effects
LMM1	Duration of dyadic association events	'hoo' produced by the subject or his partner (yes/no) + subject's sociability * subject's rank + difference in sociability between the subject and his partner + rank difference between the subject and his partner + DSIG of the dyad + DSIP of the dyad + subject groomed (yes/no) + partner groomed (yes/no)	Subject ID + Partner ID + Event ID
GLMM2	Subject terminated the association event (yes/no)	'hoo' produced by the subject or his partner (yes/no) + number of 'hoo'produced + subject's sociability * subject's rank + difference in sociability between the subject and his partner + rank difference between the subject and his partner + DSIG of the dyad + DSIP of the dyad + subject groomed (yes/no) + partner groomed (yes/no)	Subject ID + Partner ID + Departure ID
GLMM3	Subject produced a 'hoo' (yes/no)	subject's sociability * subject's rank + difference in sociability between the subject and his partner + rank difference between the subject and his partner + DSIG of the dyad + DSIP of the dyad + subject groomed (yes/no) + partner groomed (yes/no) + duration of association event	Subject ID + Partner ID + Event ID
GLMM4	Subject groomed his partner (yes/no)	subject's sociability * subject's rank + difference in sociability between the subject and his partner + rank difference between the subject and his partner + DSIG of the dyad + DSIP of the dyad + subject produced a 'hoo'(yes/no)+ partner produced a 'hoo' (yes/no) + partner groomed (yes/no) + duration of association event	Subject ID + Partner ID + Event ID
LMM5	Duration of association after the last 'hoo' produced	'hoo' production (one/ both individuals called) + number of 'hoo' produced + last caller's sociability * last caller's rank + difference in sociability between the last caller and his partner + rank difference between the last caller and his partner + DSIG of the dyad + DSIP of the dyad + last caller groomed (yes/no) + his partner groomed (yes/no) + presence of female (yes/no)	Subject ID + Partner ID + Last call ID

Table S4.4. Summary results of the previously presented models (Table 4.1) reran on a subset of the data including only association events during which no 'travel hoo' was produced.

	Estimate	SE	LCI	UCI
LMM1b - Duration of dyadic association events				
(Best fitting model: AICc = 307)				
Production of 'hoo' (Yes)	0.25	0.05	**0.15**	**0.35**
GLMM2b - Probability of the subject terminating the association				
(Best fitting model: AICc = 126)				
Production of 'hoo' (Yes)	-22.29	4.97	**-32.02**	**-12.55**
Number of 'hoo' produced	0.69	1.35	-1.96	3.34
Subject's elo-rating	17.48	4.12	**9.40**	**25.57**
Rank difference between the subject and his partner	1.91	1.43	-0.90	4.72
GLMM3b - Probability of the subject producing a 'rest hoo'				
(Best fitting model: AICc = 167)				
Duration of dyadic association event	0.003	0.001	**0.005**	**0.013**
The partner groomed the subject (Yes)	15.270	4.563	**0.417**	**1.936**
Subject's elo-rating	-6.880	2.348	**-0.728**	**-0.043**
GLMM4b - Probability of the subject grooming his partner				
(Best fitting model: AICc = 125)				
The partner groomed the subject (Yes)	6.94	1.46	**4.08**	**9.80**
Rank difference between the subject and his partner	-1.32	0.42	**-2.14**	**-0.50**
LMM5b - Time spent in association after the last 'rest hoo' produced				
(Best fitting model: AICc = 305)				
Both individuals produced a 'hoo' (Yes)	0.332	0.211	-0.081	0.745
Caller's elo-rating	0.252	0.120	**0.017**	**0.487**

LCI: lower 95% confidence interval; UCI: upper 95% confidence. Informative variables are in bold.

Chapter 5. General discussion

Male chimpanzees are very gregarious and form strong and stable social relationships with each other (Goodall, 1986; Mitani, 2009a). These social bonds have a great influence on males' partner choice in most activities, such as grooming (Watts, 2000b, 2000a), cooperative hunting (Boesch, 1994; Hobaiter et al., 2017) and intragroup or intergroup conflicts (Gilby et al., 2013; Muller & Mitani, 2005; Samuni et al., 2021; Watts & Mitani, 2001), and thus have important consequences on their fitness (Feldblum et al., 2021; Gilby et al., 2013; Mitani, 2009b). However, how males choose their social partners and the way they establish and maintain these bonds is not fully understood yet. The goal of my PhD project was to investigate how male chimpanzees use vocal communication to manage social cohesion with other males in different contexts. I first looked at the vocal production of both short and long distance calls by male chimpanzees upon their arrival at food trees (chapter 2). I then described the vocal production of 'rest hoos', a context-specific vocalisation given during resting (chapter 3). Finally, I observed the patterns of short-term dyadic associations between males (chapter 4). This work provides crucial evidence for the use of vocal signals by male chimpanzees to navigate their intricate social world and promote cohesion.

Summary of the findings

Call production upon arrival at food trees

The goal of chapter 2 was to investigate the production of food-associated calls, i.e., rough grunts and pant-hoots, by males either joining or being joined in a food tree. I analysed whether social and ecological variables had an effect on the production of these calls. Male chimpanzees produced both close-range rough grunts and long-distance pant hoots more often when actively joining a food tree than when passively being joined (Figure 2.1) and both call rates were higher in small, rather than large, parties (Figures 2.2, 2.3, 2.4 and 2.5). Arriving males produced more pant hoots when socially important individuals (i.e. social bond partners and/or high-ranking males) were not present (Figure 2.2) whereas rough grunt production seem to be mainly driven by the subject's dominance rank in this context, with low-ranking males calling more than high-ranking ones (Figure 2.3). When being joined in a food tree, both pant hoot and rough grunts were mainly produced by low-ranking individuals upon the arrival of high-ranking males (Figures 2.4 and 2.5).

'Rest hoo' vocalisations

In chapter 3, I explored the production of context-specific rest hoo vocalisations to identify the function of this call and to determine if it was produced intentionally. I analysed whether the identity of the signaller and the composition of the audience affected call production and how these calls influenced the behaviour of both the signaller and the receivers. Males seemed to direct 'rest hoo' vocalisations at an audience, since calls were mainly produced in presence of other individuals, especially when resting in small parties (Figure 3.1) or with preferred social partners (Figure 3.3). 'Rest hoo' production appeared to prolong resting, as males rested longer when they produced (Figure 3.4) or heard this vocalisation (Figure 3.6), even more so when the subject called several times (Figure 3.5), when the resting partner responded to the call (Figure 3.4) or when the caller was a preferred social partner (Figure 3.7). Moreover, this calling behaviour was more common among low-ranking, asocial (i.e., low grooming index) males (Figure 3.2).

Male short-term association patterns

Lastly, in chapter 4, I expanded on the findings of chapter 3 by investigating how 'hoo' vocalisations and grooming affected males' dyadic association patterns. To do so, I observed how much time males spent together depending on the identity of their partners and on their vocal and tactile behaviours. Overall, associations lasted longer when a 'hoo' vocalisation (i.e., 'travel' or 'rest hoo') was produced (Figure 4.1), especially when the caller was high-ranking or when both partners called (Figure 4.5). However, high-ranking males were the ones to terminate the associations most of the time (Figure 4.2). Males produced these 'hoo' vocalisations more often when they were low-ranking or when being groomed by their partner (Figure 4.3) and callers were less likely to terminate the associations (Figure 4.2). Males groomed their association partners more often when being groomed or when their partners were higher-ranking (Figure 4.4), however, grooming interactions did not seem to directly affect the time males spent in association.

Social function of vocalisations

Dual function of food-associated calls

Chimpanzees produce two different types of food-associated calls: long-distance pant hoots, which can also be produced in a variety of other contexts, and short-distance rough grunts, which are specific to feeding contexts (Goodall, 1986; Marler & Tenaza, 1977; Reynolds & Reynolds, 1965).

In chapter 2, I found that, upon the arrival of new individuals at food trees, the production of both calls seemed to be directed towards specific individuals, therefore meeting one of the key criteria for intentionality (Townsend et al., 2017). When joining a food tree, males produced pant-hoots to recruit absent socially important individuals (i.e., high-ranking males and social bond partners) to the food tree, whereas males already present in the tree, mostly called when being joined by high-ranking males, probably to strengthen their relationships by chorusing with them. These results are in line with previous studies showing that pant-hoots play a role in regulating spatial proximity and cohesion between males (Eckhardt et al., 2015; Fedurek et al., 2014; Mitani & Nishida, 1993). Rough grunts were mostly produced by low-ranking males, whether they were joining or already present in the food tree, most likely to avoid aggression by high-ranking males. This interpretation is in line with Ischer et al. (2020)'s study, which formulated the hypothesis that these calls can be produced to manage aggressive and competitive interactions during feeding.

Feeding, and especially the arrival of new individuals during feeding, can represent a very complex social situation for male chimpanzees as these events can represent an opportunity either for cooperation and bonding (Samuni et al., 2018; Wittig et al., 2014) or for competition and aggression (Muller & Mitani, 2005). Our study showed that males produced 'pant hoots' and 'rough grunts' during these events to achieve different social functions, to regulate both competitive and cooperative interactions, thus playing an important role in managing social cohesion between males.

Hoo vocalisations and social cohesion

Chimpanzees produce three acoustically distinct 'hoo' variants in different contexts (Crockford et al., 2018): 'alert hoos' are produced intentionally to inform ignorant group members about a danger (Crockford et al., 2012,

2015; Schel, Townsend, et al., 2013), 'travel hoos' are produced to initiate joint travel with bond partners (Gruber & Zuberbühler, 2013) and 'rest hoos' are produced during resting.

I found that rest hoos seemed to be produced in an audience and in a goal directed way, to prolong resting with preferred social partners (chapter 3), thus meeting the key criteria for intentional signalling (Townsend et al., 2017). I further found that both 'travel' and 'rest hoos' did not only allow males to coordinate at the level of isolated activities (i.e., travel and rest) but these calls seemed to be part of a strategy to maintain social associations over longer periods of time, across activities (chapter 4). Overall, the three different 'hoo' variants all seem to be preferentially directed towards specific social partners (Crockford et al., 2012; Gruber & Zuberbühler, 2013) to facilitate social cohesion in different contexts. The results presented in this thesis support the theory developed by Crockford et al. (2018), stating that the three hoo variants would all signal the same underlying intention, i.e., to stay together, but should elicit different behavioural responses from receivers depending on the context of production, which would explain why the three acoustically distinct variants evolved. Upon hearing a 'travel hoo', the recipient should start traveling towards the signaller (Gruber & Zuberbühler, 2013), whereas an individual hearing a 'rest hoo' should stay resting in the proximity of the signaller (chapter 3) and 'alert hoos' should elicit a careful approach of the recipient (Crockford et al., 2015). Cooperation between chimpanzees is paramount for many activities and requires a certain degree of cohesion among them, which could have favoured the differentiation of acoustically distinct and context-specific signals, thus driving the evolution of these three 'hoo' variants.

Male social bonds

Researchers use various methods to study animal social bonds (Silk et al., 2013; Whitehead, 2008). Affiliative relationships between chimpanzees are often characterised by two key behaviours: proximity and grooming (Gilby & Wrangham, 2008; Goodall, 1986; Mitani, 2009b). Proximity generally refers to individuals who are in spatial proximity with each other, either by being in the same subgroup (i.e., party-level association), or within the same specific radius (e.g., five meter proximity), which can indicate a higher degree of tolerance than the one required for party level association alone. These patterns can, in part, result from individual social decisions, such as traveling together, and can thus reveal partner preferences (Newton-Fisher, 1999). However, they can also reflect more passive behaviours, such as the simultaneous presence at the same feeding tree, which might not indicate social affinities. On the other hand, grooming requires a higher level of effort and tolerance than proximity and has been considered a strong indicator of social bonds (Crockford et al., 2013; Fedurek & Dunbar, 2009). In some studies, the two behaviours were combined to calculate a single composite index (Heesen et al., 2021; Luef & Pika, 2017; Silk et al., 2013; Webb et al., 2017) although each behaviour might reflect distinct aspects of the bonds, hence combining them may not correctly depict the relationships between individuals (Bray & Gilby, 2020; Lehmann et al., 2007; Mitani, 2009a; Sandel et al., 2020).

In my studies, I analysed both behaviours separately and calculated two different indices to quantify male dyadic relationships (i.e., DSI_P based on proximity and DSI_G based on grooming). The results showed that the relationships established through these two behaviours revealed different patterns of social preferences depending on the context. For instance, males seemed to produce more 'pant hoots' to recruit absent preferred grooming partners upon their arrival at food trees (chapter 2), whereas they produced more 'rest hoos' when

resting with a preferred proximity partner (chapter 3). Therefore, grooming and proximity behaviours might be part of alternative social bonding strategies and thus reflect qualitative differences in relationships. These findings, in line with previous studies (Bray & Gilby, 2020; Mitani, 2009a; Samuni et al., 2018, 2021; Sandel et al., 2020), suggest that these two behaviours should be considered separately in future studies investigating social relationships.

Another issue might arise from the way grooming is measured to assess social bonds. Indeed, although grooming has been used as a measure of social bond strength, this behaviour also functions to remove parasites (Barton, 1985; Tanaka & Takefushi, 1993) and can be traded for agonistic support (Kaburu & Newton-Fisher, 2015; Schino, 2001). Hence, not every male-male grooming interaction serves a strictly social function, which could confound attempts to quantify relationship strength using grooming. Moreover, unidirectional and mutual grooming do not present the same payoffs and may thus not have the same function in social bonding. Since mutual grooming was correlated with other affiliative behaviours (i.e., tolerance and proximity), Fedurek & Dunbar (2009) proposed that the purpose of mutual grooming could be to establish and maintain social relationships. However, other studies (Allanic et al., 2020; Machanda et al., 2014) refuted these findings as they found more evidence in favour of the immediate investment hypothesis, meaning that mutual grooming would indicate a willingness to prolong the grooming bout. Nevertheless, Machanda et al. (2014) found that unidirectional grooming might play a role in social bonding, as it was preferentially directed at long-term association partners. Therefore, the functions of unidirectional and mutual grooming remain unclear and further research is needed to disentangle their role in social bonding.

If grooming and proximity behaviours are commonly used to measure social relationships, vocalisations, on the other hand, are very rarely considered (Cheney & Seyfarth, 2018). The reason behind this omission seems to be based on the assumptions that vocalisations are redundant or even irrelevant and that non-vocal behaviours are sufficient to describe the strength and quality of social bonds. Given that vocalisations are a prominent feature of chimpanzee social life, this exclusion is puzzling. Compared to grooming, vocal signals are contextually more flexible and are a less costly way to maintain social relationships (Slocombe et al., 2010). Moreover, Fedurek et al. (2013) demonstrated that specific vocal exchanges (i.e., pant hoot chorusing), but not grooming, were associated with other affiliative behaviours (i.e., coalitions and tolerated co-feeding) on a short-term basis. In line with these findings, the results of chapter 4 showed that ‘hoo’ production was correlated with longer association events, whereas grooming did not significantly predict the duration of associations. Overall, as it has been previously pointed out (Allanic et al., 2020; Fedurek et al., 2013), my findings suggest that the social indices frequently employed to examine chimpanzee social bonds (i.e., based on proximity or grooming) may not always be pertinent, particularly when studying short-term social dynamics. Instead, I propose that the production of particular vocalisations, such as ‘hoo’ calls, could be a better predictor of short-term affiliative relationships. Since it is not always possible to identify the intended recipient of a vocal signal, it may be more pertinent to take into account vocal interactions like ‘pant-hoot’ chorusing (Fedurek et al., 2013) or other calls that can elicit immediate vocal responses, such as 'hoo' vocalisations (Bouchard & Zuberbühler, 2022; Gruber & Zuberbühler, 2013).

Theoretical implications

Animals display a wide range of communication systems, which vary significantly in terms of both the type and quantity of signals they send out (McComb & Reby, 2005; Oller & Griebel, 2008; Snowdon, 2017). Phylogenetic history, sexual selection and environmental factors have long been acknowledged for their roles in influencing interspecific variation in communicative systems (Brown & Waser, 2017; Hews & Martins, 2013; Snowdon, 2004), whereas social complexity has only been identified more recently as a potential key element promoting signal diversification (Fichtel & Kappeler, 2022; Freeberg et al., 2012; Peckre et al., 2019; Sewall, 2015). According to the 'social brain hypothesis', primate complex social environment placed a high demand on their cognitive abilities, which resulted in a strong selection pressure for larger brains (Dunbar, 1998). This theory predicts that larger group sizes, which are associated with a greater diversity of relationships among individuals, requires higher signalling complexity, to be able to effectively manipulate others' behaviours as well as to detect and process the signals of others (Freeberg et al., 2012, 2019; Peckre et al., 2019). Vocal exchanges are one type of vocal interaction that has recently received a lot of attention, due to their intricate organisation, potential prosocial role, and implications for our comprehension of language evolution (Chow et al., 2015; Pougnault et al., 2022). Vocal exchanges are based on the notion of turn-taking and have been observed in various primate species (Pougnault et al., 2022). Turn-taking-based vocal exchanges are interesting to study in order to evaluate the hypothesised relationship between sociality and vocal complexity, as they play a role in within-group socio-spatial coordination (Pougnault et al., 2020). Dunbar's 'grooming-at-distance' hypothesis (Dunbar, 1996) shed light on the potential role of vocal interactions in the evolution of primate communication systems. This hypothesis suggested that gestural grooming, which plays an important role in establishing and maintaining social bonds in most primate species, (Dunbar, 1991), could be partially replaced by vocal exchanges in large social groups with enduring social bonds. Indeed, with an increase in group sizes and social networks, it would have become impossible for individuals to allocate enough time to groom all their partners, which would have favoured the development of vocal exchanges. In line with this theory, studies on several primate species have found that vocal exchanges happened most often between non-randomly chosen interlocutors, based on their affiliative relationships (Arlet et al., 2015; Briseno-Jaramillo et al., 2018; Kulahci et al., 2015; Levréro et al., 2019). The data presented in this thesis show that 'hoo' vocalisations could elicit immediate vocal responses and could thus be part of vocal exchanges. These vocal exchanges seemed to have a cohesive function, as they prolonged resting bouts (chapter 3) and association events (chapter 4). Even though I did not specifically investigate how social relationships affected the patterns of vocal exchanges, I found that, globally, 'hoo' vocalisations produced during resting bouts were preferentially produced towards preferred social partners (chapter 3). Overall, these results highlight the importance of considering social factors when studying the evolution and development of vocal exchanges and provide strong support for the 'grooming-at-distance' hypothesis. As Pougnault et al. (2022) recently pointed out, vocal interaction patterns are a promising field of research, which will help us better understand how sociality has shaped the evolution of communication.

Moreover, these findings reveal that 'hoo' vocalisations may actually be produced to influence others and even to seek a shared commitment to remain together rather than simply indicating the signaller's motivation to rest or travel independently of others' activities. Dyadic associations provide the basis for various joint action, which require males to coordinate their individual behaviours and intentions. To do so, males need to be able to predict

others' behaviour and potential partners should thus communicate to reach a mutual understanding that they will engage and commit to a specific joint action (Clark, 2006). In humans, joint action is usually composed of three distinct phases: the entry phase (to establish the joint commitment), the main body (the action itself) and the exit phase (to disengage the partner) (Clark, 1996). Recent studies have suggested that this process is not unique to humans but is also present in apes (Genty et al., 2020; Heesen et al., 2020, 2021). While these studies have focused on grooming and play interactions, we suggest here that dyadic associations might provide a bedrock from which male chimpanzees can engage in joint actions. Vocal exchanges of 'hoo' vocalisations might indeed operate at the underlying motivational level, by creating a joint commitment to engage or to maintain an association. Humans not only communicate to initiate and maintain joint actions, but also to dissolve them and future studies should investigate if males communicate, vocally or with other modes, forthcoming disengagements from a dyadic association.

The results presented in this thesis also contributed to the corpus of evidence that chimpanzees are able to produce vocalisations intentionally, as call production seemed to be audience and goal-directed (Townsend et al., 2017). However, recent studies pointed out several issues in the way intentional communication is operationalised and suggested that research on intentionality should adopt a multi-modal approach and focus on communicative interactions by considering the recipient's reactions and the signaller's response (Graham et al., 2019; Rodrigues & Fröhlich, 2021; Sievers, 2022; Sievers et al., 2017, 2018). Indeed, for the recipient to be able to respond to the signaller's behaviour in a flexible manner, the recipient needs to be aware of the intentional aspect of this behaviour. As the recipient's reactions are anticipated to induce changes in the signaller's behaviour, this may result in a turn-taking sequence of communicative and non-communicative behaviours. This should be especially relevant in cases where the signaller's and the recipient's motivations diverge (Rodrigues & Fröhlich, 2021; Sievers et al., 2017). For instance, Sievers et al. (2018) investigated communicative disagreement during travel initiations in chimpanzees and discovered substantial evidence of back-and-forth negotiations as attempts to win the other individual over. These interactions might reflect the basic aspects of human conversations in terms of their turn-taking structure and their overt nature. Similarly, when investigating the production of 'rest hoos' (chapter 3), I recorded several instances of individuals producing calls in response to other group members traveling away and this vocal behaviour was either successful (i.e., targeted individuals then stopped travelling and joined the signaller to rest) or ineffective (i.e., targeted individuals kept traveling), which could constitute a case of disagreement between the interactors. Together, these results show that resting events seem to provide an ideal setting for the study of communicative disagreement, as individuals seem to communicate to convince others both to start traveling with them or to stay and rest with them. In agreement with Sievers (2022), I suggest that communicative disagreements are a clear demonstration of overt communication, where the intentional nature of a communicative behaviour could be established through repeated back-and-forth interactions, and empirical studies should thus adopt interactional approaches to investigate intentional communication.

Limitations and future directions

The studies presented in this thesis offer new insights into the function of vocal communication in chimpanzees, specifically in relation to social bonding. Nonetheless, they present some limitations that need to be highlighted, but also bring new questions that offer promising research avenues for future studies.

One clear limitation is that the studies focused only on adult males. Although male chimpanzees are more vocal and more gregarious than females, which made them better candidates to study vocal production and social cohesion, it would be interesting to know how females use these vocalisations and if they have similar patterns of production. Indeed, the social dynamics and the stakes of competition and cooperation are very different in females than in males and their vocal behaviour and association patterns might differ accordingly. Moreover, data was only collected on the Sonso community and future studies should be conducted in different field sites to adopt a comparative approach and determine if and how patterns of association and call production differ between chimpanzee communities.

Additionally, I found some evidence that male chimpanzees seem to produce 'rest hoos', 'pant hoots' and 'rough grunts' in an audience directed way and towards specific goals, thus supporting the idea that they can have voluntary control of their vocal production and that chimpanzees might produce these calls intentionally (Crockford et al., 2012; Gruber & Zuberbühler, 2013; Schel, Machanda, et al., 2013). I based my approach on observational data and, even though it provided crucial knowledge on vocal production patterns, experimental studies are now needed. For instance, playback studies could be used to further investigate the behavioural responses to the calls studied here and develop a more comprehensive understanding of their function.

Previous studies have shown that pant hoots can be produced in chorus with a pant hoot initiated by another individual (Arcadi, 1996) and these choruses might be a low-cost bonding behaviour to maintain social relationships (Fedurek et al., 2013; Mitani & Brandt, 1994; Mitani & Gros-Louis, 1998). The results of chapter 2 showed that, in a feeding context, 'pant hoots' seemed to be produced to help manage social cohesion with preferred social partners and might thus play a role in social bonding between males, however I did not take into account whether the calls were produced in response or in chorus with other calls. Studies investigating pant hoot choruses, and pant hoot response patterns in general, during feeding are necessary.

The other food-associated call studied in chapter 2, i.e., rough grunts, seem to play a role in managing competitive interactions during feeding (chapter 2). These results are in line with a previous study (Ischer et al., 2020) but further research is needed to investigate the relationship between calling and aggressive interactions as to confirm, or refute, these hypotheses. Future studies should also take into account differences in competitive pressures by investigating the effect of party size as well as fruit availability or tree crown size. Moreover, a recent study has shown that rough grunt and pant hoots could be produced in combination (Leroux et al., 2021) and further research is needed to determine the function of these call combinations and to disentangle the meaning of the calls when combined or produced in isolation. More broadly, call combinations should be taken into consideration when studying the function of chimpanzee vocalisations.

Overall, across the different studies presented in this thesis, I showed that male chimpanzees used vocalisations to manage social cohesion in different contexts. However, during the majority of the events recorded in these studies, whether they were resting bouts, arrival at food trees or association events, no vocalisations were produced. This would suggest that chimpanzees might use other signals not considered in these studies to regulate proximity with their social partners. Indeed, gestural and facial signals play an important role in chimpanzee communication and they might also be used to manage social cohesion, especially when in close proximity. Furthermore, the results of chapter 3 and 4 reveal an interesting relationship between vocal and tactile

behaviours, which highlights the importance of adopting a multimodal approach when studying communication (Fröhlich & van Schaik, 2018; Liebal et al., 2013; Slocombe et al., 2011). Studies investigating all communication channels, including follow-up behaviours (e.g., audience checking), are necessary to acquire a more complete picture of how chimpanzees regulate social distance.

In conclusion, by providing detailed observations and analyses of the use of vocalisations to manage social cohesion in chimpanzees, these results help to better understand the communication system of our closest relatives and offer interesting avenues for future research. The studies conducted as part of this thesis show that vocal communication seems to achieve various complex social functions, such as managing social cohesion and mediating both cooperative and competitive interactions, and thus plays a key role in chimpanzee fission-fusion societies. Our findings also contribute to the body of research showing that chimpanzee vocal production can be driven by intentional cognitive processes. Finally, my results suggest that vocal communication might be an alternative strategy to tactile-based social bonding and thus provide more evidence that the use of vocalisations to manage social bonding and cohesion has emerged in highly social species. By extending such work beyond chimpanzees and even primates, we could gain a better understanding of how sociality has shaped the evolution of animal communicative systems.

References

Allanic, M., Hayashi, M., & Matsuzawa, T. (2020). Investigating the Function of Mutual Grooming in Captive Bonobos (***Pan paniscus***) and Chimpanzees (***Pan troglodytes***). *Folia Primatologica*, *91*(5), 481–494. https://doi.org/10.1159/000506308

Arcadi, A. C. (1996). Phrase structure of wild chimpanzee pant hoots: Patterns of production and interpopulation variability. *American Journal of Primatology*, *39*(3), 159–178. https://doi.org/10.1002/(SICI)1098-2345(1996)39:3<159::AID-AJP2>3.0.CO;2-Y

Arlet, M., Jubin, R., Masataka, N., & Lemasson, A. (2015). Grooming-at-a-distance by exchanging calls in non-human primates. *Biology Letters*, *11*(10), 20150711. https://doi.org/10.1098/rsbl.2015.0711

Barton, R. (1985). Grooming site preferences in primates and their functional implications. *International Journal of Primatology*, *6*(5), 519–532. https://doi.org/10.1007/BF02735574

Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, *48*(3), 653–667. https://doi.org/10.1006/anbe.1994.1285

Bouchard, A., & Zuberbühler, K. (2022). An intentional cohesion call in male chimpanzees of Budongo Forest. *Animal Cognition*, *0123456789*. https://doi.org/10.1007/s10071-022-01597-6

Bray, J., & Gilby, I. C. (2020). Social relationships among adult male chimpanzees (Pan troglodytes schweinfurthii): variation in the strength and quality of social bonds. *Behavioral Ecology and Sociobiology*, *74*(9), 112. https://doi.org/10.1007/s00265-020-02892-3

Briseno-Jaramillo, M., Ramos-Fernández, G., Palacios-Romo, T. M., Sosa-López, J. R., & Lemasson, A. (2018). Age and social affinity effects on contact call interactions in free-ranging spider monkeys. *Behavioral Ecology and Sociobiology*, *72*(12), 192. https://doi.org/10.1007/s00265-018-2615-2

Brown, C. H., & Waser, P. M. (2017). Primate habitat acoustics. In *Primate hearing and communication* (pp. 79–107). Springer, Cham.

Cheney, D. L., & Seyfarth, R. M. (2018). Flexible usage and social function in primate vocalizations. *Proceedings of the National Academy of Sciences*, 201717572. https://doi.org/10.1073/pnas.1717572115

Chow, C. P., Mitchell, J. F., & Miller, C. T. (2015). Vocal turn-taking in a non-human primate is learned during ontogeny. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1807), 20150069. https://doi.org/10.1098/rspb.2015.0069

Clark, H. H. (1996). *Using Language*. Cambridge University Press.

Clark, H. H. (2006). Social Actions , Social Commitments. In N. J. Enfield & S. C. Levinson (Eds.), *Roots of Human Sociality: Culture, Cognition and Interaction* (pp. 126–150). Berg.

Crockford, C., Gruber, T., & Zuberbühler, K. (2018). Chimpanzee quiet hoo variants differ according to context. *Royal Society Open Science*, *5*(5), 172066. https://doi.org/10.1098/rsos.172066

Crockford, C., Wittig, R. M., Langergraber, K. E., Ziegler, T. E., Zuberbühler, K., & 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. https://doi.org/10.1098/rspb.2012.2765

Crockford, C., Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology*, *22*(2), 142–146. https://doi.org/10.1016/j.cub.2011.11.053

Crockford, C., Wittig, R. M., & Zuberbühler, K. (2015). An intentional vocalization draws others' attention: A playback experiment with wild chimpanzees. *Animal Cognition*, *18*(3), 581–591.

https://doi.org/10.1007/s10071-014-0827-z

Dunbar, R. I. M. (1991). Functional Significance of Social Grooming in Primates. *Folia Primatologica*, *57*(3), 121–131. https://doi.org/10.1159/000156574

Dunbar, R. I. M. (1996). *Grooming, gossip, and the evolution of language* (Harvard University Press. (Ed.)).

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

Eckhardt, N., Polansky, L., & Boesch, C. (2015). Spatial cohesion of adult male chimpanzees (Pan troglodytes verus) in Taï National Park, Côte d'Ivoire. *American Journal of Primatology*, *77*(2), 125–134. https://doi.org/10.1002/ajp.22316

Fedurek, P., Donnellan, E., & Slocombe, K. E. (2014). Social and ecological correlates of long-distance pant hoot calls in male chimpanzees. *Behavioral Ecology and Sociobiology*, *68*(8), 1345–1355. https://doi.org/10.1007/s00265-014-1745-4

Fedurek, P., & Dunbar, R. I. M. (2009). What Does Mutual Grooming Tell Us About Why Chimpanzees Groom? *Ethology*, *115*(6), 566–575. https://doi.org/10.1111/j.1439-0310.2009.01637.x

Fedurek, P., Machanda, Z. P., Schel, A. M., & Slocombe, K. E. (2013). Pant hoot chorusing and social bonds in male chimpanzees. *Animal Behaviour*, *86*(1), 189–196. https://doi.org/10.1016/j.anbehav.2013.05.010

Feldblum, J. T., Krupenye, C., Bray, J., Pusey, A. E., & Gilby, I. C. (2021). Social bonds provide multiple pathways to reproductive success in wild male chimpanzees. *IScience*, *24*(8), 102864. https://doi.org/10.1016/j.isci.2021.102864

Fichtel, C., & Kappeler, P. M. (2022). Coevolution of social and communicative complexity in lemurs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*(1860). https://doi.org/10.1098/rstb.2021.0297

Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1597), 1785–1801. https://doi.org/10.1098/rstb.2011.0213

Freeberg, T. M., Gentry, K. E., Sieving, K. E., & Lucas, J. R. (2019). On understanding the nature and evolution of social cognition: a need for the study of communication. *Animal Behaviour*, *155*, 279–286. https://doi.org/10.1016/j.anbehav.2019.04.014

Fröhlich, M., & van Schaik, C. P. (2018). The function of primate multimodal communication. *Animal Cognition*, *21*(5), 619–629. https://doi.org/10.1007/s10071-018-1197-8

Genty, E., Heesen, R., Guéry, J.-P., Rossano, F., Zuberbühler, K., & Bangerter, A. (2020). How apes get into and out of joint actions. *Interaction Studies. Social Behaviour and Communication in Biological and Artificial Systems*, *21*(3), 353–386. https://doi.org/10.1075/is.18048.gen

Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, *67*(3), 373–381. https://doi.org/10.1007/s00265-012-1457-6

Gilby, I. C., & Wrangham, R. W. (2008). Association patterns among wild chimpanzees (Pan troglodytes schweinfurthii) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology*, *62*(11), 1831–1842. https://doi.org/10.1007/s00265-008-0612-6

Goodall, J. (1986). *The chimpanzees of Gombe: patterns of behavior*. Harvard University Press.

Graham, K. E., Wilke, C., Lahiff, N. J., & Slocombe, K. E. (2019). Scratching beneath the surface: intentionality in great ape signal production. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1789), 20180403. https://doi.org/10.1098/rstb.2018.0403

Gruber, T., & Zuberbühler, K. (2013). Vocal Recruitment for Joint Travel in Wild Chimpanzees. *PLoS ONE*, *8*(9), e76073. https://doi.org/10.1371/journal.pone.0076073

Heesen, R., Bangerter, A., Zuberbühler, K., Iglesias, K., Neumann, C., Pajot, A., Perrenoud, L., Guéry, J.-P., Rossano, F., & Genty, E. (2021). Assessing joint commitment as a process in great apes. *IScience*, *24*(8), 102872. https://doi.org/10.1016/j.isci.2021.102872

Heesen, R., Bangerter, A., Zuberbühler, K., Rossano, F., Iglesias, K., Guéry, J.-P., & Genty, E. (2020). Bonobos engage in joint commitment. *Science Advances*, *6*(51). https://doi.org/10.1126/sciadv.abd1306

Hews, D. K., & Martins, E. P. (2013). Visual and chemical signals of social communication: providing the link to habitat and environment. In W. I. Lutterschmidt (Ed.), *Reptiles in research* (pp. 111–141). Nova Science Publishers, Inc. http://link.springer.com/10.1007/s00265-011-1150-1

Hobaiter, C., Samuni, L., Mullins, C., Akankwasa, W. J., & Zuberbühler, K. (2017). Variation in hunting behaviour in neighbouring chimpanzee communities in the Budongo forest, Uganda. *PLOS ONE*, *12*(6), e0178065. https://doi.org/10.1371/journal.pone.0178065

Ischer, G., Zuberbühler, K., & Fedurek, P. (2020). The relationship between food calling and agonistic behaviour in wild chimpanzees. *Behavioural Processes*, *178*(May), 104182. https://doi.org/10.1016/j.beproc.2020.104182

Kaburu, S. S. K., & Newton-Fisher, N. E. (2015). Egalitarian despots: hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, Pan troglodytes. *Animal Behaviour*, *99*, 61–71. https://doi.org/10.1016/j.anbehav.2014.10.018

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

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour*, *74*(6), 1617–1629. https://doi.org/10.1016/j.anbehav.2006.10.025

Leroux, M., Bosshard, A. B., Chandia, B., Manser, A., Zuberbühler, K., & Townsend, S. W. (2021). Chimpanzees combine pant hoots with food calls into larger structures. *Animal Behaviour*, *179*, 41–50. https://doi.org/10.1016/j.anbehav.2021.06.026

Levréro, F., Touitou, S., Frédet, J., Nairaud, B., Guéry, J.-P., & Lemasson, A. (2019). Social bonding drives vocal exchanges in Bonobos. *Scientific Reports*, *9*(1), 711. https://doi.org/10.1038/s41598-018-36024-9

Liebal, K., Waller, B. M., Burrows, A. M., & Slocombe, K. E. (2013). Primate communication: a multimodal approach. In *Evolutionary psychology : an international journal of evolutionary approaches to psychology and behavior* (Vol. 11, Issue 3). https://doi.org/10.1017/CBO9781139018111.010

Luef, E. M., & Pika, S. (2017). Reciprocal greeting in chimpanzees (Pan troglodytes) at the Ngogo community. *Journal of Neurolinguistics*, *43*, 263–273. https://doi.org/10.1016/j.jneuroling.2016.11.002

Machanda, Z. P., Gilby, I. C., & Wrangham, R. W. (2014). Mutual grooming among adult male chimpanzees: the immediate investment hypothesis. *Animal Behaviour*, *87*(C), 165–174. https://doi.org/10.1016/j.anbehav.2013.10.028

Marler, P., & Tenaza, R. (1977). Signaling behavior of apes with special reference to vocalizations. In *How*

Animals Communicate (pp. 965–1033). Indiana University Press.

McComb, K., & Reby, D. (2005). Vocal communication networks in large terrestrial mammals. In *Animal Communication Networks* (pp. 372–389). Cambridge University Press. https://doi.org/10.1017/CBO9780511610363.021

Mitani, J. C. (2009a). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, *77*(3), 633–640. https://doi.org/10.1016/j.anbehav.2008.11.021

Mitani, J. C. (2009b). Cooperation and competition in chimpanzees: Current understanding and future challenges. *Evolutionary Anthropology: Issues, News, and Reviews*, *18*(5), 215–227. https://doi.org/10.1002/evan.20229

Mitani, J. C., & Brandt, K. L. (1994). Social Factors Influence the Acoustic Variability in the Long-distance Calls of Male Chimpanzees. *Ethology*, *96*(3), 233–252. https://doi.org/10.1111/j.1439-0310.1994.tb01012.x

Mitani, J. C., & Gros-Louis, J. (1998). Chorusing and Call Convergence in Chimpanzees: Tests of Three Hypotheses. *Behaviour*, *135*(8), 1041–1064. https://doi.org/10.1163/156853998792913483

Mitani, J. C., & Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. *Animal Behaviour*, *45*(4), 735–746. https://doi.org/10.1006/anbe.1993.1088

Muller, M. N., & Mitani, J. C. (2005). Conflict and Cooperation in Wild Chimpanzees. In *Advances in the Study of Behavior* (Vol. 35, pp. 275–331). https://doi.org/10.1016/S0065-3454(05)35007-8

Newton-Fisher, N. E. (1999). Association by male chimpanzees: a social tactic? Behaviour. *Behaviour*, *136*(6), 705–730. https://doi.org/10.1163/156853999501531

Oller, D. K., & Griebel, U. (Eds.). (2008). *Evolution of Communicative Flexibility*. The MIT Press. https://doi.org/10.7551/mitpress/9780262151214.001.0001

Peckre, L., Kappeler, P. M., & Fichtel, C. (2019). Clarifying and expanding the social complexity hypothesis for communicative complexity. *Behavioral Ecology and Sociobiology*, *73*(1), 11. https://doi.org/10.1007/s00265-018-2605-4

Pougnault, L., Levréro, F., & Lemasson, A. (2020). Conversation among primate species. In N. Masataka (Ed.), *The Origins of Language Revisited* (pp. 73–96). Springer.

Pougnault, L., Levréro, F., Leroux, M., Paulet, J., Bombani, P., Dentressangle, F., Deruti, L., Mulot, B., & Lemasson, A. (2022). Social pressure drives "conversational rules" in great apes. *Biological Reviews*, *97*(2), 749–765. https://doi.org/10.1111/brv.12821

Reynolds, V., & Reynolds, R. (1965). Chimpanzees of the Budongo Forest. In *Primate behavior: field studies of monkeys and apes* (pp. 368–424). Rinehart & Winston.

Rodrigues, E. D., & Fröhlich, M. (2021). Operationalizing Intentionality in Primate Communication: Social and Ecological Considerations. *International Journal of Primatology*. https://doi.org/10.1007/s10764-021-00248-w

Samuni, L., Crockford, C., & Wittig, R. M. (2021). Group-level cooperation in chimpanzees is shaped by strong social ties. *Nature Communications*, *12*(1), 539. https://doi.org/10.1038/s41467-020-20709-9

Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R. M., & Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1888). https://doi.org/10.1098/rspb.2018.1643

Sandel, A. A., Langergraber, K. E., & Mitani, J. C. (2020). Adolescent male chimpanzees (Pan troglodytes) form social bonds with their brothers and others during the transition to adulthood. *American Journal of Primatology*, *82*(1), 1–12. https://doi.org/10.1002/ajp.23091

Schel, A. M., Machanda, Z. P., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour*, *86*(5), 955–965. https://doi.org/10.1016/j.anbehav.2013.08.013

Schel, A. M., Townsend, S. W., Machanda, Z. P., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee Alarm Call Production Meets Key Criteria for Intentionality. *PLoS ONE*, *8*(10), e76674. https://doi.org/10.1371/journal.pone.0076674

Schino, G. (2001). Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour*, *62*(2), 265–271. https://doi.org/10.1006/anbe.2001.1750

Sewall, K. B. (2015). Social Complexity as a Driver of Communication and Cognition. *Integrative and Comparative Biology*, *55*(3), 384–395. https://doi.org/10.1093/icb/icv064

Sievers, C. (2022). Interaction and ostension: the myth of 4th-order intentionality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*(1859), 4–6. https://doi.org/10.1098/rstb.2021.0105

Sievers, C., Gruber, T., & Zuberbuhler, K. (2018). The Informative Value Of Communicator Disagreement in Great Apes For The Study Of The Evolution Of Human Intentional Communication. *Proceedings of the 12th International Conference on the Evolution of Language (Evolang12)*, *May*. https://doi.org/10.12775/3991-1.112

Sievers, C., Wild, M., & Gruber, T. (2017). Intentionality and Flexibility in Animal Communication. In *The Routledge Handbook of Philosophy of Animal Minds* (pp. 333–342). Routledge. https://doi.org/10.4324/9781315742250-32

Silk, J. B., Cheney, D. L., & Seyfarth, R. M. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology: Issues, News, and Reviews*, *22*(5), 213–225. https://doi.org/10.1002/evan.21367

Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., Squibbs, P., & Zuberbühler, K. (2010). Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behavioral Ecology and Sociobiology*, *64*(12), 1959–1966. https://doi.org/10.1007/s00265-010-1006-0

Slocombe, K. E., Waller, B. M., & Liebal, K. (2011). The language void: the need for multimodality in primate communication research. *Animal Behaviour*, *81*(5), 919–924. https://doi.org/10.1016/j.anbehav.2011.02.002

Snowdon, C. T. (2004). Sexual selection and communication. In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp. 57–70). https://onlinelibrary.wiley.com/doi/10.1002/evan.10023

Snowdon, C. T. (2017). Vocal communication in family-living and pair-bonded primates. In *Primate hearing and communication* (pp. 141–174). Springer, Cham.

Tanaka, I., & Takefushi, H. (1993). Elimination of External Parasites(Lice) Is the Primary Function of Grooming in Free-ranging Japanese Macaques. *Anthropological Science*, *101*(2), 187–193. https://doi.org/10.1537/ase.101.187

Townsend, S. W., Koski, S. E., Byrne, R. W., Slocombe, K. E., Bickel, B., Boeckle, M., Braga Goncalves, I., Burkart, J. M., Flower, T., Gaunet, F., Glock, H. J., Gruber, T., Jansen, D. A. W. A. M., Liebal, K., Linke, A., Miklósi, Á., Moore, R., van Schaik, C. P., Stoll, S., … Manser, M. B. (2017). Exorcising Grice's ghost: an empirical approach to studying intentional communication in animals. *Biological Reviews*, *92*(3), 1427–1433. https://doi.org/10.1111/brv.12289

Watts, D. P. (2000a). Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. *International Journal of Primatology*, *21*(2), 189–210. https://doi.org/10.1023/A:1005469302911

Watts, D. P. (2000b). Grooming between male chimpanzees at Ngogo, Kibale National Park. II. Influence of male rank and possible competition for partners. *International Journal of Primatology*, *21*(2), 211–238. https://doi.org/10.1023/A:1005421419749

Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, *138*(3), 299–327. https://doi.org/10.1163/15685390152032488

Webb, C. E., Romero, T., Franks, B., & De Waal, F. B. M. (2017). Long-term consistency in chimpanzee consolation behaviour reflects empathetic personalities. *Nature Communications*, *8*(1), 1–8. https://doi.org/10.1038/s41467-017-00360-7

Whitehead, H. (2008). *Analyzing animal societies: quantitative methods for vertebrate social analysis*. University ofChicago Press, Chicago. http://choicereviews.org/review/10.5860/CHOICE.46-5619

Wittig, R. M., Crockford, C., Deschner, T., Langergraber, K. E., Ziegler, T. E., & Zuberbühler, K. (2014). Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1778), 20133096. https://doi.org/10.1098/rspb.2013.3096