Try a little tenderness: Investigating the evolution of empathy through comparing consolation and reassurance in our closest relatives, bonobos (Pan paniscus) and chimpanzees (Pan troglodytes)

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How to cite:

BROOKER, JAKE,STEPHEN (2023) *Try a little tenderness: Investigating the evolution of empathy through comparing consolation and reassurance in our closest relatives, bonobos (Pan paniscus) and chimpanzees (Pan troglodytes)*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/14972/

Try a little tenderness:

Investigating the evolution of empathy through comparing consolation and reassurance in our closest relatives, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*)

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Thesis submitted to Durham University for the Degree of
Doctor in Philosophy

Research conducted with the Department of Psychology

December 2022

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Preface & Acknowledgments

"A man is the product of all the people that he ever loved."—Jason Isbell

I've been fortunate enough in my 29 and a bit years to encounter some of the loveliest and kindest people around the world. They include people I met at border crossings in the Middle East, in miombo woodland in Africa, and at school in Barking and Dagenham.

The journey towards this thesis technically started in 2014 when I met Tatyana Humle and enrolled on a Master's Degree at the University of Kent to embark on a new path. Thanks to Tatyana, Sarah Johns, Brandon Wheeler, and Donna Kean for the company and encouragement during this phase. After the Master's, there was quite a gap to the next chapter. I spent some time exploring alone and with friends and working a nice, comfortable job. I'm forever grateful to the good people at DV247 Music Store—particularly Dave, James, Andy, and Dan—including for their support when I chose to move on in December 2017.

I knew that choice would unsettle most, if not all, of the safe harbour I had formed in the south of England. Either way, I bought a new Tilley hat and some rubber boots and disappeared into the savannah-forest mosaic of Comoé National Park in Côte d'Ivoire to aid habituation and research of wild chimps (a lifelong dream of mine), who were once thought to be extinct in this region. Thank you to Juan for teaching me and trusting me with managing his project for a period. Thanks too to Janne and Wender for making the evenings pleasant with their friendly company and dark humour. Also, thank you to the Miller family and Faye for being part of the journey.

Around this time, I started reading about humanism and empathy. I discovered the work of Zanna Clay, Christine Webb, and Frans de Waal; three leading experts in empathy. I reached out to Zanna and after some back and forth over almost a year, I was accepted to join their Templeton-funded project for my PhD. Thank you to Frans for the help and fascinating insights. Thank you to Christine for the reassurance, supervision, and welcoming me to Cambridge and Harvard just before the world went mad. And thank you to Edwin van Leeuwen for showing me the ropes in Zambia and collaborating on some fascinating projects—I can't wait for the next one to commence in 2023! Thank you to Templeton World Charity Foundation for the funding behind my research.

"*It's a bit of a slog*." I heard that a few times, from various people and in various forms over the last four years. I knew the PhD journey would be long and arduous. Maybe it shouldn't be that way, but I was desperate to be challenged again—and that certainly worked out. I signed up to the academic test, but the journey of social connections and self-discovery, and ultimately acceptance, was a welcome surprise. Thank you to all that came along for the ride.

The most crucial of those is my incredible supervisor, mentor, and friend, Zanna Clay. I cannot thank Zanna enough for placing so much faith, trust, and patience into me on this project. I started as Zanna's second PhD student and have seen the C4D lab grow exponentially over four years. We've both been on a journey of development together during this time, albeit at different stages, and seen each other grow into our roles. I could not have asked for a better and more inspirational mentor during my journey. I'm ecstatic that I will stay in Durham for at least two more years as a postdoctoral researcher to continue our collaboration and see what is next for the lab!

I must thank other past and present members of the C4D lab, including Carlo Vreden, Raphaela Heesen, and Chris Krupenye. Thank you to Georgia Sandars and Emma Doherty for their company during our shared trip to Chimfunshi. A huge thanks also to Stephanie Kordon for collecting the bonobo data in Lola, coding a lot of it, and being the second, more talented half of Pan Pals, the best acoustic duo in Durham.

During my PhD, I was lucky enough to spend eight cumulative months at Chimfunshi Wildlife Orphanage in Zambia, collecting data on chimpanzees in 2019 and 2021. I arrived for my first field season feeling like a bonafide imposter, but the wonderful staff, researchers, and volunteers quickly made it a genuine home. Special thanks to Innocent, Thalita, Thom, Lameck, Dennis, Sylvia, Sara, Rosie, Mwaona, Ana, Zeus, Skinny, The Bears, and the late Sheila Siddle; for all she did for the chimps and welcoming me into her home. Thank you to Hélène, Nora, Yana, Sanne, and Chloé for swinging/coding the peanut swing. And, though I never made it there physically, I'd like to thank the good people at Lola ya Bonobo Sanctuary in the DRC, especially Heritier Izansone for his contribution to this thesis. I hope I can one day visit or work at Lola in person!

I spent the rest of my time in Durham experiencing life pre-pandemic, followed by a few lockdowns and the subsequent slow progression towards normality. Thank you to: Craig Withers, my musical soulmate and friend after meeting on just my second day in Durham; Ben Walton for his companionship, the fancy meals, and pub quizzes; Alastair Stewart and Anna Kranz for being lovely housemates during a crazy time for us all; Siobhán McAteer, my Office Wife, for the statistical insights, baking experiments, and many runs; Connor Armstrong for tolerating my nonsense and the fun times we had in Ustinov together; Diana Martinez-Trejo for being a great friend and source of many laughs; Josh and The Observatories, Brian and Los Aluxes del Norte, and every other musician I've had the pleasure of playing and performing with over the past four years; Lennie and Kristine for the many pints of Guinness and late-night pool matches we shared; Matt, Jess, and Jack for the much-needed distractions; Rafa, and welcome to Durham; Ariane (Barry), my boulder buddy; Chris and Sue for the part-time employment during my continuation; and Julia Clay for help with proofreading. A special thanks also to Diane, for helping me make this beautiful city a home from my first day.

As my career changes paths and people come and go, I've known and grown with some wonderful characters over more than 25 years in some cases. They are the source of some of my most treasured memories, even if they still think I'll be a student forever. Unfortunately for them, as I submit this, I am officially no longer a student, but I'm sure the jokes will continue. I'm so proud of these friends and the paths they've taken in their own lives and grateful that we keep this ever-strengthening network together. Thank you to Tommy and Connor for always being there and, despite growing, never changing. Special love and thanks to Mullen, Martina, Charlie, Kieran, Simmons, Langan, Danny, Duhig, Trevor, Amy, David, Ian, Emma, Becki, Doige, Paul, Josh, and Irwin. Thanks also to Frank Marsters for inspiring me to not just sit around and wait for the lights to go green.

I met Zoë Goldsborough at Ndola Airport as we both arrived in Zambia to start five months living together in the bush, and I don't think either of us quite expected that two years later I'd make a 22-day journey to her wedding, but here we are. Beyond our academic collaboration, the many non-work chats and occasional times we've been able to hang out in person since leaving Zambia have been incredibly vital. Thank you, Zoë, my Research Wife.

The last friend I must acknowledge is Cameron Hollis. The near-daily phone calls during the first lockdowns and weekly Zoom gatherings with our fellow degenerates made a rough time much easier. Regardless of the distance, Cam's unwavering support and dedication to winding me up helped me push to the end. Cheers for always listening.

Thank you to the Brookers, Lawrences, and Hollingsworths for their love and quirks. Extra thanks to Dean and Ellen for employing me before I moved to Durham! Thank you to my mum, my biggest and most important cheerleader, who apparently always suspected I would become a doctor (but I don't think she expected a comparative psychologist…); my dad, who never questions but always supports the strange directions I have taken over the years; Colette and the Brewsters, who make our circle more complete; and to Alex, for challenging me, encouraging me, but never once doubting me.

Finally, during my PhD I came to know over 100 chimpanzees at Chimfunshi Wildlife Orphanage. Each chimp has their own personality and story and learning each was a pleasure. For the most part, to them, I was nothing significant—just a keen, scruffy tourist with a silly hat who liked to be there early and late. To me, though, they are a constant reminder of why I continue to choose this path. If I could thank any individually, it would be Brian—for always keeping me on my toes.

This thesis is dedicated to three people we lost along the way:

To Margery Hollingsworth, who taught me about empathy and tolerance when I was a child;

to Anna Karen, my first mentor, who showed me that there is life outside of my shell;

and to Joseph Irwin, who always reminded me how important it is to have fun on the journey.

Abstract

Empathy—the ability to share, understand, and respond to the emotions and states of others—is often considered a cornerstone of the human experience. As our closest living relatives, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) are often used as models for the evolution of human behaviour, and comparative research often seeks to identify interspecific variation. However, comparisons often consist of single groups of small captive populations, and recent investigations have indicated substantial within-species differences in bonobo and chimpanzee cognitive and emotional behaviour. In this thesis, to contribute to the investigation of empathy's evolution, I provide the first comprehensive systematic comparison of sanctuary-living groups of bonobos and chimpanzees regarding their use of reassuring body contact during two periods of social tension: post-conflict consolation and pre-feeding affiliation. Using a combination of naturalistic observations and an experimental method, I show the *Pan* apes share similar tendencies to engage in consolation and pre-feeding reassurance, including the use of genital contacts during social tension. Instead, considerable variation lies at the individual, dyadic, and group levels. Two bonobo communities varied in consolatory tendencies, and whilst younger individuals offered consolation more than older individuals, young male chimpanzees consoled more than other chimpanzees. Results also indicate that contact affiliation around feeding is associated with reduced conflict and promotes an individual's access to a competitive feeding zone. Furthermore, contact affiliation between socially central sex pairings in each species—bonobo females, and chimpanzee males—were associated with group-level social tolerance, indicating that reinforced affiliative bonds between dominant individuals in both species promotes more crowded, peaceful feeding. My findings support considering individual variation and multiple groups of diverse populations when making species-level comparisons in ethology. A bottom-up approach assessing species- and group-specific abilities could reveal the ancient ancestry of empathy, and what factors promote or inhibit its emergence.

“Piglet sidled up to Pooh from behind.

"Pooh!" he whispered.

"Yes, Piglet?"

"Nothing," said Piglet, taking Pooh's paw. "I just wanted to be sure of you."

— A.A. Milne, The House at Pooh Corner

Glossary of terms

Term	Definition	Behaviour
Altruism	Behaviour that increases the recipient's fitness at a cost to the performers.	de Waal (2008)
Celebration	Behaviours associated with positive social events, such as mating, successful cooperation, or arriving at a food source.	de Waal (1992)
Consolation	Spontaneous offering of reassuring body contact from an uninvolved bystander towards an individual who is distressed due to conflict or other circumstances.	de Waal & Aureli (1996)
Empathy	A complex psychological process, involving both cognitive and emotional components, that facilitates the ability to understand and share the emotions and states of others.	Cuff et al. (2016)
Pre-feeding affiliation	Affiliative behaviours that occur prior to feeding, such as grooming and huddling.	Goodall (1986)
Prosociality	Voluntary behaviour intended to benefit another individual or group.	Eisenberg et al. (2006)
Reassurance	Affiliative body contact used to reduce anxiety or aggressive tendencies in another individual.	de Waal (1989a); van Hooff (1967)
Reconciliation	The process of restoring social bonds following a conflict or aggression.	de Waal (1989a)
Sexual behaviour	Conceptive and non-conceptive genital contact occurring within and between the sexes.	Andersson (1994)
Triadic contact	A social interaction involving three individuals, often in the context of conflict resolution or cooperation.	de Waal (1982)

Chapter 1: General introduction

1.1 The link between primate empathy and affiliative body contact

Parts of this section have been published as a book chapter, of which I was lead author, in an edited volume entitled "Primate Cognitive Studies", edited by Bennett L. Schwartz and Michael J. Beran.

Book chapter published as:

Brooker, J. S., Webb, C. E. and Clay, Z. (2022). Primate empathy: A flexible and multi-componential phenomenon. In B. L. Schwartz & M. J. Beran (Eds.), Primate Cognitive Studies. Cambridge University Press. Preprint version accessible at https://psyarxiv.com/bpw5x/

1.1.1 The phenomenon of empathy

From parental caregiving and comforting to marketing and politics, empathy is often considered to reflect a cornerstone of the human experience, and a capacity that sets our species apart from other animals. In the academic world, discrepancies in definition have created dissonance in the study of empathy and led to confusion with other concepts such as sympathy (Cuff et al., 2016).

Some definitions focus on more specific characteristics of empathy, such as its affective or emotion-sharing aspect, by describing empathy as the "sharing of the emotions or sensory states of another person" (Hein & Singer, 2008, p.154) or "'mimicking' of one person's affective state by that of another" (Goldman, 1993). Alternatively, other definitions focus on its cognitive aspects, by specifying empathy as the "capacity to understand and enter into another person's feelings and emotions or to experience something from the other person's point of view" (Colman, 2015, p.245). Other definitions consider these aspects integrated (Eisenberg et al., 2006, p.647) and some emphasise a behavioural component (Oliveira-Silva & Gonçalves, 2011, p.201), or specify the importance of a self-other distinction (Coplan, 2011, p.40).

These inconsistencies reflect a difficulty to isolate a complex multidimensional phenomenon consisting of a suite of socio-emotional mechanisms and behaviours into one short definition. Broadly, however, empathy is considered to represent a complex socio-emotional ability that enables individuals to match and potentially understand another individual's emotional state, which can motivate prosocial behavioural action (Cuff et al., 2016; Preston & de Waal, 2002).

The capacity to connect with and respond to others' states appears to facilitate the formation of strong social bonds (Rumble et al., 2010). Emotions are considered internal states elicited by intrinsic or extrinsic stimuli (Anderson & Adolphs, 2014), and human research has indicated that various emotional expressions can evoke empathy, including anger, disgust, happiness, sadness, and fear (Fan et al., 2011). Through empathy, it is thought that we can unconsciously merge the self and other, thereby echoing another's experiences within ourselves (de Waal, 2011). For instance, in a facial expression experiment looking at facial muscle movements (Dimberg et al., 2000), subjects mimicked happy and angry faces and reported experiencing the relative emotion even when the speed of stimulus presentation was beyond conscious perception.

It has been suggested that humans exhibit an advanced capacity for empathy, related to other capacities including perspective-taking, self-other differentiation, emotion regulation, and cognitive appraisal (Decety et al., 2012). However, recent comparative breakthroughs have revealed that many empathy-related behaviours appear to exist across mammals (Adriaense et al., 2020; de Waal & Preston, 2017), as well as some avian species (e.g., Fraser & Bugnyar, 2010). Instead of emerging independently in humans, empathy likely manifests through bottom-up processes from foundational components with a potential ancient ancestry in our evolutionary lineage (Adriaense et al., 2020; Decety & Lamm, 2006). These processes are proposed to be regulated by sophisticated top-down information processing mechanisms, which may be more pronounced in our own species.

As a wider phenomenon in many social mammals, empathy is thought to contribute towards the adaptive facilitation of strong, long-term affiliative bonds, which promotes cooperation towards joint goals (Rumble et al., 2010; Yamamoto & Takimoto, 2012). Furthermore, in humans and non-humans, empathy appears to be mediated by trait and state influences, which has led to apparent individual and group-level variation in the strength or presence of certain empathic responses (Chopik et al., 2017; Eisenberg et al., 1999; Webb et al., 2017).

As a multidimensional phenomenon, empathy can manifest as one of multiple behaviours on varying affective and/or cognitive levels (Brooker et al., 2022; de Waal, 2007). Empathy can be divided into sub-components that differ by their neurobiological, psychological, and behavioural complexity (Hecht et al., 2012; Iacoboni, 2009). The revelation that empathy likely exists beyond our species has encouraged a deeper discussion into how to model such mechanisms that facilitate emotion sharing and understanding, which may have deep and widespread phylogenetic origins (de Waal & Preston, 2017).

The Russian Doll Model (de Waal, 2007; de Waal & Preston, 2017) proposes that there are multiple levels or layers of empathy, with each level building upon the previous to create a more complex understanding of the other person's experiences. This model theorises that empathy is not a single, unitary phenomenon, but rather a multifaceted construct involving cognitive, affective, and behavioural components. Furthermore, the Perception-Action Model (PAM; Preston & de Waal, 2002) suggests that the observation of others' actions activates the same neural representations used to perform those actions, allowing individuals to understand and share the feelings and intentions of others. This can result in physiological reactions such as body surface temperature changes (Ebisch et al., 2012) and behavioural responses to provide relevant or appropriate assistance (Lindegaard et al., 2017). Studies of the Mirror Neuron System appear to support the PAM. When an individual observes an action performed by another, mirror neurons in the observer's brain fire in a way that is similar to when the individual performs the action themselves (Gallese & Goldman, 1998; Rizzolatti & Craighero, 2004). This activation of mirror neurons is thought to create a neural simulation of the observed action, which allows the observer to understand and anticipate the actions, emotions, and intentions of others (de Waal & Preston, 2017; Keysers & Gazzola, 2009). Relatedly, the PAM is further supported by neural studies demonstrating overlapping signatures for observing and experiencing states including happiness, sadness, anxiety (Morelli & Lieberman, 2013), disgust (Wicker et al., 2003), and pain (Zaki et al., 2016). It is purported that this perception-action mechanism is the core layer of the Russian Doll Model, facilitating expression of cognitive and behavioural forms of empathy, such as consolation (de Waal, 2007; de Waal & Preston, 2017).

Other models, such as Yamamoto's (2017) Three-Factor Model of Primate Empathy have challenged the linear nature of the Russian Doll view of empathy. The three-factor model views empathy as a combination of abilities that lend themselves towards particular behaviours. In this case, (1) matching with other’s states, which may manifest as synchrony and mimicry; (2) understanding other’s states, which enables perspective-taking; and (3) an inclination towards prosocial behaviour (i.e., voluntary behaviour intended to benefit another person; Eisenberg et al., 2006) and altruism (i.e., biologically defined as behaviour that increases the recipient’s fitness at a cost to the performers; de Waal, 2008). These factors are conceptualised to combine in various ways in different primates. According to Yamamoto (2017), only some species, including humans and some other great apes, may be capable of combining all three factors. This combination is suggested to manifest as true consolation (de Waal, 2008; de Waal & Aureli, 1996), elicited by matching the state of a distressed individual, understanding this feeling is independent from one’s own state, and reacting prosocially by providing reassuring affiliative contact.

Due to its complexity and definitional discrepancies, I describe empathy broadly in this thesis in line with de Waal’s (2007) Russian Doll Model, conceptualising empathy as a multidimensional system made up of different cognitive and affective components (see *Chapter 2* for further discussion). The Russian Doll Model facilitates a bottom-up, comparative approach (see *Section 1.1.2*) towards empathy, where researchers can empirically study specific empathy components across various species. Through doing so, we can conduct systematic comparisons to identify the presence or absence of empathic personalities elsewhere in the animal kingdom, and whether such behaviours are consistent across individuals and communities.

1.1.2 Evolution of empathy and the comparative approach

Empathy-driven responses, such as consolation (see *Section 1.1.3* below), have been reported in diverse mammalian taxa, including Cercopithecine primates (*Macaca tonkeana*; Palagi et al., 2014), rodents (*Microtus ochrogaster*; Burkett et al., 2016, and cetaceans (*Physeter macrocephalus*; Pace et al., 2005; also see Bearzi et al., 2017 for cases of epimeletic behaviour in cetaceans). There are also reports that some avian species console others in distress (e.g., *Corvus corax*; Fraser & Bugnyar, 2010). It has been hypothesised that the presence of offspring care may advance the development of empathy and similar behaviours associated with altruistic tendencies (Preston, 2013; Zahn-Waxler & Radke-Yarrow, 1990). The selective pressure to respond to the emotional expressions of offspring, such as smiling and crying, through their development would facilitate a strong emotional connection and could explain why empathy may be present across mammals and birds. Yet, not all species that care for their young exhibit empathy behaviours, for example consolation has not been clearly observed in Japanese macaques (*Macaca fuscata*; Palagi et al., 2014). Thus, whilst possibly being widespread throughout the animal kingdom, empathy may manifest as a flexible trait driven by the emergence of certain social and ecological pressures (Decety, 2015).

Animals within the same species may share many traits, but individuals vary as a result of ultimate and proximate intraspecific variation (Bolnick et al., 2011; Lott, 1984). Thus, at the population- or group-level, one can observe considerable within-species differences (Kaufhold & van Leeuwen, 2019). Intergroup behavioural variation has been studied in multiple primates, including activity and ranging patterns of guerezas (*Colobus guereza*; Fashing, 2001), robbing and bartering behaviour in long-tailed macaques (*Macaca fascicularis*; Brotcorne et al., 2017), and social network relationships in vervet monkeys (*Chlorocebus pygerythrus*; Borgeaud et al., 2016).

Most empirical research on nonhuman empathy has focused on primates; in particular, the bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*) have often been applied as models to examine the origins of human social cognition and behaviour (Boesch et al., 2002; Boesch, 2009; Sayers & Lovejoy, 2008; Zihlman et al., 1978). The *Pan* genus are the closest living genetic relatives to humans, with our lineages diverging between five- and eight-million years ago (Langergraber et al., 2012; Prufer et al., 2012). This close ancestral relationship has led some to consider bonobos (Zihlman et al., 1978) and/or chimpanzees (see Sayers & Lovejoy, 2008 for a review) as referential models for hominid evolution.

Chimpanzees—in particular, findings from the eastern subspecies—have been most commonly used as a model for reconstructing the evolution of our species (Boesch et al., 2002; Boesch, 2009; Sayers & Lovejoy, 2008). This "chimpocentrism" (Beck, 1982) is, in some regards, understandable due to the similarities in the human and chimpanzee genome, and discovery of multiple behaviours in chimpanzees that were once thought to be unique to humans (Boesch & Tomasello, 1998; Whiten & van Schaik, 2007). However, this bias is primarily a result of a later discovery that bonobos are a distinct species (Coolidge, 1933) as well as being comparatively understudied, both in the wild and in captivity.

Modelling the chimpanzee as an example of how our last common ancestor may have behaved excludes the insights that bonobos can contribute, as well as the independent evolutionary development of the chimpanzee since our ancestral divergence up to eight-million years ago (Gruber & Clay, 2016). A one-dimensional approach and bias towards eastern chimpanzees also excludes the broader contribution to be made by coalescing cross-community research on both *Pan* species towards a more comprehensive model of hominid evolution (Gruber & Clay, 2016). Furthermore, ape-centric models tend to approach evolution from a top-down perspective with humans at the beginning and end (Eaton et al., 2018). In contrast, a bottom-up approach allows evolutionary biologists and comparative psychologists to consider species-specific characteristics and abilities to investigate the biological foundation of behaviours and cognition (Eaton et al., 2018). This approach helps us to understand animals in their own right as opposed to tools to assess human evolution and development.

Like humans and some other primate species, bonobos and chimpanzees express remarkable behavioural diversity, not only across the chimpanzee subspecies but even between groups living in similar ecological conditions (Boesch et al., 2002; van Leeuwen et al., 2018). Some distinct cultural differences have even been shown to persist beyond regular immigration in wild chimpanzees (Luncz & Boesch, 2014). This finding, and others (Hohmann & Fruth, 2003), show that cultural traditions can feature stark diversity and longevity across *Pan* groups.

To apply the comparative approach effectively requires a deeper understanding of both species and how behaviour can vary at different levels, from the species, group, environment and individual. Systematic comparisons of *Pan* populations are relatively more common in recent years, and as a result, many previously declared species-differences, such as bonobos being more socially tolerant than chimpanzees (Hare et al., 2007), are under question. For example, cross-community research has revealed that social tolerance in the *Pan* apes appears to vary more at the group-level than at the species-level (Cronin et al., 2015; van Leeuwen et al., under review).

Given the scope for behavioural diversity, to truly understand a given species and draw conclusions about their nature, investigating more than one group is vital. However, despite detected variation in *Pan* groups, species generalisations are often still declared based on observations of small populations of one or two groups of, often captive, bonobos and chimpanzees (dicussed in Kaufhold & van Leeuwen, 2019). By contrast, humans are recognised to vary across groups and cultures in cognition and behaviours including in language, communication (Hua et al., 2019), prosociality (House et al., 2013), conformity (van Leeuwen et al., 2018), emotional expressions, and empathy (Chopik et al., 2017). It would be inappropriate to declare conclusions on human nature from a study on a single group (Hruschka et al., 2018). Given their behavioural flexibility (Boesch et al., 2002), the same approach must surely be applied to our closest cousins. Taking the comparative perspective, which accounts for between-group variation, can provide us with a greater understanding of how human social and cognitive behaviours evolved, what shapes their emergences, and to what extent they are uniquely human.

In this regard, the comparative approach is informative to investigate the evolutionary origins of empathy and related phenomena. Responding to the suffering of another individual would likely not be advantageous if it reduces one's ability to focus on one's own state, or if that individual does not share a beneficial relationship with them. Indications that empathy-related behaviours are generally biased towards close social partners (e.g., humans: Lindegaard et al., 2017; bonobos: Palagi & Norscia, 2013, Clay & de Waal, 2013; and chimpanzees: Romero et al., 2010, Webb et al., 2017) with whom an individual has an invested social relationship supports an adaptive explanation as to how empathy emerged and persisted in social animals (see *Chapter 2*).

Furthermore, whilst often associated with altruistic intentions, empathic responses may incur self-serving benefits, such as increasing social desirability, punishment avoidance, social rewards, or personal arousal reduction (Batson, 2010). Empathic responders may also receive benefits through reciprocity (Watts, 2002), and even reduce possible reactive aggression in distressed individuals, thus benefitting the community (Palagi et al., 2006). Thus, there are various selective motivations that may lead to the emergence of empathy-related behaviour.

In the rest of this section, I will outline the role and function of a particular empathy-related behaviour—consolation, also often termed "sympathetic concern"—and its link to other forms of affiliative body contact during periods of social tension. For more information about the study of empathy and its subcomponents, generally and how they manifest in the *Pan* apes, see *Chapter 2*.

1.1.3 Consolation: Reassuring body contact as empathy

One of the most common methods applied to study empathy in nonhuman animals, particularly primates, is to naturalistically observe consolation behaviour directed towards distressed conspecifics (Adriaense et al., 2020; Brooker et al., 2022; Perez-Manrique & Gomila, 2018). Consolation is defined as the spontaneous offering of reassuring body contact from uninvolved bystanders towards individuals who are distressed due to conflict or other circumstances (de Waal & Aureli, 1996). Consolation behaviour is one form of triadic contact, which are post-conflict interactions where three individuals—an aggressor, victim, and bystander—are present (de Waal, 1982). Consolation represents a specific directional form of triadic contact where a bystander offers unsolicited contact affiliation towards a victim. Other triadic contacts include reconciliation, where the aggressor and victim restore social bonds following a conflict or aggression (de Waal, 1989a). As victims are typically distressed, it is purported that consolation requires the ability to be emotionally affected by, understand, and respond to another's emotion (de Waal & Preston, 2017), therefore representing an other-oriented prosocial motivational response to improve another individual's emotional state (de Waal, 2008).

Consolation, and other forms of comforting, is common in humans (Davidov et al., 2013, 2021; Fujisawa et al., 2006; Lindegaard et al., 2017; Roth-Hanania et al., 2011; Vreden et al., in prep; Zahn-Waxler et al., 1992) and appears to already develop in the first year of life in human infancy (Davidov et al., 2021; Vreden et al., in prep). Consolation has also been demonstrated in other animals, including bonobos and chimpanzees (see *Chapter 2* for a review). Young bonobos and chimpanzees tend to console the most out of all age groups (Clay & de Waal, 2013; Webb et al., 2017; see *Chapter 4*). In addition, across humans and *Pan*, consolation is more commonly offered by individuals who share a close social relationship to the distressed individual (Fraser et al., 2008; Lindegaard et al., 2017; Palagi & Norscia, 2013). Indicative of its prosocial, tension-relieving function consolation has been shown to be effective in reducing stress markers in the target in both bonobos (Clay & de Waal, 2013) and chimpanzees (Fraser et al., 2008).

The *Pan* apes share a suite of contact affiliation behaviours during consolatory approaches, including embracing, touching, and sexual contacts (Clay & de Waal, 2013; de Waal & van Roosemalen, 1979; Palagi & Norscia, 2013; Romero et al., 2010). Sexual behaviour, especially the species-typical genito-genital rubbing, appears to be particularly pronounced in bonobo consolation compared to chimpanzees (de Waal, 1988; see *Chapter 7*). Some trends appear to be group-specific, such as possible sex differences in who consoles or is consoled (Romero et al., 2010; but see Webb et al., 2017). Proposed species differences, such as social tolerance (Hare et al., 2007; but see Cronin et al., 2015 and van Leeuwen et al., under review), social attentiveness (Kano et al., 2015), and emotional sensitivity (Kret et al., 2016; Rilling et al., 2012; Staes et al., 2014), are thought to influence species variation in empathic responding in bonobos and chimpanzees. Nevertheless, the two species have not to date been systematically compared regarding their empathic behaviour. In this thesis, I addressed this by conducting the first systematic comparison of consolation tendencies in bonobos and chimpanzees by studying groups living in ecologically similar semi-wild conditions.

As previously highlighted, consolation is thought to be mediated by individual and social factors, and not merely an automatic response. Consolation appears to be limited or even absent in non-ape primates (Brooker et al., 2022; but see Palagi et al., 2014 for the only exception in *Macaca tonkeana*), despite many studied social groups living in similar captive conditions to those of *Pan*. Thus, the direct comparison in this thesis provides extra depth to the discussion of what our closest living relatives can reveal about the evolution of our own empathic behaviour, and what circumstances facilitated its development.

1.1.4 Pre-feeding affiliation: A putative form of reassurance during social tension?

Consolation represents a functionally specific form of contact reassurance that occurs during specific periods of social tension in which a certain individual/s exhibit greater distress than others observing the event (such as after a conflict). However, reassurance—the more general phenomena that refers to the functional use of affiliative body contact to reduce anxiety or aggressive tendencies in another individual (van Hooff, 1967; de Waal, 1992)—does not only occur as a response to another's distress during post-conflict or post-distress periods. Reassurance in non-conflict periods of social tension has also been noted in *Pan* individuals, often from more dominant group members, through behaviours such as embracing and genital contact (e.g., de Waal, 1992; Goodall, 1986; Samuni et al., 2019; Sandel & Reddy, 2021), similar to those used during consolatory contacts towards distressed conflict victims.

Contextually, however, consolation occurs during a post-conflict context in response to an individual expressing distress and is driven by uninvolved bystanders (de Waal & Aureli, 1996; de Waal & van Roosemalen, 1979). In this context, consolation represents a specific form of reassurance with a specific function to reduce conspecific distress and strengthen social relationships (Clay et al., 2018; de Waal & Aureli, 1996; Romero et al., 2010). In contrast, reassurance occurs more generally during periods of social tension, which could be prior to or during post-conflict contexts (i.e., consolation and other triadic affiliative contacts are specific forms of reassurance) but also during intergroup and predator encounters (de Waal, 1992; van Hooff, 1967). Reassurance has been purported to have multiple functions including to reduce aggressive tendencies in the target as well as anxiety in the self or other (de Waal, 1992; van Hooff, 1967).

Aggression is especially common during periods of feeding competition, and both bonobos and chimpanzees have been reported to engage in heightened levels of contact affiliation during these periods (de Waal, 1992; de Waal et al., 2000; Goodall, 1986). Although pre-feeding affiliation—defined as affiliative behaviours occurring prior to feeding, such as grooming and huddling—has been discussed in the literature (Watts & Mitani, 2002), little is known about how it is targeted or operationalised to potentially moderate social tension, nor its relation to consolation. Sometimes referred to as 'celebration', pre-feeding affiliation is thought to promote social bonding and cooperation, thereby reducing the costs of competition over food resources (de Waal, 1992; Watts & Mitani, 2002).

In both species, pre-feeding affiliation often manifests as a collective behaviour, where multiple individuals affiliate spontaneously across age and sex classes (Brooker, personal observation). Individuals notably affiliate with multiple individuals and thus determining the specific function of one interaction, and whether it reduces an individual's anxiety or aggressive tendency, is challenging. Despite this challenge, studying the use of pre-feeding contact affiliation on a group and dyadic level may provide further nuance to the evolutionary emergence of specific forms of reassurance, such as consolation.

Therefore, in this thesis, in addition to comparing consolation behaviour in bonobos and chimpanzees, I have systematically compared the tendencies for bonobos and chimpanzees to engage in contact affiliation (reassurance) during a controlled period of social tension. To explore how this affiliation may be used to manage social tension and possibly prevent conflict, I compared the tendencies for these behaviours to occur in relation to conflict behaviour during a competitive pre-feeding context. These observations were made during a regulated feeding experiment to assess group-level cofeeding tolerance, known as the *peanut swing* (Cronin et al., 2014). Experimental sessions involve the distribution of a finite food resource across a limited spatial plane, to record the density that groups gather in to feed before the resource has been mostly consumed. Groups higher in social tolerance are expected to gather in higher densities than those that are more despotic (Cronin et al., 2014; de Waal & Luttrell, 1989; DeTroy et al., 2022). Prior to cofeeding, great apes are known to engage in contact affiliation (Clay & de Waal, 2015; de Waal, 1989b, 1992; Palagi et al. 2006). Thus, I designed a systematic pre-feeding period for this experiment to compare tendencies of pre-feeding contact affiliation in sanctuary-living bonobos and chimpanzees.

1.2 The study species: Bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*)

In this section, I briefly introduce bonobos and chimpanzees, my study species. *Chapter 2* provides a more thorough overview of bonobo and chimpanzee expressions of empathy-related behaviours and other relevant aspects of their social cognition. Here, I briefly describe their ecology and social systems to provide a backdrop to my comparative research on these species. Aspects of *Pan* social lives that are relevant to my empirical research are also elaborated on in each chapter respectively.

1.2.1 The *Pan* genus

The great ape taxonomic family comprises four genera of extant species: *Pongo*, consisting of Bornean (*Pongo pygmaeus*), Sumatran (*Pongo abelii*), and Tapanuli orangutans (*Pongo tapanuliensis*); *Gorilla*, consisting of eastern (*Gorilla gorilla berengei*) and western gorillas (*Gorilla gorilla gorilla*); *Pan*, consisting of bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*); and *Homo*, of which only modern humans (*Homo sapiens*) remain. Bonobos were once believed to be a subspecies of chimpanzee, primarily due to their morphological similarities, until Coolidge (1933) discovered extensive anatomical differences between the two species. Since, comparative investigations have revealed many morphological, behavioural, and genetic distinctions and the two species are currently estimated to have diverged from a common ancestor around 0.9–1 million years ago (Hey, 2010; Prüfer et al., 2012; Wegmann & Excoffier, 2010; Won & Hey, 2005).

1.2.1.1 Bonobos (*Pan paniscus*)

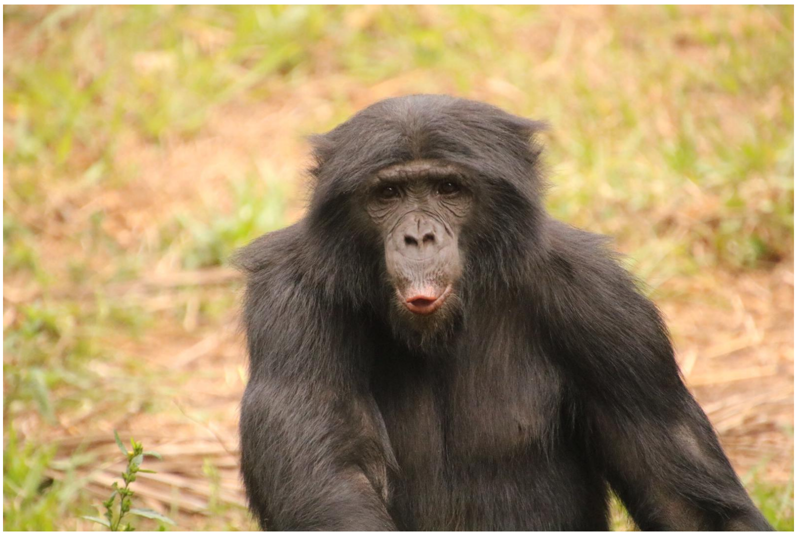

Figure 1.1. Lomako, an 11-year-old wild-born male bonobo living in group 3 (B3) at Lola ya Bonobo Sanctuary in the Democratic Republic of the Congo. Photo by S. Kordon.

Bonobos are often characterised as more slender, or gracile, generally reaching a similar height as chimpanzees (73–80 cm), but with a slimmer build, blacker hair and face, and paler lips than their chimpanzee counterparts (de Waal & Lanting, 1997). Whilst chimpanzees are widespread through sub-Saharan Africa, bonobos are only found on the left bank of Congo River in the Democratic Republic of the Congo. Their primary habitat comprises primary and secondary tropical forest, however they also can occupy forest mosaic and savannah habitats (Hashimoto et al., 1998; Thompson, 2002). Their diet consists of fruits, leaves, herbaceous vegetation, honey, mushrooms, and even the meat of small mammals and other primates through hunting (Kano, 1992; Lucchesi et al., 2021; Serckx et al., 2015; Surbeck & Hohmann, 2008).

Both bonobos and chimpanzees live in large multi-female, multi-male communities, which are, contrary to most primate societies, characterised by male philopatry and female migration (Furuichi et al., 1998; Goodall, 1986; Kano, 1992). Both species live in fission-fusion social systems—where the whole group generally fractures into smaller subgroups that regularly fuse together—and each group can occupy a home range of up to 31.5 km^2

(Hashimoto et al., 1998). Unlike typical patterns in male philopatric species, the strongest bonds in bonobo groups are between females, who are the most gregarious, despite often joining their respective groups as immigrants (Hohmann et al., 1999; Furuichi, 1989; White, 1996). Whilst male bonobos generally do not form strong affiliations with other males (Hohmann et al., 1999; Kano, 1992), males often form strong bonds with females, particularly their mothers, which typically positively influences their hierarchical rank (Furuichi, 1989, 1997; Hohmann & Fruth, 2003).

The dominance structure of bonobo societies is more flexible and dynamic than that of chimpanzees and other similar social systems (Paoli & Palagi, 2008; Stevens et al., 2007; Vervaecke et al., 2000). On an individual level, females and males commonly share relatively equal social status (Furuichi, 1989; Surbeck et al., 2012; White, 1996). Collectively, clusters of females generally dominate bonobo groups in contexts of foraging and alliance-forming (White & Wood, 2007), with older females occupying the highest-ranking positions (Furuichi, 2011; Surbeck et al., 2012; Vervaecke et al., 2000). However, dominance patterns are typically non-linear and depend on context, such as during feeding or oestrus periods (Parish, 1996; Vervaecke et al., 2000; White & Wood, 2007). In contrast to chimpanzees, aggression, particularly severe aggression, is lower (Wilson et al., 2014). The enhanced dominance status of female bonobos compared to their chimpanzee counterparts may be facilitated by low male motivation for status and a lack of male-male alliances (de Waal, 1997; Paoli et al., 2006; Parish, 1994).

1.2.1.2 Chimpanzees (*Pan troglodytes*)

Figure 1.2. Tilly, an 18-year-old female chimpanzee born in captivity living in group 2 (C2) at Chimfunshi Wildlife Orphanage Trust in Zambia. Photo by J. S. Brooker.

Current chimpanzee habitat stretches across sub-Saharan Africa, in forested and savannah ecosystems: western chimpanzees (*Pan troglodytes verus*) remain in parts of West Africa (Humle et al., 2016a); eastern chimpanzees (*Pan troglodytes schweinfurthii*) in Central and East Africa (Plumptre et al., 2016); the Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*) in Cameroon and Nigeria (Oates et al., 2016); and the central chimpanzee (*Pan troglodytes troglodytes*) in Central and South-West Africa (Maisels et al., 2016).

Like bonobos, chimpanzees also live in fission-fusion communities and home range size can vary. Examples include 15.5–19.0 km^2 for a western subspecies group in Guinea-Bissau (Vieira et al., 2019) and 25.2–27.4 km^2 for an eastern subspecies group in Mahale, Tanzania (Nakamura, 2012). Wild chimpanzees have culturally varied diets, generally tending to consume a variety of fruits and vegetation, as well as honey, bark, seeds, insects, and the meat of mammals, primates, and even birds and their eggs (Goodall, 1986; McGrew, 1983; Nishida & Uehara, 1983).

Unlike bonobos, but typical of other male-philopatric species, chimpanzee males form the strongest social relationships with other males in their groups, which facilitates cooperation and alliance formation (Goodall, 1986, Mitani et al., 2000; Reynolds, 2005; Watts, 2002). In contrast, females tend to live semi-solitary lives, travelling often with just their offspring and avoiding unrelated adult males outside of oestrus, seemingly to avoid being aggressed (Williams et al., 2002). However, this appears to vary in wild chimpanzees as females in Taï National Park have been shown to have strong, long-lasting grooming and association relationships (Lehmann & Boesch, 2009). The closeness between males is known to extend to food sharing and conflict support, as well as territorial protection by collectively engaging in cooperative boundary patrols and hunting (Boesch, 2009; Nishida, 2011).

Adult male chimpanzees typically dominate over all females, and hierarchies are considered to follow strict linear patterns headed by an alpha male and his closest allies (Boesch, 2009; Nishida, 2011). This dominance structure is accompanied by characteristically high rates of male aggression, typically directed towards other males but also females (Goodall, 1986; Sabbi et al., 2021). Lethal aggression has been recorded in multiple wild communities, usually in cases of infanticide or during intergroup conflict (Wilson et al., 2014). Notably, whilst western chimpanzees appear less prone to within- and between-group lethal aggression (Wilson et al., 2014), intergroup and intragroup killing has been recorded in Taï National Park, Côte d'Ivoire (Boesch, 2009) and Fongoli, Senegal (Pruetz et al., 2017) respectively. Tendencies to defend home ranges and higher rates of aggression in chimpanzees, including harassment of females, is purported to have adaptive benefits, such as strategic and adaptive responses to competition over territory, resources, and mating opportunities (Williams et al., 2004). More information on bonobo and chimpanzee social living is provided in *Chapter 2*, where I critically review the literature on empathy behaviour in these two species.

1.2.2 The role of sanctuaries in comparative research

Bonobos and all chimpanzee subspecies are considered endangered according to the IUCN Red List of Threatened Species (bonobos: Fruth et al., 2016; chimpanzees: Humle et al., 2016b). Threats include poaching, habitat loss, and disease (Fruth et al., 2016; Humle et al., 2016b). Killing, capturing, and consuming bonobos and chimpanzees is illegal, however poaching remains the biggest threat. Slow reproductive rates and low population densities mean hunting can lead to the eradication of entire *Pan* groups. When bonobos or chimpanzees are killed for meat, any infants left behind are typically captured and trafficked into the pet trade. The price for an infant bonobo and chimpanzee can reach over £10,000 in the exotic pet and entertainment industries, and over the past six years it is estimated that over 14,000 chimpanzees have been captured by the illegal wildlife trade (David Shepherd Wildlife Foundation, 2022). Whilst many confined bonobos and chimpanzees are confiscated, many are eventually abandoned when they reach sub-adulthood due to their unmanageable strength. Consequently, hundreds of rescued bonobos and chimpanzees now reside in sanctuaries, which provide veterinary care and semi-wild naturalistic enclosures to offer a resemblance of natural life with other conspecifics (see *Section 3.1* for details of two examples of African sanctuary sites).

Whilst much research on nonhuman primates over the past century was centred on individuals kept in laboratory conditions, focus gradually shifted towards behavioural observations and experimental trials more commonly being concentrated on captive zoo populations (Hopper, 2017; Lankau et al., 2014). However, the conservation crisis has led to rapid growth of sanctuary-living great apes in recent decades. The management and caregiving staff at great ape sanctuaries generally focus their efforts on rescue, rehabilitation, and husbandry. Over time, these sites have become increasingly important as locations to conduct behavioural and experimental studies of social and cognitive behaviours (Ross & Leinwand, 2020).

The use of sanctuaries for research is popular as they typically provide ecologically similar conditions to what great apes might experience in the wild, compared to other forms of captive living. Sanctuary groups are generally housed within large outdoor enclosures encompassing habitat representative of what individuals might encounter in the wild, whilst being supported by caregivers who provide supplemental feeding and veterinary care. However, in some locations, residents can engage in naturally occurring ecological behaviour such as foraging, independent nesting, and even vigilance from natural threats such as snakes.

Sanctuaries provide suitable locations to conduct between-group and even between-species comparative research on social and cognitive behaviour. Examples include cognitive comparisons of human children with sanctuary-living orangutans and chimpanzees (Haun et al., 2012), and comparisons of communication task performance in dogs with sanctuary-living chimpanzees (Wobber & Hare, 2009). Sanctuary-based research has yielded many revelations regarding great ape socio-cognitive behaviour, including use of tools for corpse cleaning in chimpanzees (van Leeuwen et al., 2017), differences in socio-cognitive development in the *Pan* apes (Wobber et al., 2010), and failure for orangutans to pass the 'floating peanut task' (Hanus et al., 2011).

Multiple chimpanzee sanctuaries exist across Africa, (PASA, 2022; see *Chapter 3*) but also in the United States, such as Chimp Haven in Louisiana and Ape Initiative in Iowa. By comparison, only one sanctuary housing bonobos currently exists; Lola ya Bonobo Sanctuary in the Democratic Republic of the Congo (see *Chapter 3*). Thus, there is potential for conducting systematic comparisons across multiple groups of semi-wild populations of the *Pan* apes, between- and within-species. Groups will typically feature diverse social compositions of bonobos and chimpanzees across age and sex classes, and incorporate wild-born and captive-born individuals. Furthermore, the enclosures at African location are more likely to typically represent a reflection of the natural habitat that these apes were taken from.

1.3 Outline of the thesis

With this thesis, I set out to conduct a systematic comparison of sanctuary-living bonobos and chimpanzees in their use of affiliative body contact during tense social contexts. I investigated two specific contexts of social tension where reassurance is notably common: "consolation", defined as unsolicited post-conflict reassurance spontaneously offered by an uninvolved bystander towards a distressed conspecific (de Waal & Aureli, 1996; Romero et al., 2010; Zahn-Waxler et al., 1992); and "pre-feeding contact affiliation", defined as contact affiliative behaviour occurring prior to a feeding where competition, and thus social tension, is likely (de Waal, 1986b, 1992). I provide a brief overview of each chapter of this thesis below. I am first author for all review and empirical articles included in this thesis. A prospective list of authors for each paper is provided prior to each chapter, as relevant.

Chapter 2: The expression of empathy in human's closest relatives, bonobos and chimpanzees: Current and future directions.

I start with a review article about the study of empathy-related behaviours in bonobos and chimpanzees. As a multi-dimensional phenomenon, comprising affective and cognitive components, empathy is observed in animals through a suite of behaviours related to emotional responding. As our closest living relatives, bonobos and chimpanzees could provide a model to explore the origins of Hominid social cognition, including empathy.

This review synthesises the literature and suggests future directions for the study of empathy in *Pan*, as well as other animals. This review also provides context for my empirical studies.

Chapter 3: General methods

Chapter 3 provides a broader overview of the field sites, data collection methods, and coding approaches that I used to address my research questions. Each empirical chapter includes a specific methods section related to that study's questions.

Chapter 4: Within-species variation eclipses between-species differences in Pan consolation

This empirical chapter is a systematic comparison of bonobo and chimpanzee consolation. I investigated both between-species variation in consolation tendencies and the extent of within-species variation including group, age, sex, rank, and other social factors. I found that tendencies to offer consolation were consistent between sanctuary-living bonobos and chimpanzees at the species-level. However, I found that groups of bonobos differed in their tendencies to console, as well as species differences in which individual and social variables influence consolation. I discuss these results in their relevance to the wider literature on *Pan* and primate empathy.

Chapter 5: Sanctuary-living bonobos and chimpanzees manage social tension with affiliative body contact

Next, I compare the use of contact affiliation during a 5-minute pre-feeding window prior to a competitive feeding context in sanctuary-living *Pan* groups. Using a cofeeding paradigm to measure social tolerance—the *peanut swing*—I designed a controlled period of social tension that could be applied comparatively across sanctuary groups. During this period (the 5-minute pre-feeding window), we could record all affiliative and agonistic social interactions. My analyses revealed stark overlaps in general tendencies to engage in pre-feeding contact affiliation across species and groups.

My findings also revealed marked species and group differences in the forms of contact affiliation and who affiliates with whom. Same-sex pairings of the typically more socially dominant sex in each species (i.e., bonobos = female-female; chimpanzees = male-male) were more likely to affiliate than other respective sex-pairings. Group-level analyses revealed that these sex trends were only present in the most socially tolerant groups, which I discuss. I also found group differences in the use of specific types of reassurance as well as the temporal distribution of contacts. I discuss these results in their relevance to social bonding in great apes, and how they may function to prevent social conflict during competitive contexts.

Chapter 6: Pre-feeding reassuring body contacts facilitate cofeeding tolerance in sanctuary-living bonobos and chimpanzees

In this chapter, I investigate whether pre-feeding affiliative contact interactions proximately increase *Pan* cofeeding tolerance. I did so using the *peanut swing experiment;* explained in *Chapter 3* and *Chapter 6*. Data collected for this experiment also contributed to a larger cross-group comparison of sanctuary- and zoo-living bonobos and chimpanzees. The paper (van Leeuwen et al., under review) of which I am a co-author focusses specifically on co-feeding tolerance across groups and showed marked between-group differences but between-species similarities. In my thesis, I refer to these findings for context of how the groups compare in tolerance. My findings, which focus on pre-feeding affiliation behaviour (reassurance) indicate that an individual's number of contact partners and absolute numbers of contacts positively associate with increased access to the cofeeding zone for both bonobos and chimpanzees. Group-level analyses indicate group-specific trends that may be associated with wider social dynamics. I discuss these findings as a potential window in the proximate mechanisms that encourage greater social tolerance in our closest living relatives.

Chapter 7: Sexual healing: Genital contacts during periods of social tension in sanctuary-living bonobos and chimpanzees

Bonobos are famous for using sexual behaviour---e.g., genito-genital contact, genital touching, and mounting---during periods of social tension (Hohmann & Fruth, 2003; Clay & de Waal, 2015). Genital touching and mounting are also common in chimpanzees in tense contexts, including post-conflict periods, intergroup encounters, or prior to boundary patrols (see Sandel & Reddy, 2021). Using data from post-conflict observations and sessions of the peanut swing experiment, I compared tendencies for bonobos and chimpanzees to use sexual contacts during consolation and pre-feeding affiliative interactions relative to non-sexual contact behaviours. Bonobos were more likely to use sex as consolation, however the two species did not differ in tendency to use sex as pre-feeding affiliation. These findings indicate apparent context variation in the function of sociosexual behaviour between semi-wild bonobo and chimpanzee groups. I discuss these findings in their relevance to the wider literature of *Pan* sexuality and reassurance.

Chapter 8: Fellatio among male sanctuary-living chimpanzees during a period of social tension

During my observations at Chimfunshi in 2019, I observed an instance of male-male fellatio among two adult chimpanzees. Whilst sexual behaviours are common in both *Pan* species, fellatio is rarely described in either and had previously never been explicitly referred to in the literature for chimpanzees. The fellatio occurred during a post-conflict observation of a distressed conflict victim. The behaviour was not coded as consolation as the victim initially solicited affiliative contact with the uninvolved bystander. Nonetheless, the nature of the fellatio represented a form of post-conflict affiliation between the pair.

Anecdotes in primatology and related disciplines can provide rich, qualitative observations of rare or potentially unique behaviours that may influence the way we consider a species (Ramsay & Teichroeb, 2019). I thereby reported the observation for a special issue on anecdotes of animal behaviours for the journal *Behaviour*, which was published online in 2020 (Brooker et al., 2020). I discuss this use of fellatio in a post-conflict context in its relevance to the role of social tolerance and sexual behaviour in chimpanzee social tension management strategies.

Chapter 9: General discussion

This thesis concludes with a broad discussion of the implications of my empirical studies and how they relate to the wider literature on empathy, reassurance, and sexuality. Within these topics, I highlight their relevance to the study of social tolerance and the importance of studying multiple groups of the same species for a comprehensive image of inter- and intraspecific variation. I discuss the limitations of my methods and how they made be overcome. Throughout this chapter, I offer directions for future research, in particular testing directly the functions of reassurance behaviour outside of conflict contexts.

Chapter 2: The expression of empathy in human's closest relatives, bonobos and chimpanzees: Current and future directions

The chapter constitutes a review article to be submitted for publication with the following authorship:

Brooker, J. S., Webb, C. E., de Waal, F. B. M., & Clay, Z. The expression of empathy in human's closest relatives, bonobos and chimpanzees: Current and future directions.

Abstract

Empathy is a complex, multi-dimensional capacity that facilitates the sharing and understanding of others' emotions. As our closest living relatives, bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*) provide an opportunity to explore the origins of hominid social cognition, including empathy. Despite certain assumptions that bonobos and chimpanzees may differ empathically, these species appear to overlap considerably in certain socio-emotional responses related to empathy. However, few studies have systematically tested for species variation in *Pan* empathic or socio-emotional tendencies. To address this, I synthesise the growing literature on *Pan* empathy to inform our understanding of the selection pressures that may underlie the evolution of hominid empathy, and its expression in our Last Common Ancestor. As bonobos and chimpanzees show overlaps in their expression of complex socio-emotional phenomena such as empathy, I propose that group comparisons may be more meaningful than species comparisons when it comes to understanding evolutionary pressures for such behaviour. Furthermore, key differences, such as how humans and *Pan* communicate, appear to distinguish how we experience empathy compared to our closest living relatives.

2.1 Introduction

Empathy is a socio-emotional capacity that involves recognising and being emotionally influenced by the emotions of others, enabling corresponding prosocial responses and cooperative behaviour (Preston & de Waal, 2002). Despite definitional inconsistencies, most scholars characterise empathy as an automatic, affective response to emotional stimuli, shaped by top-down control processes, which may trigger a prosocial behavioural response (Cuff et al., 2016). Empathy is thus important for developing and maintaining strong, long-term cooperative relationships among social animals (Rumble et al., 2010).

A leading model to describe empathy is the Perception-Action Model (PAM; Preston & de Waal, 2002). According to the PAM, empathic processes arise from perceiving another's external state or action. This evokes representations of such states or actions in oneself, which then result in a corresponding response. Relatedly, the Russian Doll Model of empathy describes this perception-action pairing as the core mechanism that facilitates more other-oriented behaviours, including targeted helping and sympathetic concern (de Waal, 2007). Critically, behavioural research suggests that many social mammals, and primates in particular, are capable of all of these layers of empathy (Adriaense et al., 2020).

Affective states can spread from one individual to another spontaneously and consciously, yet various factors can mediate the expression of empathy. Experiencing the suffering of others indiscriminately would not likely be advantageous if it depletes one's own socio-emotional resources or puts them at risk. The empathy mechanism appears to be influenced by individual and social factors such as an empathy gradient, which has been identified in humans and some non-human species (Fraser et al., 2008; Lindegaard et al., 2017; Palagi & Norscia, 2013). This gradient alludes to a heightened emotional representation of another's state if they have a strong relationship with oneself, such as close social partners or kin (de Waal, 2012; de Waal & Preston, 2017). This trend offers a selective explanation as to how a potentially costly behaviour may have emerged among social animals. Primates thus provide suitable models for study here, as most species, especially apes, invest in long-term social cooperative relationships with kin and other group members throughout their lifetimes.

In recent decades, scientific discoveries have uncovered social and cognitive capacities, such as culture, in other animals that were once thought to be unique to humans (Whiten & van Schaik, 2007). In the case of empathy, inconsistencies in defining and operationalising empathy in empirical research (Cuff et al., 2016), and a lack of systematic comparative designs, have limited direct between-species comparisons, which are needed to identify the breadth of empathy in animals. Despite these hurdles, our closest living primate relatives—the *Pan* apes, bonobos and chimpanzees—provide suitable models for testing open questions about the ancestral roots of empathy and social cognition. Comparative research on great apes helps us uncover clues about what types of social behaviours our last common ancestor with *Pan* may have exhibited. In addition, whereas *Pan* overlap with each other and humans in many aspects of their social dynamics and behaviour, these species provide a further window into how variations in social structures may foster changes in expressions of phenomena like empathy. This review will outline current insights into understanding empathic behaviour in *Pan* with some proposed new directions, that can provide a more nuanced and broader view about animal empathy. As cross-species investigations are vital for revealing how human empathy may have evolved, the rationale for more systematic comparisons of the two species is also advocated.

2.2 *Pan* similarities and distinctions

Like most primate species, bonobo and chimpanzee societies are characterised by long-term social bonds among group members. However, unlike most primate species, the males of both *Pan* species are the philopatric sex, with females typically emigrating at sexual maturity (Gruber & Clay, 2016). Both species live in large multi-male, multi-female fission-fusion societies, with subgroupings that vary in membership over time (Boesch et al., 2002). While male philopatry predicts males to be the most socially-bonded sex, among *Pan* this pattern is only expressed in chimpanzees, where males exhibit strong social bonds and occupy the highest status positions (Boesch et al., 2002; Goodall, 1986). By contrast, bonobo societies are characterised by female-female and mixed-sex bonding, with dominance hierarchies that are typically female-centric (Boesch et al., 2002). Male-male alliances in chimpanzees and female-female alliances in bonobos between dominant individuals are crucial for their respective intragroup social stability (Gruber & Clay, 2016). Given this striking variation in bonding and hierarchical structure between *Pan*, one might expect sex-biased variation in socio-emotional tendencies between the two species, including empathy.

Compared to chimpanzees, bonobos are less aggressive (Wilson et al., 2014) and have been considered to be the more empathic species—the "make love not war" ape (de Waal & Lanting, 1997), that uses sexual behaviour to resolve social conflicts (Hohmann & Fruth, 2000). Whilst they also engage in aggression (Fruth & Hohmann, 2003; Hare et al., 2012), bonobo societies are regularly described as having a more peaceful nature (Furuichi, 2011) with lower inter- and intragroup aggression levels than those described for chimpanzees (Hare et al., 2012). Bonobos also appear to be relatively tolerant of other groups, having been observed peacefully interacting with neighbouring groups at artificial and natural feeding locations (Idani, 1990; Lucchesi et al., 2020; Sakamaki et al., 2018). Furthermore, no observation of intra-species killing has yet been confirmed for bonobos (Furuichi, 2011; Wilson et al., 2014).

By comparison, chimpanzees are depicted as more aggressive and despotic, with much empirical focus on their patriarchal hierarchies and antagonistic interactions within and between groups (de Waal, 2005). Intergroup competition is a ubiquitous feature among chimpanzee communities and encounters are often hostile with threat vocalisations and or physical aggression likely to occur (Wilson & Wrangham, 2003). Chimpanzees have been documented killing group and non-group members (Boesch et al., 2007; Pruetz et al., 2017), with their behaviour explained as strategic and adaptive responses to competition over territory, resources, and mating opportunities (Williams et al., 2004). In addition, whilst social bonding is key to chimpanzee nature, bonobos have been reported as more socially attentive than their *Pan* counterparts (Kano et al., 2015).

Despite these differences, bonobos and chimpanzees appear to overlap more in terms of social tolerance than previously thought (van Leeuwen et al., under review). Previously, bonobos had commonly been considered the more tolerant species due to their decreased aggressivity, their potential to coalesce with other groups, and their rapid responsiveness towards others' emotional expressions (Kret et al., 2016). However, a recent study of cofeeding tolerance in zoo- and sanctuary-living populations revealed greater variation within species than between (van Leeuwen et al., under review).

In bonobo societies, the prevalence of non-conceptive sexual behaviour, which occurs among all age and sex combinations (de Waal, 1990; Hohmann & Fruth, 2000), is thought to facilitate cooperation and reduce aggression compared to chimpanzees (Clay & de Waal, 2015; de Waal, 1995). However, chimpanzees also engage in genital contacts, with observations from both the wild and captivity (Anestis, 2004; Zamma & Fujita, 2004). In both species, sexual contacts are particularly common during periods of social tension, indicating a shared strategy of tension management through sexual interactions (Clay & de Waal, 2015; Samuni et al., 2019).

Here I review the literature on the different components of empathy in *Pan*. Chimpanzees feature more prominently, due to a study bias towards chimpanzees in empirical socio-cognition studies (Clay et al., 2022). Bonobos and chimpanzees appear to have certain marked species differences in behaviours that may influence empathic expressions, such as socio-emotional attentiveness. However, I propose that marked within-species variation, behavioural flexibility, and the possible existence of variable social cultures are of greater interest than direct species differences between chimpanzees and bonobos. I offer some proposed future directions, that may provide a more nuanced and broader way of thinking about *Pan* empathy and its relevance to understanding how empathy has evolved.

2.3 Studying empathy in *Pan*

2.3.1 Mimicry and behavioural contagion

Emotional responses can occur automatically (Lamm et al., 2007), as seen in some observations of mimicry and contagion in human and nonhuman animals. Mimicry is considered the involuntary copying of the physical appearance of others, for example by replicating facial expressions or vocalisations (Chartrand & Bargh, 1999; Zentall, 2003). Similarly, mimicking self-directed or social motor actions, typically known as behavioural contagion, has been observed in humans and other primates (Amici, et al., 2014). Whilst some examples of delayed mimicry could imply conscious application (Palagi et al., 2019), both mimicry and contagion are broadly assumed to be involuntary and reflexive. In this review, I describe mimicry and behavioural contagion together, as manifestations of the most basal empathic mechanisms that facilitate more complex behaviours.

Mimicry and behavioural contagion have been studied in humans (Norscia & Palagi, 2011), as well as in captive and semi-wild *Pan* populations (Madsen et al., 2013; Tan et al., 2017). A number of studies have proposed links between mimicry, empathy, and emotion contagion (Adriaense et al., 2020). It remains unclear whether, and to what extent, mimicry and corresponding internal states are directly linked, in humans and other animals alike (Adriaense et al., 2020). Evidence of a specific physiological or behavioural response would be needed to support an association with these phenomena (Isern-Mas & Gomila, 2019). Yet, as a building block towards perspective-taking abilities, reflexive state-matching behaviours may have been favoured, due to influences in social bonding (Seyfarth & Cheney, 2013). This may assist immature individuals in learning the correct contexts and usage for social behaviours and in forming affiliative relationships (Want & Harris, 2002). Mimicry and behavioural contagion could thus contribute to the foundations of empathic expressions due to their involvement in affiliative bonding.

When responding empathically, we may unconsciously merge the self and other, thereby echoing another's experiences within ourselves (de Waal, 2011). The Russian Doll model proposes that mimicry acts as a prerequisite for more complex socio-emotional behaviours (de Waal, 2007; de Waal & Preston, 2017), which may explain why facial mimicry is a common reflex after observing emotional expressions. Looking at facial muscle movements, Dimberg & Thunberg (2012) found that human participants mimicked happy and angry faces and reported experiencing the equivalent emotion even when stimuli were presented to them too quickly for conscious perception.

Akin to the neonatal human studies by Meltzoff & Moore (1977; but see Davis et al., 2021), small samples of captive neonatal chimpanzees appeared to attend to social stimuli and mimicked model facial expressions (Bard, 2007; Myowa, 1996). Even newborn chimpanzees appeared to copy and discriminate the basic facial expressions from human models (Myowa-Yamakoshi et al., 2004), although such work requires further replication. This mimicry process generally stops after two months, indicating that this behaviour is possibly an adaptive reflex. In addition, a study of social behavioural contagion in captive chimpanzees (Videan et al., 2005) found that hearing grooming and aggressive vocalisations from an outgroup, triggered individuals to reproduce these respective behaviours in their own group. These responses could be stimulated by feelings of intergroup threat, but they may also be driven by similar mechanisms to other behaviour and emotion contagion effects, such as those that facilitate yawn contagion and physiological state matching.

Whilst these behaviours may not reflect a full empathic response, there is a strong correlative link between mimicry and behavioural contagion with emotional contagion (Palagi et al., 2020; see *Section 2.3.2*). This motor contagion is purported to have served as an exaptation for emotional contagion when viewing the emotional internal states of others, such as facial expressions (Hess & Fischer, 2013). Thus, mimicry and behavioural contagion may facilitate the outer layers of empathy, as per the Russian Doll model (de Waal, 2007), by representing contagion of a similar emotional state (Palagi et al., 2020). Furthermore, Palagi et al. (2020) suggest that mimicry and behavioural contagion may inform emotional contagion, as opposed to merely synchrony, as these responses tend to be distributed unevenly across individuals. As such, I now discuss findings in *Pan* regarding more specific study areas on mimicry and behavioural contagion; rapid and delayed facial mimicry, and yawn contagion.

2.3.1.1 Rapid and delayed facial mimicry

Primate mimicry research has generally focused on the play-face, which is considered homologous to human facial laughter and appears to evoke positive affective states in the perceiver (Parr & Waller, 2006). The play-face may reveal internal positive affect that can rapidly and accurately be interpreted by observers and potentially triggering matching conspecific reactions. Play-face mimicry may therefore have adapted to convey honest intentions of positive interactions, reducing the risk of misunderstandings and conflict (Palagi, 2008). Chimpanzees have been observed to display both rapid facial mimicry (RFM; occurring within 1-second) and delayed facial mimicry (DFM; within 5-seconds), with each seeming to serve separate functions (Palagi et al., 2019). The authors of this research suggested that RFM helps to prolong play sessions and communicate a playful motivation, whilst DFM modulates sessions at later stages.

Whilst play-face mimicry has not been reported in bonobos, RFM of the bared-teeth expression has been observed during sexual encounters. Among captive bonobos in Wilhelma Zoo, the duration of sexual contacts appeared to increase when homo- and heterosexual partners rapidly mimicked the silent bared-teeth facial expression, particularly among female-female dyads (Palagi et al., 2020). Therefore, by prolonging such interactions, facial mimicry in a sexual context may strengthen social relationships and, in the case of heterosexual dyads, increase likelihood of conception.

2.3.1.2 Yawn contagion

Yawn contagion, whereby one individual yawns in a relaxed or experimental context and triggers a matched response in the observer (Massen & Gallup, 2017), is the most prevalent approach to studying facial mimicry and contagion in humans and other species. Although yawning itself appears to have physiological and social functions (Gallup, 2011), the contagion of yawning seems to be a social phenomenon associated with emotional affinity and social responsiveness (Norscia et al., 2020; Norscia & Palagi, 2011). In humans, even just thinking or reading about yawning can trigger contagion (Provine, 1986). Neuroscientific research has found that viewing a yawn activates neural regions associated with self-processing and theory of mind (Massen & Gallup, 2017). This may explain why yawn contagion is more prevalent among human participants with higher perspective-taking skills and lower recorded schizotypal traits (Platek et al., 2003). Types of behavioural contagion therefore could be associated with other-oriented processes.

A comparative study of the four nonhuman great apes showed that, when exposed to various voluntary and involuntary motor actions, only chimpanzees showed response facilitation, and only when exposed to yawning (Amici, et al., 2014). Moreover, this effect was only present when the model stimulus was a conspecific. However, other studies have demonstrated both *Pan* species responding contagiously to conspecifics yawning through experimental (Campbell et al., 2009; Palagi et al., 2014) and nonexperimental means in captive groups (Campbell & Cox, 2019; Demuru & Palagi, 2012).

Like humans, *Pan* yawn contagion may be enhanced by social closeness (Demuru & Palagi, 2012; Palagi et al., 2014), which could indicate a possible association with empathy (de Waal, 2008; Tan et al., 2017). Meanwhile, other reports have found no social bias in contagion response for chimpanzees (Madsen et al., 2013; Massen et al., 2012). In chimpanzees, this social bias appears to be limited to ingroup/outgroup membership, whereby within-group social relationships do not influence the contagion effect, but outgroup conspecific models do not trigger contagion (Anderson et al., 2004; Campbell & de Waal, 2011, 2014; Madsen et al., 2013; Massen et al., 2012). In addition, other bonobo studies have revealed a lack of social bias in yawn contagion responses (Norscia et al., 2022), and some sanctuary-living individuals even respond to strangers (Tan et al., 2017). These findings have been purported to reflect the apparent xenophilic nature of bonobos.

There also appears to be an effect of sex interacting with species. In chimpanzees, the yawns of male chimpanzees are more contagious than those of females (Massen et al., 2012); whereas the opposite is the case for bonobos (Demuru & Palagi, 2012). This may be due to differences in social attention biases between the two species, with males more socially-central and dominant in chimpanzee groups and females taking this role in bonobo groups (Boesch et al., 2002). Interestingly, whilst human research suggests empathy increases with age (Oh et al., 2020), yawn contagion effects are strongest in young individuals and decrease linearly with age (Bartholomew & Cirulli, 2014). Conversely, whilst age effects have not been observed in zoo-living bonobos (Demuru & Palagi, 2012), yawn contagion was not observed in infant sanctuary-living chimpanzees (Madsen et al., 2013). However, this may be unsurprising, given that yawn contagion only seems to emerge in human infants around 3-years-of-age (Cordoni et al., 2021). Whilst we must consider alternative explanations for why contagious yawning may be recorded—such as coinciding stress-relief or boredom (Adriaense et al., 2020)—if yawn contagion truly reflects emotional contagion, this phenomenon would support previous claims of automatic mimicry having adaptive origins.

2.3.2 Emotional contagion

Emotional contagion refers to what occurs when one individual matches with another individual's emotional state, triggering similar states in oneself (Hatfield et al., 1993). Emotional contagion is thought to foster emotional synchrony between individuals (Hatfield et al., 1993). Cortisol and alpha-amylase, salivary hormones associated with internal stress, appear to increase in humans observing conspecifics engaged in stress-inducing tasks (Buchanan et al., 2012). These increases were associated with self-reported empathic concern and perspective-taking abilities, indicating that affective state-matching may be associated with appraisal of others' situations.

Detecting emotion is difficult in any species. Recent innovative methods to explore how physiological states change in response to emotional stimuli have indicated the existence of emotional contagion in humans and other animals. One such physiological approach is pupil mimicry, the automatic and unconscious synchronization of pupil size between two individuals in response to emotional or social cues (Bradley et al., 2008; Harrison et al., 2006). Whilst relation to emotional contagion is under debate (Derksen et al., 2018), effects are stronger between close social partners (Harrison et al., 2006; Kret et al., 2015), indicating that pupil mimicry may be associated with social bonding and emotional engagement. Humans and chimpanzees have both been shown to mimic the pupillary dilation of conspecifics (Kret et al., 2014), and this has been associated with increased attention, arousal, and activation of brain regions associated with social engagement and the theory-of-mind network (Prochazkova et al., 2018; see *Section 2.3.3* for more information on 'theory-of-mind'). Whilst emotional contagion studies usually feature limited sample sizes and effects, these findings indicate that pupil mimicry may facilitate instantaneous communication of internal states, which may provide adaptive benefits of improving the quality of social interactions.

Another technique to monitor physiological reactions is infrared thermography (IRT). This non-contact approach allows detection of activity of the autonomic nervous system in response to affective stimuli (Speakman & Ward, 1998). Studies show that human facial temperatures change in response to socio-emotional situations. A study of maternal response to infant distress suggested that mothers and children affect-match during specific emotional contexts (Ebisch et al., 2012). So far, the core regions of interest for IRT in detecting possible emotional responses include the nasal, perinasal, orbital, periorbital, and maxillary regions of the face (Ioannou et al., 2014). Drops in nasal and maxillary area temperatures have been associated with exposure to upsetting social contexts and other negatively valenced stimuli (Ioannou et al., 2016, 2013).

Dezecache et al. (2017) found significant changes in the ear and nose surface temperatures of wild chimpanzees in response to naturally occurring conspecific vocalisations. Aversive calls, such as aggressive barks, were associated with the largest changes in nasal temperatures (Dezecache et al., 2017). In captivity, nasal tip temperatures in chimpanzees dropped significantly in response to playbacks of conspecific agonism (Kano et al., 2016). Further activation of the sympathetic nervous systems was noted, as heart-rate variability and behavioural arousal also occurred (Kano et al., 2016). Other video playback experiments have revealed vicarious responses in chimpanzee viewers, whereby emotional images appeared to trigger decreased skin temperatures and increased tympanic membrane temperatures (Parr, 2001; Parr & Hopkins, 2000).

However, other aversive stimuli, such as viewing an injury on a human experimenter appears to reduce nasal temperature in captive chimpanzees (Sato et al., 2019). In addition, chimpanzees can distinguish between scream variants that form a graded continuum, being more attentive to severe victim screams than acoustically similar tantrum screams (Slocombe et al., 2009). Therefore, contextual cues and further control conditions are needed, to make it possible to rule out arousal responses to aversive events that may be unrelated to the conspecifics state, and more to one's own personal negative experiences. Applying non-invasive arousal detection techniques alongside behavioural experiments may make it possible to detect whether social responses to emotional stimuli are associated with underlying affective state-matching responses.

2.3.3 Consolation

While detecting the underlying mechanisms of empathy requires careful experimentation and/or physiological markers, some behavioural manifestations of empathy can be observed by watching how individuals respond to conspecifics in distress. One such behaviour is consolation, which refers to bystanders offering friendly contact to someone in distress, which is effective in reducing the recipient's distress (Romero et al., 2010; Zahn-Waxler et al., 1992). de Waal & Yoshihara (1983) developed the post-conflict/matched-control (PC/MC) method during early studies of zoo-living rhesus macaques (*Macaca mulatta*) to test if bystander-initiated affiliation was more common towards certain individuals during a standardised post-conflict period compared to a matched control recorded at a similar time in the following days. It is suggested that consolation requires the ability to be emotionally affected by, understand, and respond to another's emotion (de

Waal & Preston, 2017). Consolation has thus been equated with sympathetic concern as it appears to represent an other-oriented prosocial motivational response to improve another individual's emotional state (de Waal, 2008).

Although the cognitive complexity of consolation remains under debate, genuine consolation (i.e., that which has a tension reducing function in the receiver and cannot be otherwise clearly explained as having an alternative function) appears to be rare in the animal kingdom, including among primates (Adriaense et al., 2020). Thus far, humans, bonobos, and chimpanzees are three of the few species known to use consolation in their day-to-day social lives (for a review of consolation studies in all animals, see Adriaense et al., 2020). Although ape research is generally limited to captive and semi-wild populations, wild chimpanzees have been shown to console (Taï National Park, Ivory Coast: Wittig & Boesch, 2003; Mahale Mountains, Tanzania: Kutsukake & Castles, 2004). The eastern chimpanzee subspecies at Budongo do not appear to use consolation or explicit gestures during post-conflict interactions (Arnold & Whiten, 2001). Although wild bonobos have not been explicitly tested, multiple captive and semi-wild bonobo populations have been shown to console (Clay & de Waal, 2013; Palagi et al., 2004). Similar consolation behaviours are seen across *Pan* including embracing, touching, and patting. However, bonobos are much likelier to use sexual contacts to console conspecifics regardless of the age or sex of the victim or consoler (de Waal, 1988; see *Chapter 7*).

In humans, research has generally been limited to developmental studies in young children (Davidov et al., 2013, 2021; Fujisawa et al., 2006; Roth-Hanania et al., 2011; Zahn-Waxler et al., 1992). However, a recent study showed that adult human consolatory tendencies following robberies resemble those seen in chimpanzee post-conflict studies (Lindegaard et al., 2017). Consolation emerges early in human development, as early as nine months (Davidov et al., 2013; Davidov et al., 2021; Vreden et al., in prep). Such early responses are also seen in bonobos and chimpanzees, with consistent age effects showing that consolatory tendencies appear to be highest in young individuals and decrease as apes age (Clay & de Waal, 2013; Webb et al., 2017).

Observations of infant humans, apes, and other mammals offering comfort to distressed others contradicts a common assumption that consolation requires complex cognitive processes (de Waal & Preston, 2017). Instead, with age, consolation may become a more conscious and targeted response, whereas in infants it may be more reflexive. Like humans, male chimpanzees have been shown to become more selective in their social interactions as they age, favouring social partners with whom they have a strong reciprocal bond (Rosati et al., 2020). In contrast, younger males tend to have more one-sided relationships. This increasing selectivity may therefore manifest in reduced consolatory tendencies, particularly as recipients of aggression are often younger males and females that older individuals may not have developed a close relationship with (Sabbi et al., 2021).

Subsequently, the recipients of these responses may be more likely to be those with whom the initiator has a stronger reciprocal social bond.

Social closeness has been shown to predict consolation in both human (Lindegaard et al., 2017) and nonhuman apes (Fraser et al., 2008; Palagi & Norscia, 2013). These trends reflect the view that empathic responses are more likely between individuals that share close relationships (Preston & de Waal, 2002). Therefore, empathic behaviours, like consolation, may help to strengthen interpersonal bonds and group cohesiveness. Consolation also appears to be used as a substitute for reconciliation in human children. A developmental study found reconciliation and consolation increased significantly in 5-year-olds, compared to 3- and 4-year-olds, and consolation more often occurred when no reconciliation had taken place (Fujisawa et al., 2006). However, other studies have indicated that consolation does not serve as a replacement for reconciliation in chimpanzees (Koski & Sterck, 2007) or bonobos (Clay & de Waal, 2013).

Sex differences in *Pan* consolation have been suggested but remain unclear. In one study, female chimpanzees seemed to console more than males (Romero et al., 2010). However, other studies have suggested either no sex differences (Webb et al., 2017). Romero et al. (2010) found that despite females appearing to be the most consolatory, high-ranking males offered consolation the most. Therefore, it may be likely that structural differences in dominance distribution and social composition across captive groups may facilitate varying tendencies across sex classes. On a similar note, consolation, like other behavioural empathic expressions, is believed to be influenced by levels of social tolerance (de Waal & Aureli, 1996). The presence of consolation in these species indicates that increased tolerance may facilitate empathic responses that might otherwise be inhibited due to intimidation or fear of aggression. This appears to be the case beyond apes, as socially tolerant Tonkean macaques (*Macaca tonkeana*) are another species shown to use true consolation, whereby their despotic counterparts do not (Palagi et al., 2014). Furthermore, higher tolerance towards infants and juveniles in bonobos and chimpanzees, and therefore lower risk of redirected aggression, may explain why consolation is more prevalent in younger age classes.

Consolation enables us to study empathy from a more nuanced perspective; whilst consoling behaviour may be prosocial, motivations may not be strictly altruistic. Victim-directed affiliation may also result in punishment avoidance, social rewards, or personal arousal reduction (Batson, 2010). Consolers may receive benefits through reciprocity, such as receiving post-conflict affiliation in the future (Watts, 2002). Furthermore, consolation may reduce potential reactive aggression in the victim, thereby benefiting the consoler and the group as a whole (Palagi et al., 2006). Empathy need not be used benevolently; it may be used by humans and other animals for personal or inclusive fitness benefits that are not necessarily associated with comforting a distressed victim. Consolation is one such behaviour that may be mediated by individual and social factors and not as an indiscriminate response brought about by emotional sensitivity.

2.3.4 Perspective-taking

The ability to ascribe mental states to others, known as Theory of Mind (ToM), enables one to take another's perspective (Premack & Woodruff, 1978). ToM can emerge from understanding of what others think and what their actions might be, and knowledge of others' mental states, or "putting oneself in someone's shoes" (Goldman, 1989). ToM thereby facilitates the capacity to distinguish between the states of oneself and others, a building block for empathy (Batson et al., 1997; Decety & Svetlova, 2012). Human studies indicate this ability can increase altruistic motivation—when one is able to imagine how another feels during a period of need (Batson et al., 1997). Cognitive appraisal of another's need thereby enables one to offer targeted assistance to specific needs (de Waal, 2008). However, if perspective-taking goes too far, and one imagines directly being in another's position without clear self-other distinction, personal distress may increase (Batson et al., 1997). Therefore, effective self-regulation of one's own affective state and a distinction between one's own state and another's is needed for genuine other-oriented concern.

Captive chimpanzees appear capable of understanding the goals of conspecifics (Yamamoto et al., 2012) and can process what other individuals can see and not see (Bräuer et al., 2007; Hare et al., 2000). For example, subordinate chimpanzees are able to process what dominant conspecifics perceived during social food problem-solving tasks, including in competitive contexts (Bräuer et al., 2007; Hare et al., 2000). In this experiment, the subordinates preferentially approached food that they knew the dominants had not seen. Subjects even seemed able to keep track of who had seen what, as they consistently chose the hidden options when the dominant individual was replaced with another dominant. This perspective-taking also occurred when the competitors were humans (Hare et al., 2006). Comparatively, bonobos appear to be more adept than chimpanzees in similar tasks, achieving higher scores in gaze following and tasks on understanding others' goals and intentions (Herrmann et al., 2010).

Therefore, both species appear capable of learning others' visual perspectives and of using this information strategically to navigate social and competitive situations. Chimpanzees also appear to be capable of processing what other individuals can hear. When presented with "noisy containers" and "silent containers", both containing desirable food, chimpanzees preferred to search from the silent containers when human experimenters were facing the other way, indicating both a visual and auditory understanding (Melis et al., 2006). Whilst such research has not yet been conducted with bonobos, one might expect they would be likely to show such capacities, due to their similarities with chimpanzees as well as their other aforementioned documented perspective-taking abilities.

By 9 months of age, human infants can separate the preferences of different agents without generalising (Buresh & Woodward, 2007; Henderson & Woodward, 2012). By 18 months, infants can understand that individuals can have desires and preferences different to one's own (Repacholi & Gopnik, 1997; but see Ruffman et al., 2018). Explicit false belief understanding, that is being able to explicitly attribute two conflicting views of the world—one's own, aligning with reality, and one that does not—seems to develop from 4 years of age onwards (Baillargeon et al., 2010; Scott & Baillargeon, 2017). However, a rise in use of non-traditional techniques has uncovered evidence that infants as young as 9 months of age have some capacity of implicit false belief understanding (see Scott & Baillargeon, 2017 for a review). Using similar eyetracking techniques, Krupenye et al. (2016) found evidence of implicit false belief understanding in great apes. Bonobos, chimpanzees, and orangutans showed anticipatory looking to a location where an actor falsely believed an object to be hidden, even though the apes knew it was no longer there.

In summary, humans and *Pan* seem to share a capacity of taking the perspectives of others into account, such as desires and the presence of false beliefs. Humans possess perspective-taking capacities so far not demonstrated in other species, including explicit false-belief understanding (Krupenye, 2021). However, theory of mind tests of preverbal infants and apes have shown that some forms of perspective-taking can exist without human language. For apes, many assessments have been conducted in captivity and test responses to experimental stimuli. In the wild, bonobos and chimpanzees navigate their interconnected social worlds seemingly without communication systems that are as complex and multi-faceted as those of humans. For example, chimpanzees coordinate hunts with individuals fulfilling specific roles to ambush and capture prey (Boesch, 1994). Thus, the true extent of how great apes can fully understand the perspectives of others is still unclear. Continued investigation of the most advanced perspective-taking skills in more groups of apes in varying living conditions may yet reveal their presence.

2.3.5 Targeted helping

By accurately discerning another's states and needs, individuals can tailor their active prosocial responses to meet a recipient's specific requirements (de Waal, 2008). This is termed targeted helping (de Waal, 2008), and is thought to require accurate perspective-taking of another individual's situation in order to provide an effective response (Yamamoto et al., 2012). Bonobos' and chimpanzees' helping behaviour has generally been studied experimentally using food-related paradigms, expressing both positive (bonobos: Tan & Hare, 2013; chimpanzees: Claidière et al., 2015; Greenberg et al., 2010; Horner et al., 2011; Melis et al., 2011; Warneken & Tomasello, 2006; Yamamoto et al., 2009, 2012) and negative other-regarding preferences (bonobos: Amici et al., 2014; chimpanzees: Amici et al., 2014; Jensen et al., 2006; Silk et al., 2005; Vonk et al., 2008).

In a seminal study, Yamamoto et al. (2012) found that captive chimpanzees, whilst able to provide targeted help by providing conspecifics with specific tools, generally only helped others when directly requested. Therefore, these responses cannot count as targeted helping as the responses are not spontaneous, despite suggesting an understanding of the needs of others. In contrast, bonobos have been observed to voluntarily aid strangers with obtaining food, even when not overtly solicited (Tan et al., 2017). Furthermore, bonobos have also been seen to share food with unfamiliar conspecifics in return for social interactions, even unselfishly helping strangers reach inaccessible food (Tan & Hare, 2013). In a comparative study, bonobos outperformed chimpanzees on cooperation tasks when food was monopolisable (Hare et al., 2007). Such behaviour may relate to why bonobos appear more willing to interact positively with strangers and build wider social networks.

Distinguishing empathy-related targeted helping from other prosocial responses depends upon whether the action is fine-tuned to an individual's specific situation and need (Pérez-Manrique & Gomila, 2018). Such flexible behaviours have primarily been reported as case studies and anecdotes in the form of rescuing and epimeletic behaviour, including caring for ill or injured individuals and pre-emptive protection (de Waal, 2019; Pruetz, 2011). There are several qualitative reports of chimpanzees spontaneously affiliating with and helping injured group members (Boesch, 1991; Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1985). Injury and wound attendance may reflect an understanding of another's suffering and care directed towards an individual and may reflect a motivation to alleviate or ease that suffering. Wound cleaning is a common behaviour in wild chimpanzees, whereby individuals will inspect injuries of conspecifics by licking and grooming them (Boesch, 1991; Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1985).

Nonhuman apes have been anecdotally observed to respond to the specific needs of others, such as a young male chimpanzee assisting an unrelated female by carrying her infant (Pruetz, 2011). Neither the female nor infant had expressed any markers of distress, and this behaviour was reported as unusual for this male and did not appear to bring him any direct benefits. Similarly, a group of chimpanzees have been observed to wait for an injured group member who was unable to keep up (Boesch, 1992). In addition, Hirata (2009) has outlined a variety of instances where chimpanzee mothers have rescued infants from dangerous circumstances by observing their behaviour and responding accordingly. There are also case reports in both wild bonobos and chimpanzees, where they have helped remove snares from trapped groupmates (bonobos: Tokuyama et al., 2012; chimpanzees: Amati et al., 2008).

Furthermore, in bonobos, de Waal (2019) reported an anecdote where a captive dominant male at San Diego Zoo attracted a keeper's attention as some juvenile conspecifics had fallen into a dry moat. The juveniles were unable to get out and if the moat had been filled, they would have drowned due to an inability to swim. Whilst some of these responses may be related to maternal instincts (Hirata, 2009), the notion of providing pre-emptive protection may represent an epimeletic form of targeted helping (Pérez-Manrique & Gomila, 2018), which could reflect a form of empathy; understanding imminent risk and consequences and actively taking prosocial steps to avoid them. These case reports represent instances where individuals may have taken pre-emptive altruistic steps to help others, when the consequences of not helping could have been severe.

It is conceivable to think that our closest living relatives may be able to flexibly respond to the emotional needs of others. Whilst still distantly related to bonobos and chimpanzees, fossil records indicate that severely injured and disabled Neanderthals were able to survive for relatively long periods, suggesting they were supported by their community (Spikins et al., 2018). Furthermore, the injury or death of fellow group members has been shown to cause observable distress in wild (Boesch, 1991), captive (Anderson et al., 2010), and semi-wild chimpanzees (van Leeuwen et al., 2016), as seen by vocalisations, agitation, and anxiety-related behaviours. Individuals can be attentive and affiliative towards dying conspecifics and even guard their corpses (Anderson et al., 2010; Boesch, 1991). One case report from sanctuary-living individuals even recorded corpse cleaning behaviour using tools to remove debris from the teeth of the deceased groupmate (van Leeuwen et al., 2017). Whilst the individual 'cleaning the corpse' may have been separately motivated to acquire food from the teeth or even learn about death, the individual notably forfeited high-quality food offered by caretakers in attempts to lure her away from the body. Such care towards injured, weak, and deceased individuals is common in humans and may have ancient evolutionary origins.

It is difficult to systematically measure targeted helping in real-life contexts, such as responding to injuries among humans and *Pan*, due to their rarity. However, experimental studies indicate promising directions for studying empathic responses to others' pain. Human research has shown that observers of painful contexts experience arousal (Hein et al., 2011; Kupfer, 2018), via measuring heart-rate (Preis & Kroener-Herwig, 2012), pupil diameter (Azevedo et al., 2013) and skin temperature changes (Salazar-López et al., 2015). In human children, prosocial behaviour appears to be motivated by other-oriented concern and inner arousal, as measured in this case by pupil dilation (Hepach et al., 2013). Sato et al. (2019) found chimpanzees spontaneously attended to injured conspecifics more so than to non-injured conspecifics; moreover, thermal imaging revealed that chimpanzees exhibited greater reduction in nasal temperature reduction when viewing an injury rather than a control stimulus. Currently there is no explicit programme for studying emotional targeted helping in animals systematically, in both natural and experimental conditions. In addition, like consolation, forms of helping and cooperative behaviour may lead to personal fitness benefits beyond other-oriented concern, such as reciprocity (Wedekind & Milinski, 2000). However, using these paradigms to compare internal and external responses to the emotions of others across multiple populations within and between species, may help to uncover the affective mechanisms and possible emotional motivations that may underlie *Pan* helping behaviours.

2.4 Future directions

Some components of empathy have been studied at length in chimpanzees and to a lesser extent in bonobos. Cross-species comparisons indicate greater emotional attentiveness and perspective-taking abilities in bonobos than in chimpanzees, but systematic comparisons across these components are generally lacking. I describe here examples of where future research may focus, to uncover whether species differences are pronounced in these behaviours, as well as additional approaches that could reveal deeper insight into *Pan* emotional understanding.

2.4.1 Socio-cultural aspects of empathy

Great ape societies have been shown to vary socio-culturally, whereby social and even arbitrary behaviours emerge and are culturally transmitted, such as grooming traditions (van Leeuwen et al., 2017) and the "grass-in-ear" behaviour observed by van Leeuwen et al. (2014). If consolation involves a learned component, it could well follow similar group-specific functions and individual responses may vary across social cultures. As consolation has been observed among most *Pan* communities tested (Fuentes et al., 2002), yet differs in rarity (Arnold & Whiten, 2001; Kutsukake & Castles, 2004), its expression may be dependent on variable social dynamics. Empathy expressions have been shown to vary across human cultures (Chopik et al., 2017). It is likely that proclivity of behaviours such as consolation and emotional contagion may vary across the diverse societies of our closest living relatives too, being contingent on social composition and group structure. Cultural differences may also be reflected in the trends observed between different groups, such as inconsistencies in sex effects. The dominance structure in the captive group studied by Romero et al. (2010), may facilitate a more tolerant environment for females and they may play a more involved role in conflict management than in other groups. To understand these species at more length, it may be appropriate to focus less on how they differ between species but how collective temperaments and inter-individual dynamics vary between groups.

The '*Social Constraints Hypothesis*' (de Waal & Aureli, 1996) posits that consolation depends on the social tolerance levels of a given social structure. In social primates, the risks of further aggression for potential bystanders appear to be lower in more tolerant societies (Fraser et al., 2009), and this may have facilitated the emergence of consolation in the most tolerant species. Palagi et al. (2014) compared two macaque species differing in social tolerance in their social structures. They found that consolation was present in the tolerant Tonkean macaques (*Macaca tonkeana*) and absent in the despotic Japanese macaques (*Macaca fuscata*). Consolation was biased towards close grooming partners and predicted a reduction in victim self-scratching, therefore following the trends seen in *Pan*.

Whilst bonobos were traditionally considered generally more socially tolerant than chimpanzees (Hare et al., 2012), collective temperaments and social tolerance have been shown to vary across sanctuary-living *Pan* groups (van Leeuwen et al., under review), even indicating greater differences within-species than between. As tolerance has been linked with prosocial and empathic responses (Martin et al., 2021; Palagi et al., 2014), one might expect that more tolerant groups of chimpanzees or bonobos would show more consolatory tendencies than less tolerant groups.

Empathic responsiveness may fluctuate if social developments culminate in a higher personal and or interpersonal benefit through engaging in more consolatory responding. For example, in the case of consolation, the proclivity for redirected or renewed aggression may differ depending on collective temperaments and the individual personalities of the involved parties. However, research demonstrates that consolatory tendencies are temporally stable across chimpanzee lifespans (Webb et al., 2017), indicating that empathic behaviour may reflect individual personality characteristics and are not as vulnerable to group/cultural changes. Longitudinal studies across multiple groups in parallel with objective measures of collective temperaments are needed. Such data can be compared with records of affective responses through the non-invasive methods highlighted previously, so as to assess the longevity and association of individual responsiveness and what factors may influence it over time.

2.4.2 Reassurance

A consistently observed behaviour across *Pan* and human cultures is the use of reassurance behaviour—affiliative body contact used to reduce anxiety or aggressive tendencies in another individual (de Waal, 1989a; van Hooff, 1967)—during socially tense situations. Aggression can be common for large groups of primates living in environments that foster competition. To alleviate such tension during high-anxiety periods and prevent conflicts, individuals may offer and seek social reassurance, often from more dominant group members (de Waal, 1986b, 1992; Goodall, 1986). Reassurance can occur through gestural and physical body contacts and has been observed in wild chimpanzees responding to the vocalisations of unfamiliar conspecifics (Herbinger et al., 2009). Despite being regularly referenced in the literature, little is known about whether affective mechanisms underlie these behaviours nor how they may relate to consolation, which itself represents a context-specific form of reassurance.

As discussed, pre-emptive protection has been considered a measure of empathic targeted helping. Whilst conflict resolution has been documented extensively in the human and animal literature, pre-emptive prevention of conflicts – which may involve protecting the self as well as kin or other group members – through emotional recognition and action has rarely been discussed. Yet, through studying reassurance, we may be able to tap into a different level of emotional awareness and uncover the strategies that chimpanzees and bonobos use to alleviate social tension, prevent conflicts from occurring, and thus maintain group cohesion and stability.

An extensive repertoire of reassurance behaviours for both species has been identified, with significant overlap, including mount and embrace, genital inspection, and begging (de Waal, 1988; Goodall, 1989). Bonobos tend to engage in greater sexual reassurance, including ventro-ventral genital rubbing (de Waal, 1988). Post-conflict affiliation, including consolation, is a context-specific form of reassurance between victims of conflicts and uninvolved bystanders (Clay & de Waal, 2013; Romero et al., 2010). In these situations, they appear to be deployed to reduce conspecific distress, which in turn may prevent redirected aggression towards other group members or future instances of the consoler being aggressed. In non-conflict high-tension contexts, these behaviours may be used to alleviate anxiety in the initiator and receiver alike, during a period at high-risk of aggressive interactions.

Reassurance offers the opportunity to look at a potential means of pre-emptive protection of the self, kin, and other group members, through understanding the anxiety felt in conspecifics and taking prosocial actions to help reduce that anxiety. As has been highlighted, empathic behaviour need not be entirely altruistic, so reassurance contacts may just be motivated by self-protection. Nevertheless, individuals may need to comprehend conspecific anxiety and assess the relative risk of aggression faced. Therefore, it would be reasonable to predict that reassurance contacts may increase with individual- and/or group-level tension, measurable by observing markers of anxiety, such as self-directed behaviours and particular vocalisations and gestures. Furthermore, the differences in resource value and distribution may also influence the propensity to engage in these behaviours. Individuals may also be likelier to direct their attention towards those most likely to be aggressive but would also be expected to seek reassurance from kin and close social contacts (Preston & de Waal, 2002).

Reassurance behaviour among primates, including chimpanzees and bonobos, is especially common during periods of high anxiety such as pre-feeding (de Waal et al., 2000; Paoli et al., 2007). Studying reassurance would be most appropriate in these settings as they typically offer disciplined feeding schedules that would provide enough pre-feeding time for observations (Young et al., 2018). Great ape sanctuaries are particularly suited to this type of research with varying group sizes and fluctuating food competition, thereby likely influencing the form, function, and frequency of reassurance behaviours. Systematic comparisons can be made between groups as well as settings and species, as seen in social tolerance comparative research in bonobos and chimpanzees (van Leeuwen et al., under review).

2.5 Discussion

As with humans, strong social support networks are important for our closest living primate relatives. The empathy-related behaviours outlined in this review facilitate the growth of such relationships. These behaviours have consistently been observed in both species, including mimicry, consolation, and targeted helping (Gruber & Clay, 2016). However, direct comparisons so far only indicate that bonobos have greater perspective-taking abilities. Observational and experimental reports indicate that, across other empathy paradigms, neither species excels over the other. The lack of clarity is primarily due to a lack of direct species comparisons. Some of these behaviours, such as the case reports of epimeletic helping, are impossible to study systematically as they rely on opportunistic observations. However, wild *Pan* individuals have been observed to offer support to fellow group members following or during distressing and difficult circumstances.

Bonobos appear to have greater social attentiveness to conspecifics than chimpanzees (Kano et al., 2015), and show rapid responses towards others' emotional expressions (Kret et al., 2016). These tendencies may be facilitated by different biological mechanisms, whereby chimpanzees, but not bonobos, appear to have deletion of the DupB region in the *AVPR1A* gene, which facilitates a microsatellite called RS3 (Staes et al., 2014). RS3 is associated with social bonding, and increased levels in bonobos may support their reported xenophilia. This is further supported by neurological research, which shows that bonobos have twice the density of serotonergic axons in the amygdala (Stimpson et al., 2016). In addition, Rilling et al. (2012) found that, compared to chimpanzees, bonobos have more grey matter in the right dorsal amygdala and right anterior insula, regions associated with perceiving distress in oneself and others. Further, the pathway linking the amygdala with the ventral anterior cingulate cortex is also larger in bonobos. This pathway is implicated in the control of reactive and proactive aggressive impulses. Therefore, these differences support increased emotional sensitivity and inhibition in bonobos but may also explain why more severe conflicts and escalation of conflicts tend to occur in chimpanzees.

These neuroanatomical differences may reflect interspecies differences in emotional regulation and social cognition, including empathy-related behaviours. However, other characteristics that appear to facilitate empathy do not vary between species as much as previously thought. Bonobos have previously been declared to be the more socially tolerant species (Hare et al., 2007), a factor that appears to be crucial for facilitating behavioural manifestations of empathy. A recent cofeeding within-group experimental study tested captive and semi-wild populations of bonobos and chimpanzees and found social tolerance levels in fact appeared to vary more within species than between them (van Leeuwen et al., under review). It should be noted that this tolerance overlap extends only to within group conspecifics. Whilst chimpanzees are exclusively hostile to outgroups and many bonobo intergroup encounters result in agonism and threat vocalisations (Clay et al., 2016; Furuichi, 2020), some bonobo societies have been seen to have more tolerant intergroup encounters, typically when feeding competition is lower (Lucchesi et al., 2020; Sakamaki et al., 2018).

Furthermore, the opportunity to provide empathy-related responses, such as consolation and helping behaviour, may be disproportionately larger in chimpanzees than bonobos, due to the difference in social dynamics. The need to console and reduce social tension is possibly much higher in chimpanzees due to the structure of their hierarchies and a much higher risk of aggression and injury (Hare et al., 2012; Wilson et al., 2014). The politics of a chimpanzee society may lend itself to increased rates of empathic behaviour, as individuals seek to maintain group cohesion and protect their personal status and kin.

Bonobos and chimpanzees are two of the most studied primate species when it comes to empathy and other emotional capacities. It has been suggested that bonobos may be more empathic than chimpanzees due to generally exhibiting less severe aggression (Hare et al., 2012; Parish et al., 2000), and what seems to be a neurological predisposition for stronger social and emotional attentiveness (Kano et al., 2015; Kret et al., 2016). Yet, thus far there is no direct comparative evidence to support such a statement. Whilst many primates have been observed responding in more basal empathy-related paradigms, such as mimicry and contagion, the *Pan* species have consistently been observed to use multiple forms of empathy. Some of these responses, including consolation, emerge early developmentally and appear to remain consistent ontogenetically (Webb et al., 2017). The early development of sensitivity to the emotions of others may facilitate the emergence of different empathic responses and emotional understanding at younger ages.

A combination of new and established empathy research methods offers a broader and more nuanced approach to understanding the functions of empathy. Whilst bonobos excel (relative to chimpanzees) in perspective-taking and emotional sensitivity, the species appear to overlap in how they respond to the states of others. Both bonobos and chimpanzees appear to perceive the states of others in sophisticated ways. Furthermore, whilst bonobos may have better perspective-taking abilities, both species appear capable of comprehending and processing other's beliefs. Finally, when fellow group members are in distress or need specific assistance or support, both species provide consolation and targeted help.

Studying our closest living relatives provides insights into the origins of our own social and emotional behaviour. As we share a close evolutionary history with bonobos and chimpanzees, studying their expressions of empathy may elucidate the journey of how modern human empathy developed through our ancestral lineage. However, we share more than this close genetic history with *Pan*. We overlap with many aspects in our social structures and capacity for physical and social cultures. We also appear to share empathy-related behaviours, ranging from mimicry and contagion, to comforting of distressed conspecifics and epimeletic helping.

Still, there seems to be a divide between human and ape empathy. Some socio-cognitive behaviours, such as false belief understanding based on explicit behavioural choices, are yet to be identified in *Pan*. Similarly, true helping in experimental tasks has been difficult to determine, due to task design and use of biased samples, consisting of apes raised in restricted, man-made environments. Importantly, though, certain behaviours once thought to be facilitated by language have been shown to be present in preverbal infants and nonhuman apes (Scott & Baillargeon, 2017). The continued use of non-traditional techniques for tasks such as perspective-taking, may continue to reveal that these capacities can emerge in the absence of human language through underlying shared mechanisms.

With the progression of animal empathy research has come the understanding that animals possess the building blocks of morality, as concepts such as reciprocity, conflict resolution, and cooperation are incorporated into animal societies (de Waal, 2008). Yet, despite the growth of research into ape social cognition, a systematic programme that truly incorporates all we know about great ape empathy is lacking. More cross-species investigations would be insightful for making comparisons across phylogeny. The multidimensional view of empathy as a process, varying in levels and combinations of complexity, from emotional contagion to theory of mind, enables us to study behaviours in other species, and thereby evaluate the origins of human social and moral nature.

Chapter 3: General methods

3.1 Study sites and team

For this thesis, I analysed data from two African great ape sanctuaries. I collected data on chimpanzees during a field season at Chimfunshi Wildlife Orphanage Trust (hereafter: Chimfunshi) in Zambia between March and August 2019 alongside a collaborator, Zoë Goldsborough (hereafter: ZG). In addition, another collaborator, Stephanie Kordon (hereafter: SK), led data collection on bonobos at Lola ya Bonobo Sanctuary (hereafter: Lola ya Bonobo) in the Democratic Republic of the Congo between July and September 2019 which I subsequently analysed. At Lola ya Bonobo, SK supervised a research assistant named Heritier Izansone (hereafter: HI), who assisted with experimental sessions and observations of social relationships. ZG and I logged 800 hours of observations at Chimfunshi and SK and HI logged 600 hours of observations at Lola ya Bonobo. I supervised all data collection and led all of the analyses and authorship for the studies included in this thesis. Here I describe the general structure of these sanctuaries regarding the set-up of their facilities, the composition of the study groups, and the general diet and enrichment they provide for their residents.

CHIMFUNSHI
gives a home to chimpanzees in need

3.1.1 Chimfunshi Wildlife Orphanage Trust, Copperbelt Province, Zambia

3.1.1.1 Background

Chimfunshi was founded in 1983 by David and Sheila Siddle, cattle farmers based in the Copperbelt Province of Zambia, approximately 58 kilometres from Chingola, the nearest city. A game ranger brought a wounded infant chimpanzee to the Siddles, who named him Pal and nursed him back to health. This triggered the formation of a sanctuary for orphaned chimpanzees rescued from the pet and bushmeat trades, as well as circuses and dilapidated zoos from around the world. To date, Chimfunshi is one of the largest (9300 ha / 93 km^2) and oldest chimpanzee sanctuaries in the world, housing over 140 individuals across eight forested enclosures. Whilst most of the original chimpanzees were rescued, many have been subsequently born onsite.

3.1.1.2 Group composition and facility set-up

Four of the groups at Chimfunshi are open to researchers for naturalistic observations and experimental data collection. Designed to mimic their natural environment, Chimfunshi's outdoor enclosures (ranging from 19–77 ha / 0.19–0.77 km^2, see *Figure 3.1*) comprise miombo woodland forest, a mixture of grassland, trees, and bushes (*Figure 3.2*). Each enclosure is supplemented with an indoor handling facility with lockable compartments to allow supplementary feeding, veterinary care, and social integration. If an individual requires ongoing health treatment, they may be kept in the indoor handling facility for a period of time as required. Otherwise, all groups spend most of their time outside, where they can forage and nest independently.

Figure 3.1. Satellite view of the four chimpanzee enclosures at Chimfunshi Wildlife Orphanage Trust, Zambia. Enclosure area sizes: 1 (Group C1) = 77 ha / 0.77 km^2; 2 (Group C2) = 65 ha / 0.65 km^2; 3 = 19 ha / 0.19 km^2; 4 = 25 ha / 0.25 km^2. Satellite image obtained through Google Maps and edited in Adobe Photoshop.

Figure 3.2. Photo of chimpanzee cousins, Chitalu (left) and Camilla (right) from group 2 (C2), surrounded by the miombo forest that makes up their enclosure at Chimfunshi Wildlife Orphanage Trust, Zambia. Photo by J. S. Brooker.

For my thesis, I analysed data collected from two groups. For consolation observations, with ZG, I studied group 2 (hereafter: C2) comprising 50 individuals at the start of our field season (28% wild-born; 72% captive-born). For prefeeding affiliation observations, we conducted the *peanut swing* experiment at group C2 and group 1 (hereafter: C1) comprising 25 individuals at the start of our field season (20% wild-born; 80% captive-born). Across both groups, three mothers gave birth between May and July 2019. We did not collect data on any of these infants. Exclusions due to absences or limited sampling are provided in each empirical chapter. A full list of IDs and matrilineal relationships is provided in *Table 3.1*.

Table 3.1. Group composition of the two chimpanzee study groups at Chimfunshi Wildlife Orphanage in Zambia. Deceased individual included in parentheses to show sibling relationship. Infants born during study period presented in *italics* and were not studied. Em-dash (“—“) indicates individual is infant of the above mother. Age denoted in years. Groups feature chimpanzees of all subspecies. Asterisk (*) denotes wild-born individual.

Group 1 (C1)		
Name	Sex	Age
(Big Jane)[a] *		
— BJ	F	12
— Bob	M	17
Booboo *	M	37
Brenda	F	23
Chrissie	F	12
Girly *	F	37
— Genny	F	22
— Gloria	F	3
— Gonzaga	F	11
— Gerard	M	16
Ingrid	F	28
— Ida	F	3
— Ilse	F	16
— Ian	M	4
— Innocentia	F	12
— *Isaac*	*M*	—
— Irene	F	7
Pal *	M	38
Rita *	F	36
— Renate	F	22
—Rachel	F	6
—Regina	F	13
—Ricky	M	1
— Rogers	M	1
— Rusty	M	12
Tobar *	M	37

Group 2 (C2)		
Name	Sex	Age
Coco *	F	34
— Carol	F	22
— Camilla	F	2
— Charity	F	11
— Claire	F	16
— *Charlie*	*F*	—
— Chitalu	F	4
Debbie	F	17
— Don	M	3
Diana *	F	28
— Daisey	F	14
— David	M	17
— Diz	F	11
Dora *	F	30
— Danny	M	6
— Dolly	F	22
— Doug	M	16
Little Jane *	F	34
— Little Jenkins	F	12
— Little Joey	M	1
— Little Jones	M	8
— Little Judy	F	24
— Little Jacky	M	7
— *Little Jake*	*M*	—
— Long John	M	13
Maggie *	F	33
— May	F	6
— Merial	F	1
— Moyo	M	11
Masya *	F	28
— Mary	F	13
— Mumba	M	2
Mikey *	M	21
Misha *	F	31
— Martin	M	6
— Max	M	12
— Maxine	F	17
Noel *	F	42
— Nikkie	F	21
— Nina	F	16
— Nancy	F	2
Pan *	M	30
Pippa *	F	30
Tess	F	21
— Tina	F	3
Trixie *	F	29
— Tilly	F	18
— Tom	M	4
Violet *	F	28
— Victoria	F	1
— Vis	M	14
Zsabu *	M	29

3.1.1.3 Diet and enrichment

Chimpanzees of all groups can independently forage for naturally occurring fruits, leaves, herbaceous vegetation, and bark. Onsite keepers provide supplementary feedings twice per day, once in the morning typically from 1130–1200 and once in the afternoon typically from 1330–1400. Feedings consist of various seasonal fruits and vegetables, seeds, nuts, and nshima (a staple food in Zambia made from maize flour and water). Water fountains are installed in the outdoor part of each enclosure, which the chimpanzees operate themselves. During the dry season (June–September), pools in the outdoor enclosure may be filled with water for the chimpanzees to drink from or play in. The Chimfunshi volunteer programme was ongoing during my field season, which included the construction of enrichment stimuli and puzzle feeders. No enrichment was provided to groups C1 or C2 during our study period.

LOLA YA BONOBO
Les Amis des Bonobos

3.1.2 Lola ya Bonobo Sanctuary, Kinshasa, Democratic Republic of the Congo

3.1.2.1 Background

Lola ya Bonobo was founded in 1996 and is currently the largest bonobo facility in the world (30 ha / 0.3 km^2) housing over 70 bonobos. Most bonobos at Lola ya Bonobo are wild-caught infant or juvenile orphans, typically victims of the pet and bushmeat trades, as well as rescues from biomedical facilities. Infant arrivals are rehabilitated in a nursery group, where each bonobo is assigned a surrogate human mother. Following successful rehabilitation, individuals are integrated into diverse, mixed social groups. Groups at Lola ya Bonobo have been fluid over the years, with composition changing regularly. During our field season in 2019, the groups were considered relatively stable (though some males were prone to escaping). Lola ya Bonobo also manage a release site in the DRC, named Ekolo ya Bonobo, where, since its inception, more than 30 rescued bonobos have successfully been released back into wild primary rainforest.

3.1.2.2 Group composition and facility set-up

Lola ya Bonobo is located 30 km from Kinshasa, the capital city of the DRC in the Bas-Congo region. During the daylight hours, three groups of bonobos are free to roam in outside enclosures (ranging from 5–15 ha / 0.05–0.15 km^2, see *Figure 3.3*), comprising primary natural rainforest, lakes, swamps, streams, and open fields (*Figure 3.4*). Bonobos at Lola ya Bonobo sleep in separate indoor dormitories (approximately 75 m^2) connected to each enclosure.

Figure 3.3. Satellite view of the three enclosures at Lola ya Bonobo, Democratic Republic of the Congo. Enclosure area sizes: 1 (Group B1) = 10 ha / 0.10 km^2; 2 (Group B2) = 15 ha / 0.15 km^2; 3 (Group B3) = 5 ha / 0.05 km^2. Satellite image obtained through Google Maps and edited in Adobe Photoshop.

Figure 3.4. Photo of the enclosure of group 2 (B2) at Lola ya Bonobo, showing the combination of fields and primary rainforest that make up enclosures at the sanctuary. Photo by S. Kordon.

For my thesis, I analysed data collected from all three groups. For consolation observations, SK observed group 1 (hereafter: B1) comprising 22 individuals (77.7% wild-born; 22.3% captive-born) and group 2 (hereafter: B2) comprising 18 individuals (66.7% wild-born; 33.3% captive-born). Two male bonobos were excluded from all analyses due to long periods of absence from their main groups (62–95% of observation time). For prefeeding affiliation observations, SK and HI conducted the *peanut swing* experiment at groups B1 and B2 as well as group 3 (hereafter: B3) comprising 14 individuals (64.3% wild-born; 35.7% captive-born). Other relevant exclusions due to absences or limited sampling is provided in each empirical chapter. A full list of IDs and matrilineal relationships is provided in *Table 3.2*.

Table 3.2. Group composition of the three bonobo study groups at Lola ya Bonobo in the DRC. Em-dash ("—") indicates individual is infant of the above mother. Age denoted in years. All individuals that are not denoted as offspring were brought to the sanctuary as orphans.

Group 1 (B1)		
Name	Sex	Age
Bandundu	F	21
— Likunzi	M	2
— Moseka	F	6
Bikoro	M	5
Katako	F	14
Kikwit	M	20
Kinsele	M	7
Kinzia	F	8
Lalia	F	6
Lopori	M	8
Lubi	F	7
Manono	M	24
Matadi	M	18
Ndjili	F	8
Opala	F	23
— Pole	M	13
Oshwe	M	11
Salonga	F	21
Semendwa	F	22
— Elikya	F	13
Waka	F	13
— Kitoko	M	3

Group 2 (B2)		
Name	Sex	Age
Boma	F	9
Bombo	M	10
Dilolo	M	17
Eleke	M	15
Garamba	M	9
Kalina	F	20
— Baraka	F	3
— Bolingo	M	8
— Malaïka	F	11
Keza	M	30
Kimya[a]	F	8
Kodoro	M	11
Liyaka	F	8
Mabali	M	15
Maniema	M	16
Minova	F	8
Nyota	F	7
Singi	M	9

Group 3 (B3)		
Name	Sex	Age
Boende	M	18
Chibombo	M	13
Fizi	M	18
Isiro	F	21
Kinshasa	F	14
— Mobondisi	F	3
Likasi	F	17
— Elonga	F	6
Lomako	M	11
Makali	M	36
Tshilomba	F	30
— Minzoto	F	4
— Moyi	M	11
— Sanza	F	8

3.1.2.3 Diet and enrichment

Bonobos at Lola ya Bonobo can forage independently for wild fruits, leaves, and vegetation, but are also provisioned by keepers 3–4 times daily. Feedings consist of various seasonal fruits and vegetables in the morning and afternoon. Keepers also provide water at least once per day to each individual as well as daily supplement feeds comprising seasonal fruits and nuts. The bonobos can also access water in lakes, ponds, and streams within their enclosures.

3.2 General protocols for data collection

To measure and compare post-conflict consolation and prefeeding affiliation in sanctuary-living bonobos and chimpanzees, I devised a set of research protocols designed to collect comparable data across study sites and groups. This included a combination of naturalistic observations and application of an established group-based experimental manipulation, which I modified for my specific research aims. My use of naturalistic observations was to collect data for: post-conflict and post-distress victim follows to record instances of consolation (see *Section 3.2.1.1*); social relationships to compute a measure for dyadic relationship strength (see *Section 3.2.1.2*); and aggressive tendencies to assign categorical dominance rank values to each study subject (see *Section 3.2.1.3*). My use of an experimental manipulation was to systematically record affiliative behaviour during a controlled period of social tension (see *Section 3.2.2.1*).

3.2.1 Naturalistic observations

3.2.1.1 Victim focal follows (relevant to Chapters 4, 7, and 8)

Consolation has typically been recorded using the post-conflict/matched-control (PC/MC) method (de Waal & Yoshihara, 1983). This involves focal following an individual expressing victim-related behaviour (e.g., scream, tantrum, whimper; see *Figure 3.5* for an example of a distressed chimpanzee) for a standardised period—usually 5–10-minutes. The observer records the initiator and behaviour of all affiliative interactions that occur involving the focal victim. Post-conflict periods are then compared with matched control recordings observed at a similar time and circumstance a day later. The PC/MC method has already reliably demonstrated consolation in multiple bonobo and chimpanzee communities (Clay & de Waal, 2013; de Waal & Aureli, 1996; Palagi et al., 2004; Romero et al., 2010), including in some of these sample populations (Clay & de Waal, 2013). As we were not interested in proving the existence of consolation, rather what factors influence consolatory tendencies, we decided to forego collecting matched controls in order to maximise our data collection of both post-conflict and pre-feeding affiliation observations. Typically, a victim focal follow is recorded following a social conflict. In both bonobos and chimpanzees, individuals can spontaneously become distressed for non-conflict reasons. Thus, my data collection protocol included collecting focal follows of these events too, where possible, which I refer to as post-distress (PD) events. Previous studies of consolation show that most consolatory interactions occur during the first minute after distress (e.g., Clay & de Waal, 2013). All victim focal follows were thus ended after the first 5-minutes following distress to optimise our limited observation time.

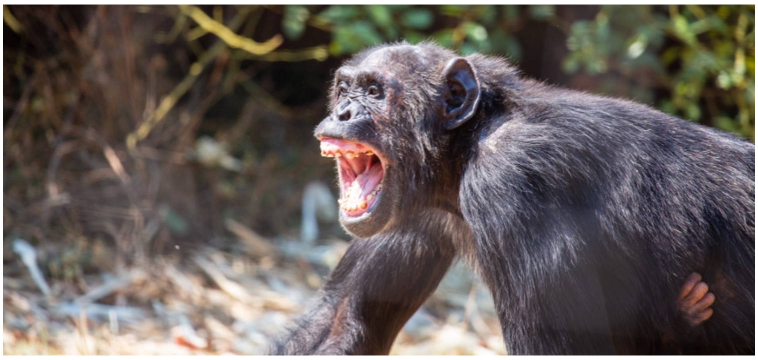

Figure 3.5. Photo of Misha, an adult female chimpanzee in group C2 at Chimfunshi Wildlife Orphanage. Misha was a distressed victim, exhibiting a scream. Photo by J. S. Brooker.

PC/PD events were all-occurrence sampled due to their unpredictable nature throughout the day. I defined agonistic encounters as the presence of at least one of the following behaviours: high-contact aggression [hit, slap, kick, trample, bite], low-contact aggression [poke, push, push away, brush aside], chase, or threat [threat bark, swagger, display, flail arm, stamp] (see *Appendix A.3*; Nishida et al., 2010; Goodall, 1986; de Waal, 1988; Kano, 1992). I only analysed post-conflict events where the victim elicited a clear victim response, identified as any combination of bared-teeth scream, whimper, tantrum, or flee from aggression (Nishida et al., 2010; Kano, 1992) following an agonistic encounter, where I coded the observation as a PC event. If victim response behaviours occurred in the absence of clear agonism, I coded the observation as a PD event. We noted the presence of all uninvolved bystanders at the onset of the event. PC/PD victim focal follows were recorded using Panasonic HC-V770 Camcorders with detachable Sennheiser MKE 400 directional shotgun microphones.

Figure 3.6. Photo of H. Izasone collecting naturalistic observations of group B2 at Lola ya Bonobo Sanctuary Zambia, using a Panasonic HC-V770 Camcorder fitted with a detachable Sennheiser MKE 400 directional shotgun microphone. Photo by S. Kordon.

3.2.1.2 Social relationships (relevant to chapters 4, 5, 7, and 8)

For chapters 4 and 8, I assessed the strength of social relationships among group members by collecting 10-minute focal scan follows (Altmann, 1974) of social behaviour to measure dyadic affiliation levels and individual gregariousness. We focal followed all individuals (except dependent infants) outside of feeding times for both species in the morning between 0800–1100 and afternoon between 1400-1700 hours. As I modelled affiliation at the dyadic-level, data accumulated on individuals who were not currently the focal subject if they associated with the focal. The focal data set consisted of 706 follows for bonobo group 1 (B1: range = 28–41; *M* = 32.1; *SD* = 11.0), 587 follows for bonobo group 2 (B2: range = 16–44; *M* = 34.2; *SD* = 11.3), and 684 follows for chimpanzees (C2: range = 9–18; *M* = 14.3; *SD* = 2.6).

Each focal follow consisted of 10 1-minute scan points. At each scan point, we recorded all social interactions the focal was engaged in including grooming (see *Figure 3.7*), play, sex, and sitting in 1-metre proximity (Martin & Bateson, 2007; Kano, 1992; Nishida et al., 1999). As social behaviours assume 1-metre proximity to the focal, we only coded either behaviour or proximity once per dyad per scan. For both behaviour and proximity, I divided the total scan points each dyad interacted for by the total scan points both individuals of the dyad were observed for (Clay & de Waal, 2013). However, when independent of one another, dyadic scores for behaviour and proximity were strongly correlated (r(375) = .43, *P* < .001). I thus collated behaviour observations and proximity observations together into one 'dyadic affiliation' observation and used this as a proxy for social relationship strength for each dyad. I computed individual gregariousness scores by dividing the total number of scans each focal subject was observed within proximity to at least one other individual by the total numbers of scans they were observed for.

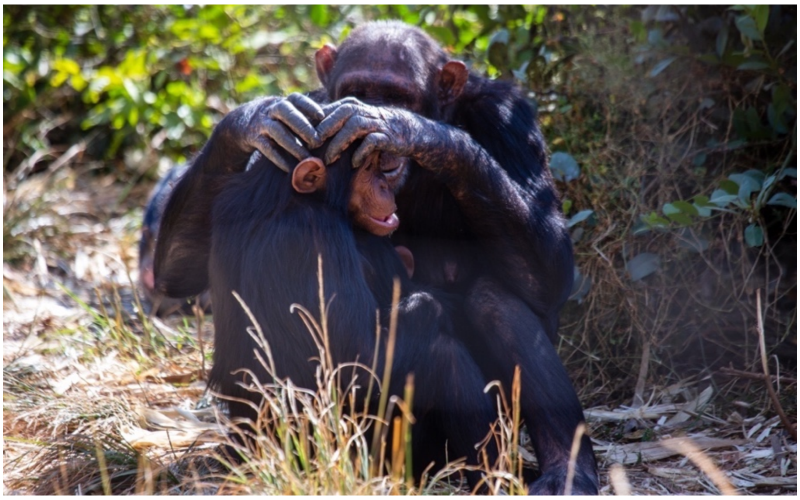

Figure 3.7. Grooming between two chimpanzees in group C2 at Chimfunshi Wildlife Orphanage, Zambia. Tess grooming the head of her daughter, Tina. Grooming is a social bonding behaviour in bonobos and chimpanzees. Photo by J. S. Brooker.

ZG and I recorded social focal scans at Chimfunshi using the free-ware tablet app Zoo Monitor (Wark et al., 2019; see http://www.zoomonitor.org/), our observations for which contributed towards long-term data collection of social relationships. At Lola ya Bonobo, due to software incompatibility, SK and HI recorded social focal scans by hand. Time constraints prevented us from collecting data on all five groups and thus we prioritised those we collected post-conflict focal follows on (B1, B2, and C2). Inter-observer reliability revealed almost perfect agreement between observers (partner identity: bonobo $\kappa > 0.80$; chimpanzee $\kappa > 0.96$; social behaviour: bonobo $\kappa > 0.95$; chimpanzee $\kappa > 0.93$).

Additionally, I was interested in the effect of kinship, and defined each dyad as 'kin' or 'nonkin' depending on whether they shared a maternal genetic relationship or not, respectively. This therefore included all mother-infant, sibling-sibling, and grandmother-grandchild pairs as 'kin'. Some dyads at Chimfunshi represented a genetic uncle-nephew dynamic and were also included as 'kin'. Full paternity data is currently unavailable at both field sites, and thus I was unable to consider paternal kin relationships.

3.2.2 Experimental manipulations

3.2.2.1 The "Peanut Swing"

The *peanut swing* is an established experimental paradigm for systematically comparing social tolerance across groups of semi-wild bonobos and chimpanzees (for full details on the *peanut swing*, including with groups from Chimfunshi, see Cronin et al., 2014, 2015; DeTroy et al., 2021; van Leeuwen et al., 2021). A trough-like receptacle, constructed from a bamboo pole, is measured to 1-metre length per five individuals and filled with 12 peanuts per individual in the group. This trough is then swung at chain-link enclosures, therefore systematically distributing a valuable, yet depletable, resource in a limited spatial zone (see *Figure 3.8* and *Figure 3.9*). Once the peanuts have landed inside the enclosure, researchers then count the total crowd size gathered within 1-metre of the fallen peanuts, in what is termed the *cofeeding zone*, at 15s intervals up to 2-minutes—typically by which time most of the peanuts have been eaten. By averaging these values and comparing across groups, one can assess the relative social tolerance of *Pan* groups, whereby more tolerant groups feature higher group proportions gathering in the cofeeding zone.

Figure 3.8. Researchers fill the trough-like receptacle with peanuts during a 5-minute prefeeding window for a peanut swing cofeeding session with group C2 at Chimfunshi Wildlife Orphanage, Zambia. Behind the researchers, ZG and I are recording social behaviours with camcorders and I am operating a stopwatch. Photo by A. Giovanetti.

Figure 3.9. Researchers push the trough-like receptacle onto the chain-link enclosure of group C2 at Chimfunshi Wildlife Orphanage, Zambia, to distribute the peanuts and initiate a peanut swing cofeeding session. To the right, I am recording social behaviours with a camcorder and operating a stopwatch. Photo by A. Giovanetti.

Through collaboration with Edwin J. C. van Leeuwen, who originally co-designed the peanut swing, we devised a protocol to apply the *peanut swing* experiment to simultaneously (1) contribute data for their ongoing comprehensive assessment of social tolerance in *Pan* and (2) compare prefeeding affiliative behaviour in sanctuary-living bonobos and chimpanzees. The comparison of our five *Pan* groups (van Leeuwen et al., under review), shows that, relative to each other, B1 and C1 share similarly despotic climates, whereas B2, B3, and C2 share similarly tolerant climates. This means that, during cofeeding sessions, crowding around the food source was considerably less likely in groups B1 and C1, and many individuals were unable to access the cofeeding zone entirely. In some cases, particularly in C1, this appeared to be driven by heightened agonistic behaviour from dominant individuals, notably the alpha male, Bob, in C1 (Brooker, personal observation). Increased bluffing and threats in the cofeeding zone co-occurred with the onset of feeding and led to many individuals of all rank classes withdrawing or fleeing. In contrast, whilst bluffing and agonism did occur in groups B2, B3, and C2, all three showed remarkably more peaceful cofeeding than B1 and C1 (Brooker, personal observation).

In this thesis, I did not explicitly compare social tolerance of our *Pan* groups. Instead, I focused on the use of prefeeding affiliation—also termed celebration— behaviours, which may serve a reassurance function (de Waal, 1992). Thus, to make systematic comparisons across groups and species, we implemented a 5-minute prefeeding window to provide a controlled arena to observe affiliative and conflict social interactions. This window was introduced by alerts and calls to the apes using words and intonations they associate with feeding, which have typically been used to attract the full groups for *peanut swing* sessions in previous studies. Every session was filmed from 2-5 angles depending on group and personnel. We used at least two stationary cameras per session covering as much of the respective enclosures as possible. In Chimfunshi, we carried extra handheld cameras to assist with identification of larger group populations. Camera operators annotated the sessions from start to finish by highlighting when individuals arrived, their identities, and what behaviours occurred. At both field sites, sessions were filmed using Panasonic HC-V770 Camcorders with detachable Sennheiser MKE 400 directional shotgun microphones.

We started a stopwatch when we first alerted the apes and began filling the trough-like receptacle with peanuts. We then engaged with the resource until 4.5-minutes, when we would lift the trough-like receptacle to deposit the contents at the 5-minute mark. At Chimfunshi Wildlife Orphanage, we ran 12 sessions at C1 and 11 sessions at C2 between 1030 and 1115 or 1330 and 1415 hours, to avoid clashing with regular feeding protocols. At Lola ya Bonobo, we ran 12 sessions at B1, 12 sessions at B2, and 13 sessions at B3 between 0800 and 1230 or 1400 and 1615 hours, to coincide with more sporadic feeding protocols. Sessions were balanced between morning and afternoon across all groups. Unlike the original design, we were unable to wait for all members of the groups to be present, due to the inclusion of the pre-feeding window. For these analyses, I excluded data from sessions with less than 80% of the group seen prior to T0 and some where equipment failed. This resulted in a total session *N* per group of: B1 = 8; B2 = 10; B3 = 10; C1 = 9; C2 = 8). More details on our application of the *peanut swing* for our research questions can be read in *Chapters 5, 6, and 7.*

3.3 General coding methods

I coded all victim focal follows and *peanut swing* sessions using the video software ELAN (*ELAN*, 2019; Wittenburg et al., 2006), which allows annotation of multimedia files with accurate timestamps. For consolation analyses (see *Chapter 4* and *Chapter 7*), I defined consolation as the onset of an affiliative interaction involving contact during the 5-minute follow that was spontaneously initiated by a bystander. Initiation was defined as the solicitation of an affiliative interaction either by gesturing or initiating physical contact with a partner. Thus, interactions initiated by the victim—e.g., the victim approached the bystander—were excluded as they do not represent spontaneous approaches by the bystander, thereby these interactions are not considered consolation (Das et al., 1998).

ELAN allows users to include up to four videos and four audio tracks in one coding file. Thereby, for *peanut swing* sessions, I could match all video files from one session for a fully synced playback meaning that I could code every social and agonistic behaviour each ape engaged in. I coded presence of a social interaction once per dyad per session alongside all behaviours and identity of the initiator for each behaviour and the recipient's response. I did not code durations due to the intensity of the coding programme, however, I coded new bouts per behaviour if there was a latency of at least 15 seconds between the same behaviour types. This enabled me to compile multiple datasets for consolation and prefeeding affiliation analyses.

I coded all chimpanzee victim focal follows myself, with inter-coder reliability (ICR) assisted by two independent coders. SK coded all bonobo victim focal follows, and I coded a subset for ICR. I coded all chimpanzee peanut swing sessions and most bonobo sessions (84.8%), whilst SK coded the remainder (15.2%). For specific detail regarding my coding approach and inter-coder reliability per research question, see empirical chapters.

For consolation and prefeeding affiliation coding, I applied an extensive ethogram to account for the myriad behaviours by either species. Contact affiliation behaviours coded as consolation or prefeeding affiliation behaviours included: body kiss, groom, embrace, finger/hand in mouth (see *Figure 3.10*), genito-genital contact (coded as rump-rump touch in chimpanzees), genital touch, pat, and touch (see *Figure 3.11*; Nishida et al., 2010). For *Chapter 5*, I also coded non-contact affiliative behaviours during *peanut swing* sessions, which included: hold out hand, hold out hand bent, sexual invitation, and submissive greeting (Nishida et al., 2010). Additionally, for *Chapter 5*, I also coded conflict behaviours, representing all forms of dyadic social agonism behaviour, including: high-contact aggression, low-contact aggression, chase, threat, and bluff display (Nishida et al., 2010). I only included an instance of conflict if an agonistic behaviour involved two clear parties.

Figure 3.10. Example of reassurance behaviour in a non-research group of chimpanzees at Chimfunshi Wildlife Orphanage, Zambia. Madonna (right) has offered her hand for Sims (left) to take into his mouth. Madonna's action is accompanied with a bared-teeth facial display, where she has retracted her lips to show her teeth to Sims. Taken by J. S. Brooker in May 2021.

Figure 3.11. Example of reassurance in group C2 at Chimfunshi Wildlife Orphanage. Violet (left, carrying her daughter Victoria) offering a touch to Misheck (right, on the back of his mother, Maxine). Taken by J. S. Brooker in July 2021.

Full descriptive ethograms of behaviours included in this thesis are included in the Appendix. See *Appendix A.1* for contact-affiliation behaviours (relevant for *Chapters 4*, *5*, *6*, and *7*), *Appendix A.2* for non-contact affiliation behaviours (relevant for *Chapter 5*), and

Appendix A.3 for conflict behaviours (relevant for *Chapter 5*). During both coding protocols, for post-conflict observation and peanut swing trials, coders recorded instances of self-directed behaviours, including self-scratching and self-touching. However, I did not incorporate these data into my analyses due to time restrictions and focus on the affiliative interactions.

3.4 Ethics

I conducted my research with full approval from the Chimfunshi Research Advisory Board (CRAB), the Senior Veterinary Advisory Team of Lola ya Bonobo Sanctuary, and the Animal Welfare Ethics and Research Board (AWERB) of Durham University. Data collection for this thesis consisted of naturalistic observations and experimental procedures that adhered to the legal requirements of the Democratic Republic of the Congo and Zambia, as well as the International Primatological Society's Principles for the Ethical Treatment of Nonhuman Primates.

Chapter 4: Within-species variation eclipses between-species differences in *Pan* consolation

This chapter constitutes an empirical article to be submitted for publication with the following authorship:

Brooker, J. S., Webb, C. E., Kordon, S., de Waal, F. B. M., & Clay, Z. Within-species variation eclipses between-species differences in Pan consolation.

Abstract

As our closest living relatives, bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*) provide a key model to test and explore open questions about the emergence of empathy in hominids. A key behavioural marker of empathy is consolation, or unsolicited bystander affiliation directed towards distressed others. Although consolation has been widely observed in bonobos and chimpanzees and some interspecific differences assumed, to date, systematic comparisons of *Pan* consolatory tendencies are absent. To address both within- and between-species variability in consolation in *Pan*, I systematically tested the consolatory tendencies of large groups of sanctuary-living bonobos and chimpanzees while taking into account social and individual factors. My results show that chimpanzees and bonobos exhibit similar overall consolation tendencies; however within-species analyses revealed further similarities and variation. Both bonobos and chimpanzees tended to console kin more than nonkin. However, whereas bonobo consolation was most often directed towards younger individuals, chimpanzee consolation was most often directed towards females. In addition, whilst males and females of both species showed decreased consolation with age, young chimpanzee males consoled more than young females. These findings suggest that within-species variation in *Pan* socio-emotional abilities is greater than between-species differences, highlighting the presence of striking behavioural diversity across our two closest cousins.

4.1 Introduction

Empathy, broadly defined as sharing and/or understanding others' emotional states, is a cornerstone of the human experience (Eisenberg & Strayer, 1990; Preston & de Waal, 2002). From politics and marketing to day-to-day social interactions, empathy allows us to effectively cooperate and communicate as well as strengthen our social relationships (de Waal, 2007). Cross-cultural and personality studies have revealed remarkable individual and cultural variation in empathic concern and perspective-taking (Chopik et al., 2017; Zahn-Waxler et al., 1992; Eisenberg et al., 1995, 1999; Knafo et al., 2008; Vreden et al., in prep). Some longitudinal studies indicate that individual differences in human empathic responding are relatively stable (Eisenberg et al., 1995, 1999; Knafo et al., 2008; Zahn-Waxler et al., 1992). As variation has been reported on individual and cultural levels, it has been suggested that both personality and cultural norms may influence empathy.

In the animal kingdom, many behaviours possibly related to empathy have been reported, mainly in mammals (Adriaense et al., 2020) though there is also some evidence in birds (e.g., consolation in *Corvus corax*; Fraser & Bugnyar, 2010). Empathy-driven behaviours emerge in the form of sub-components that represent differing expressions of emotional responsiveness and understanding (Brooker et al., 2022; de Waal, 2007). Some of these sub-components, such as emotional contagion, have been observed across many social mammals, indicating a deep evolutionary history (Adriaense et al., 2020; Brooker et al., 2022). Furthermore, some behavioural prosocial manifestations of empathy, such as consoling others in distress, have been observed in rodents (Burkett et al., 2016), elephants (Plotnik & de Waal, 2014), and some primate and great ape species (for a review, see Brooker et al., 2022).

Consolation—defined as unsolicited affiliative contact offered by an uninvolved bystander towards a distressed conspecific (de Waal & van Roosemalen, 1979)—is thought to require both a cognitive appreciation, and even understanding, of another's state combined with a prosocial orientation to improve it, such as by providing reassuring contact (de Waal, 2008). Consolation represents a specific form of post-conflict affiliation, functionally determined by a clear reduction in victim distress (Palagi et al., 2004; Romero et al., 2010; Zahn Waxler et al., 1992). If this criterion is uncertain, I hereafter refer to these interactions broadly as unsolicited post-conflict affiliation. Nonetheless, among non-human animals, our two closest relatives, the bonobos and chimpanzees, have demonstrated the capacity for consolation in a range of settings, including captivity, sanctuaries, and even the wild (Clay & de Waal, 2013; Palagi et al., 2004; Romero et al., 2010; Wittig & Boesch, 2003).

Among wild chimpanzees, both the western and eastern subspecies have been observed to initiate unsolicited post-conflict affiliation towards others, including at Taï National Park, Ivory Coast (Wittig & Boesch, 2003) and the Mahale Mountains National

Park, Tanzania (Kutsukake & Castles, 2004) respectively. Another study of the eastern subspecies in Budongo Forest, Uganda, showed that unsolicited post-conflict affiliation only occurred after 3.3% of observed conflicts, which was not significantly more than matched controls (Arnold & Whiten, 2001). In contrast, Kutsukake and Castles (2004) observed unsolicited post-conflict affiliation after around 22% of conflicts in the Mahale M-group of eastern chimpanzees (Kutsukake & Castles, 2004). This difference between the Mahale and Budongo groups indicates possible within-species behavioural flexibility and cross-community variation in consolatory tendencies. Whilst there are no studies of unsolicited post-conflict affiliation in wild bonobos, case studies of targeted prosocial behaviour, such as conspecifics attempting to remove snares from group members and searching for lost group members (Tokuyama et al., 2012) suggest consolation is likely. Moreover, consolation has been observed in sanctuary-settings (Clay & de Waal, 2013), including by wild-born immature individuals.

Evidence that immature apes engage in consolation challenges assumptions that consolation is dependent on sophisticated cognitive mechanisms. In both chimpanzees and bonobos, consolation is offered most by younger individuals (Clay & de Waal, 2013; Webb et al., 2017), suggesting that empathic orientation towards other's states may be intrinsic and adaptive. In humans, concern for others including consolation has been reported even within the first year of life, as early as nine months (Davidov et al., 2021; Vreden et al., in prep). Empathic behaviours, like consolation, may strengthen interpersonal bonds, especially for dyads that demonstrate enduring cooperative relationships. For this reason, social closeness, familiarity, or similarity has been shown to be a key predictor of empathic tendencies in humans (Lindegaard et al., 2017; Norscia & Palagi, 2011) and among nonhuman apes (bonobos: Clay & de Waal, 2013; Palagi & Norscia, 2013; chimpanzees (Fraser et al., 2008; Romero et al., 2010; Webb et al., 2017).

Bonobos and chimpanzees develop long term enduring bonds with other group members and form strong support networks (Gruber & Clay, 2016); yet there are reported differences in their social tendencies and socio-emotional orientations. For example, bonobos appear to have enhanced attentiveness to conspecific social and emotional expressions than chimpanzees (Kano et al., 2015; Kret et al., 2016). Apparent differences in sociability, socio-sexuality, and aggressive tendencies between the two species may have biological and neurological foundations. Firstly, chimpanzees, but not bonobos, have been shown to have deletion of the DupB region in the *AVPR1A* gene, which includes a microsatellite called RS3 (Staes et al., 2014). Variation in RS3 is linked with variation in social bonding, and increased levels in bonobos may support their reported xenophilia. Neurological research shows that bonobos have twice the density of serotonergic axons in the amygdala than chimpanzees (Stimpson et al., 2016). This region is associated with social cognition and emotional regulation amongst others, and this variation between species may mediate the differences in their social structures and behaviour. The ability to regulate one's own emotions—i.e., suppressing personal arousal upon exposure to an arousing situation—can vary between individuals (Eisenberg et al., 1994). However, emotional regulation appears to be crucial for empathy to emerge (Lockwood et al., 2014). In addition, bonobos have more grey matter in the right dorsal amygdala and right anterior insula than chimpanzees, as well as a larger pathway linking the amygdala with the ventral anterior cingulate cortex (Rilling et al., 2012). These regions are associated with perceiving distress in oneself and others, as well as control of reactive and proactive aggressive impulses. These differences, as well as lower general levels of aggression in bonobos, and therefore decreased risk of injury (Hare et al., 2012), may facilitate enhanced production of prosocial empathic behaviours, such as consolation and targeted helping, compared to chimpanzees.

Social tolerance is also thought to influence empathic tendencies, according to the *Social Constraints Hypothesis* (de Waal & Aureli, 1996). For example, evidence of consolation in the Tonkean macaques (*Macaca tonkeana*; Palagi et al., 2014) and not other more despotic macaque species (for a review, see Brooker et al., 2022), indicates that social tolerance may facilitate empathic responses that might otherwise be inhibited due to intimidation, fear, or aggression. Chimpanzees are often considered to be more intolerant and despotic than bonobos (Gruber & Clay, 2016), following evidence that chimpanzees have formal signals of subordinacy, through submissive gestures (Nishida et al., 2010), whereas bonobos do not (Kano, 1992). These expressions of submission are often used to assess chimpanzee hierarchies, which commonly follow a linear pattern (Goodall, 1986; Newton-Fisher, 2004; Nishida et al., 1999). Bonobos appear to have a more flexible, egalitarian dominance style (Fruth & Hohmann, 2003; Furuichi, 1989; White, 1996), which may be facilitated by their reduced aggressivity and increased sociability. Furthermore, chimpanzees tend to be xenophobic to other communities (Wilson & Wrangham, 2003). In contrast, whilst wild bonobo communities can be vocally hostile to other groups, numerous populations regularly have peaceful intergroup encounters, even cases of food sharing, and exchanges of sex, grooming, and play (Furuichi, 2011; Lucchesi et al., 2020). Some experimental paradigms have indicated that bonobos outperform chimpanzees on cooperation (Hare et al., 2007) and theory-of-mind-related tasks (Herrmann et al., 2010). Where empathy expressions are related to understanding others, emotions, and social tolerance, one might expect bonobos to be more consolatory than chimpanzees.

However, there is evidence of within-species variation. Several semi-wild chimpanzee communities have been shown to vary in interindividual tolerance measured by cofeeding proximity (Cronin et al., 2014). Similarly, a recent comparison of multiple captive and semi-wild populations revealed that levels of social tolerance overlapped between bonobos and chimpanzees (van Leeuwen et al., under review). Furthermore, as previously mentioned, unsolicited post-conflict affiliation appeared relatively absent in one population of eastern chimpanzees at Budongo (Arnold & Whiten, 2001) compared to their Mahale counterparts (Kutsukake & Castles, 2004). These communities appear to vary considerably in social tolerance and hierarchical steepness, whereby Budongo chimpanzees have steeper, and more despotic hierarchies compared to Mahale (Kaburu & Newton-Fisher, 2015). Whilst these wild groups have not been systematically compared, these findings indicate that consolation may show inter-group variation and emerge flexibly if conditions permit. As population-level variation in group social tolerance can differ within species, consolatory tendencies may vary across groups living in similar conditions.

Whilst some socio-cognitive abilities of bonobos and chimpanzees have been compared, direct systematic comparisons of their consolation tendencies has yet to occur. As coalitionary support and intermediate despotism are key factors of bonobo and chimpanzee societies, comparing them may reveal whether reduced physical aggression and increased emotional orientation in bonobos predict an increased likelihood to console. Consolation appears to be a feature of natural *Pan* social living, however wild studies are scarce and challenging due to methodological constraints. Therefore, comparing great apes in semi-wild sanctuary settings can provide a balance of natural ecological surroundings with improved observational conditions.

In this chapter, I systematically compared sanctuary-living populations of chimpanzees and bonobos with diverse social compositions. Based on evidence that bonobos show enhanced social awareness and emotional sensitivity, I predicted that unsolicited post-conflict affiliation should be more prevalent in bonobos than chimpanzees. Furthermore, following the hypothesis that empathy is socially biased, I expected higher rates of consolation between dyads that are socially bonded, either by kinship or close affiliative tendencies.

Whilst consolatory tendencies tend to decrease in each species with age (Clay & de Waal, 2013; Webb et al., 2017), previous studies have revealed a lack of general sex differences in consolation in bonobos and chimpanzees. However, as males remain in their natal groups in each species (Goodall, 1986; Kano, 1992), they might be expected to invest in building long-term social bonds already at a young age. In bonobos, males tend not to have strong social bonds beyond their mothers. They have been shown to form bonds with other females that extend their alliance relationships and improve reproductive success, however these are typically females with elevated rank positions, therefore reducing the likelihood that they would be victims of conflict (Surbeck et al., 2012; Surbeck et al., 2017). In adult chimpanzees, males are less likely to be victims of conflicts than females and immature males, implying that their closest social partners, other adult males, will have fewer opportunities to offer consolation. As such, and in line with previous findings (Clay & de Waal, 2013; Webb et al., 2017), I predicted that, regardless of sex, younger individuals of both species will show the highest tendencies to console. In addition, I predicted an interaction between bystander age and sex in both species, whereby younger individuals of both sexes would show the highest consolatory tendencies whereas in adulthood, older males of each species would show lower rates than females. By comparing between- and within-species influences on an empathic behaviour like consolation in our closest living relatives, I aim to improve our understanding of the origins of hominid empathy and emotional responsiveness.

4.2 Methods

4.2.1 Subjects and housing

Observations of chimpanzees were conducted at Chimfunshi Wildlife Orphanage Trust (hereafter, "Chimfunshi") in the Copperbelt Province of Zambia during March-August 2019. Observations of bonobos were conducted at Lola ya Bonobo Sanctuary (hereafter, "Lola ya Bonobo") in the Democratic Republic of the Congo during July-September 2019. For more information about these sanctuaries, see *Section 3.1*. For this study, I analysed data from Group 1 (hereafter: B1) and Group 2 (hereafter: B2) at Lola ya Bonobo, which housed N = 22 and N = 18 respectively, and Group 2 (hereafter: C2) at Chimfunshi, which comprised N = 50 at the start of data collection. Two bonobos and three chimpanzees were excluded from all analyses due to long periods of absence from their main groups (bonobos: 62–95% of observation time; chimpanzees: 54–65% of observation time). A further three bonobos across both groups were excluded due to limited data on their social behaviour. The age and sex composition of my sample is provided in *Table 4.1*.

Table 4.1. Social compositions[a] of groups I compared in terms of their consolation tendencies. Bonobos observed at Lola ya Bonobo Sanctuary in the Democratic Republic of the Congo and chimpanzees observed at Chimfunshi Wildlife Orphanage Trust in Zambia.

Species	**Group**	**Total**	**Age Range (in years)**	**Sex F / M[b]**
Pan paniscus	1 (B1)	22	2–24	12 / 10
	2 (B2)	18	3–30	8 / 10
Pan troglodytes	2 (C2)	50	1–42	33 / 17
Total		90	1–42	53 / 37

[a] *Table includes all individuals belonging to their respective groups from the start of observations, all of whom were considered for the main species comparison models. For the individual and social factors models (Models 2.1–2.2), five bonobos and three chimpanzees were removed due to limited observations of their social relationships.*

[b] *F = Number of females; M = Number of males*

4.2.2 Data collection

4.2.2.1 *Post-conflict and post-distress observations*

Consolation has typically been recorded using the post-conflict/matched-control method (de Waal & Yoshihara, 1983). This involves conducting focal follows of a victim for a standardised period—usually 5–10-minutes—after a conflict or spontaneous distress period, while recording the initiator and behaviour of all affiliative interactions that occur involving the focal victim. Post-conflict (PC) and post-distress (PD) periods are then compared with matched control (MC) recordings observed at a similar time and circumstance a day later. The PC/MC method has already reliably demonstrated consolation in multiple bonobo and chimpanzee communities compared with matched controls (Clay & de Waal, 2013; de Waal & Aureli, 1996; Palagi et al., 2004; Romero et al., 2010), including in some of these sample populations (Clay & de Waal, 2013). Thus, I decided that we would only collect the post-conflict and post-distress events to ensure I would have a large enough sample to compare individual and social influences on consolation tendencies.

I applied a focal all-occurrence sampling protocol (Altmann, 1974) to follow distressed individuals. For my chimpanzee sample, we collected $N = 150$ PC events and $N = 10$ PD events. For the bonobo sample, SK observed $N = 28$ and $N = 36$ PC events and $N = 36$ and $N = 16$ PD events in group B1 and group B2 respectively. My total sample of events for this study was therefore $N = 276$ across both species and all three groups. Post-conflict and post-distress events were all-occurrence sampled due to their unpredictable nature throughout the day. See *Section 3.2.1.1* for more information about my protocol for collecting victim focal follows and criteria for inclusion in analyses for this thesis.

4.2.2.2 *Dyadic social affinity and gregariousness*

Social relationships between the bystander and victim were of interest to my analyses in this study. Thus, observers collected 10-minute focal scan follows (Altmann, 1974) of social tendencies to measure dyadic affiliation levels and individual gregariousness. The data set consisted of 706 focal follows for group B1 (*range* = 28–41; $M = 32.1$; $SD = 11.0$), 587 focal follows for B2 (*range* = 16–44; $M = 34.2$; $SD = 11.3$), and 684 focal follows for C2 (*range* = 9–18; $M = 14.3$; $SD = 2.6$). Each focal follow consisted of 10 1-minute scan points. At each scan point, observers recorded all social interactions the focal was involved in including grooming, play, and sex, as well as all individuals within 1-metre. More information on the data collection protocols for social affiliation can be seen in *Section 3.2.1.2*.

As the social behaviours required proximity of 1-metre to the focal, observers only coded either behaviour or proximity once per dyad per scan during observations. Dyadic scores for behaviour and proximity were strongly correlated ($r(375) = .43$, $P < .001$). Therefore, I incorporated all social behaviour observations into one score for proximity and used that to compute unique dyadic affiliation scores for every possible dyad. I divided the number of scan points each dyad interacted for by the total number of scan points both individuals of the dyad were observed for. I also computed individual gregariousness scores by dividing the total number of scans each focal subject was observed within proximity to at least one other individual by the total numbers of scans they were observed for.

In addition, I was interested in the effect of kinship, and defined each dyad as 'kin' or 'nonkin' depending on whether they shared a maternal genetic relationship or not, respectively. This therefore included all mother-infant, sibling-sibling, and grandmother-grandchild pairs as 'kin'. Some dyads at Chimfunshi represented a genetic uncle-nephew dynamic and were also included as 'kin'.

4.2.2.3 Hierarchies

I assigned categorical rank values (high, medium, low) for each ape involved in the analysis for *Chapter 4*. For both species, I used the R package 'EloRating' to create dominance scores based on dyadic agonistic interactions involving high-contact aggression, low-contact aggression, and chases (Neumann & Kulik, 2020). Each agonism type was assigned a different optimised weighting, known as a K-value, based on intensity and likelihood of winning probabilities. We only included individuals four-years and older with at least six observed dyadic agonistic interactions in this ELO analysis. For the chimpanzees, the ordered rank output was consistent with categorical rankings acquired from the keepers and care staff. Hence, I evenly divided this output into 'high', 'medium', and 'low' rank, and used the keeper allocations to assign categorical ranks to individuals for whom we lacked sufficient ELO data for. For the bonobos, my ELO analysis revealed ordered results that were broadly but not wholly consistent with keeper and researcher observations. Whilst human judgements of social rank may be influenced by observer bias, these slight inconsistencies were likely contributed to by a relatively lower quantity of agonistic observations over our relatively short study period, therefore affording our ELO analysis lower power. However, whilst the rank order was inconsistent, categorisation into 'high', 'medium', and 'low' was fairly consistent with keeper and researcher observations. As we did not have substantial or prior quantitative data to support the ELO analysis, I decided to assign rank categories based on agreed deliberation between two long-term experienced observers of the bonobos at Lola ya Bonobo, supported by views of the sanctuary staff (see *Section 9.6.1* for a comprehensive review of rank assessment in our data collection). For both species, I assigned mother ranks to infants (apes between 0 and 2 years of age). In both cases, observer rankings were based on observations of dynamics surrounding food and resource competition.

4.3 Analysis

I conducted all-occurrence coding of affiliative and agonistic encounters during PC/PD periods in ELAN (*ELAN*, 2019; Wittenburg et al., 2006). SK coded all bonobo PC and PD events, and I coded all chimpanzee PC and PD events. To check inter-coder reliability, I coded 13.4% of bonobo events and two external coders coded 20.6% of chimpanzee events between them. Inter-coder reliability of consolation occurrence and consoler identity indicated almost perfect agreement (consolation occurrence: bonobo $\kappa = 0.86$, chimpanzee $\kappa = 0.85$; consoler identity: bonobo $\kappa = 1.00$, chimpanzee $\kappa = 0.97$).

4.3.1 Summary of statistical approaches

I used a mixed models approach to assess whether consolation was more likely to occur in the bonobo or chimpanzee groups sampled, along with species variation in consolation tendencies according to bystander and victim characteristics: sex, age, rank, gregariousness, and group, as well as bystander-victim social relationship. I collapsed my observations into two formats: event-level, where each observation row represents one PC or PD event; and dyad-level, where each observation row represents a unique bystander-victim combination. This allowed me to comparably investigate general species tendencies at the event-level and then to assess the influence of individual (e.g., bystander age, bystander sex) and social factors (e.g., kinship, affiliation score) on consolation at the dyad-level.

All models were fitted in RStudio (version 1.3.1093; RStudio Team, 2020) using the function glmer of the package lme4 (version 1.1-28; Bates et al., 2015). To avoid overconfidence regarding precision of fixed effects estimates and prevent type I error, I adopted a maximal model approach (Barr et al., 2013) and included all theoretically identifiable random slope components and their correlations with the intercepts. Theoretical identifiability was defined as at least three unique values per level of a random effect for covariate fixed effects and at least two levels with at least two observations per level of a random effect for factor fixed effects. Covariate predictors were z-transformed, and factor predictors were dummy coded and centred prior to inclusion as random slopes. Model stability was assessed using a function provided by Roger Mundry[1], which compares estimates obtained from the model based on all data with those obtained from models with the levels of the random effects excluded one at a time. Thus, I could check if removal of one level of a random effect (e.g., all cases involving Vis as an aggressor) leads to considerable change in model estimation. In my results tables, I provide *minimum* and *maximum* values for each fixed effect and random effect estimate, which represent the full

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[1] Not publicly available. For enquiries, contact Roger Mundry directly.

range of estimates found across these model comparisons. Stable significant effects would be indicated by a relatively narrow range being entirely above or below 0. Confidence intervals were derived using the bootMer function of the package lme4 using 1,000 parametric bootstraps and bootstrapping over the random effects too (Bates et al., 2015). Model complexity was checked by calculating the number of observations per estimated term. I followed the 10:1 rule for all models (e.g., Peduzzi et al., 1996), whereby observations exceeding $N = 10$ per estimated term (including fixed and random effects parameters) were deemed sufficient for avoiding overcomplexity. Whilst considered by some scholars to be too conservative (e.g., Vittinghoff & McCulloch, 2007), I chose to follow this rule due to the inclusion of a potentially complex random effects structure to prevent overfitting and likelihood of a Type I error.

4.3.2 Event-level analyses: Testing species differences

I used two Generalised Linear Mixed Models with logit link functions to investigate whether consolation was more likely to occur in bonobos or chimpanzees. The sample for this model consisted of $N = 276$ events (PC $N = 214$; PD $N = 62$) of $N = 90$ apes (bonobo $N = 40$; chimpanzee $N = 50$). The first model (hereafter: *Model 1.1*) had a binomial structure (did consolation occur, yes/no; see *Table 4.2*) to check whether one or more consolatory approach was higher in either species. The second model (hereafter: *Model 1.2*) had a Poisson structure (number of consolatory approaches per event; see *Table 4.3*) to check whether more individuals respond per event in either species, as all bystanders could potentially console. The fixed effects structures included species and the number of bystanders as a control effect. Control effects are variables included in GLMMs to reduce potential biases and isolate the unique contributions of predictor variables to the response variable. As population sizes varied across the three groups, and consolation may be likelier if there are more individuals present, I included number of bystanders as a control effect to isolate the estimated fixed effect of species. The random effects structure was crossed and consisted of random intercepts for aggressor identity and victim identity, as well as random slopes for number of bystanders within both aggressor identity and victim identity.

Table 4.2. Structure for *Model 1.1*: Binomial analysis of species differences in whether consolation occurs at least once during a PC/PD event. Fixed effects include species and number of bystanders and random effects include identities of the aggressor and victim.

Binomial model[a]	**Variable**	**Levels**
Response variable	Occurrence of consolation	0 = no; 1 = yes
Fixed effects	Species	Bonobo[b]; Chimpanzee
	Number of bystanders	*Continuous*
Random effects	Aggressor ID[c]	*Categorical*
	Victim ID[c]	*Categorical*

[a] *Respective null models retained the same structure with each fixed effect removed*

[b] *Reference group*

[c] *Includes random slope of bystanders*

Table 4.3. Structure for *Model 1.2*: Poisson analysis of species differences in the number of consolers to respond per PC/PD event. Fixed effects include species and number of bystanders and random effects include identities of the aggressor and victim.

Poisson model[a]	**Variable**	**Levels**
Response variable	Number of consolers	Poisson count (0–4)
Fixed effects	Species	Bonobo[b]; Chimpanzee
	Number of bystanders	*Continuous*
Random effects	Aggressor ID[c]	*Categorical*
	Victim ID[c]	*Categorical*

[a] *Respective null models retained the same structure with each fixed effect removed*

[b] *Reference group*

[c] *Includes random slope of bystanders*

To test for the effect of species, I used likelihood ratio tests (LRT; Dobson et al., 2018) via the drop1 function of the package lme4 (Bates et al., 2015) in R to compare full models with respective null models lacking each fixed effect whilst retaining the rest of the model structure, including all random effects and random slopes. Checks for collinearity using variance inflation factors for a standard linear model with the car package (Fox & Weisberg, 2019) revealed some correlation (2.176) between the two fixed effects but not enough to warrant corrective measures.

4.3.3 Dyad-level analyses: Testing individual and social factors

To analyse whether the proportions of consolation occurrences varied according to bystander and victim characteristics, I analysed my dyad-level data in R using two Generalized Linear Mixed Models (Baayen et al., 2008)—one for each species (see below).

Each observation row represented a particular bystander-victim combination with at least one opportunity for consolation to occur. The sample for the bonobo model (hereafter: *Model 2.1*) consisted of 461 observation rows from 35 individuals with this criterion across two groups. The sample for the chimpanzee model (hereafter: *Model 2.2*) consisted of 1485 observation rows from 47 individuals across one group. I excluded six individuals as victims and bystanders due to a lack of data on their social relationships (Baraka, Kitoko, Likunzi, Masya, Mikey, and Mumba) and a further two due to general limited observation (Dilolo and Kodoro).

I computed a response variable constituting a two-columns matrix as the number of consolations and non-consolations per individual, which was thus analysed as a binomial distribution. To test which individual and social factors influence consolatory tendencies, I analysed the data at dyad-level for each species separately. I ran separate models to compare how within-species trends vary between bonobos and chimpanzees. These full models included individual factors of the bystander (bystander age, sex, rank, and gregariousness), the victim (victim age and sex), and the social relationship of the dyad (kinship and affiliation level) as fixed effects. The interaction between bystander age and bystander sex was also included as a fixed effect in each model. The bonobo model included group as a fixed effect. I was primarily interested in factors related to the bystander and so proceeded without victim rank and victim gregariousness to prevent model overcomplexity and assist convergence. There is no evidence to suggest that victim gregariousness influences consolation. Whilst victim rank may be influential, the effect only appears present in chimpanzees (Romero et al., 2010) and my sample was limited regarding victim focal follows of high-ranking individuals, particularly males.

To obtain accurate *P*-values for each predictor, I used LRTs (as in *Section 4.3.2*) to compare full models with respective null models lacking each fixed effect but retaining the rest of the model structure (Barr et al., 2013). I included the individual identities of the bystanders and victims as random effects in a crossed structure. All theoretically identifiable random slopes were included in the full models (all victim and social factors within bystander, and all bystander and social factors within victim). The structure of the full models is displayed in *Table 4.4*.

Table 4.4. Structure for *Model 2.1* and *Model 2.2*: Dyad-level binomial matrix GLMM of within-species influences on whether consolation occurs. *Model 2.1* tested this model structure on the bonobo data and *Model 2.2* tested this model structure on the chimpanzee data. Respective null models retained the same structure with each fixed effect removed.

Full model[a]	**Variable**	**Levels**
Response variable	Two-column matrix: 1=Number of consolations; 2=Number of non-consolations	
Fixed effects	Group[a]	B1[c]; B2
	Bystander age	*Continuous*
	Bystander sex	Female[b]; Male
	Bystander age*bystander sex	
	Bystander rank	High[b]; Medium; Low
	Victim age	*Continuous*
	Victim sex	Female[b]; Male
	Dyad kinship	Kin[b]; Nonkin
	Dyad affiliation level	*Continuous*
	Bystander gregariousness	*Continuous*
Random effects	Bystander ID[c]	*Categorical*
	Victim ID[d]	*Categorical*

[a] *Only included in bonobo model (2.1)*

[b] *Reference category*

[c] *Includes random slope of victim age (2.1) and victim sex (2.1 & 2.2)*

[d] *Includes random slope of bystander age (2.1 & 2.2), dyad kinship (2.2), bystander rank (2.2), bystander sex (2.2), and dyad affiliation level (2.2)*

4.4 Results

4.4.1 Event-level results: Do bonobos console more than chimpanzees?

Across observations, consolation occurred at least once in 124 of the 276 events (44.9%). On average, *M* = 0.64 (*SD* = 0.81) consolatory approaches occurred per event in bonobos, and *M* = 0.69 (*SD* = 0.95) consolatory approaches per event in chimpanzees. *Model 1.1* revealed no effect of species on the probability of consolation (LRT comparing full and null models: $\chi2 = 0.073$, df = 1, *P* = .787; see *Figure 4.1*). Additionally, *Model 1.2* showed no effect of species on the number of consolers that responded (LRT comparing full and null models: $\chi2 = 0.002$, df = 1, *P* = .967; see *Figure 4.2*). Importantly, in each model, the inclusion of the number of bystanders did not significantly influence the outcome variables (binomial model: estimate ± SE = 0.185 ± 0.238, z = 0.777, *P* = .440; Poisson model: estimate ± SE = 0.177 ± 0.150, z = 1.182, *P* = .233), indicating consolation likelihood does not increase if more possible consolers are present. *Model 1.1* and *Model 1.2* both featured *N* = 39.43 observations per estimated term, indicating, alongside stability checks (see *Table 4.5*), no issue with model overcomplexity. All output from the event-level models can be seen in *Table 4.5*.

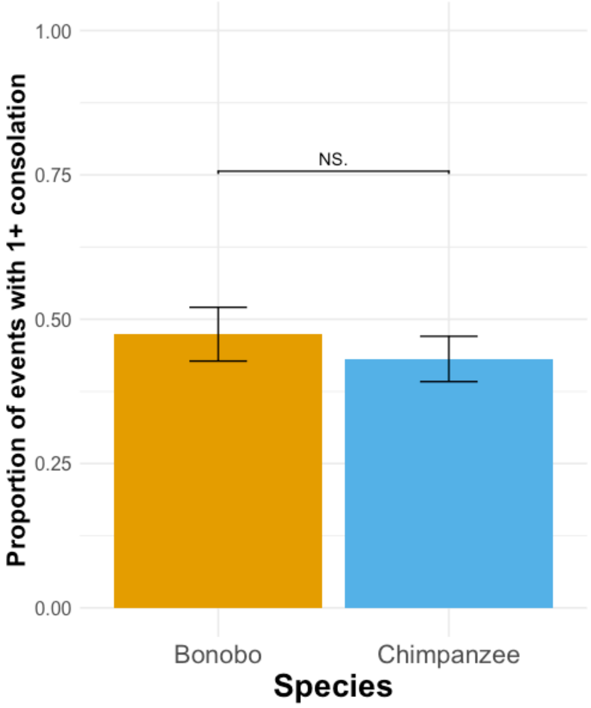

Figure 4.1. Barplot showing no significant difference (P > .05) between bonobos and chimpanzees in their relative tendency for a PC or PD event to feature 1+ consolation approach towards the distressed victim. Results obtained from *Model 1.1*. Whiskers show one standard error above and below mean.

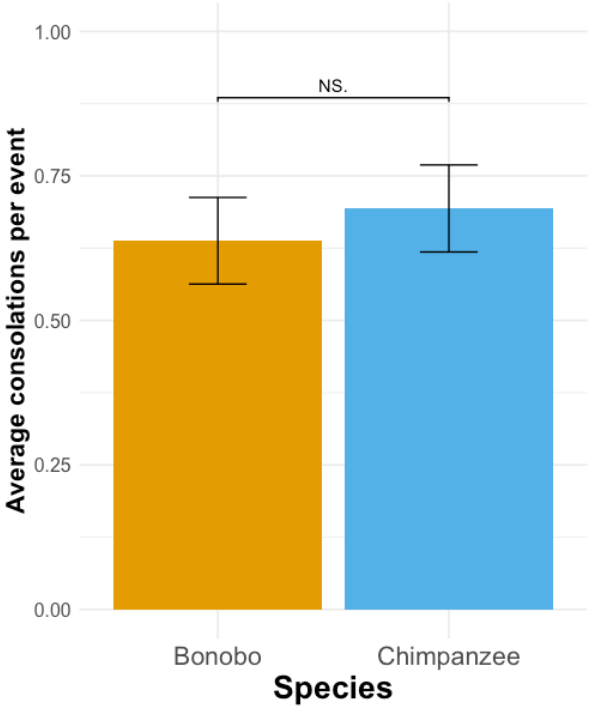

Figure 4.2. Barplot showing no significant difference ($P > .05$) between bonobos and chimpanzees in the average number of consolatory approaches made during PC or PD events. Results obtained from *Model 1.2*. Whiskers show one standard error above and below mean.

Table 4.5. Results for *Model 1.1* (did consolation occur?) and *Model 1.2* (how many individuals consoled). Model estimates and standard errors, together with confidence intervals, results of likelihood ratio tests, and the range of estimates obtained when dropping levels of random effects one at a time. Significant *P* values (< 0.05) are shown in ***italicised bold***.

***Model 1.1*: Full model testing whether consolation occurred**

Term	Estimate	SE	CI_{95}	$\chi2$	z	*P*-value	Min	Max
Fixed effects								
(Intercept)	-0.324	0.406	-1.197 to 0.421		-0.799	.424	-0.995	-0.601
Species^a	-0.152	0.561	-1.205 to 1.025	0.073	-0.270	.787	-0.192	0.321
Number of bystanders^b	0.185	0.238	-0.326 to 0.672	0.595	0.777	.440	0.094	0.271
Random effects								
Aggressor ID	0.626						0.407	0.723
Victim ID	0.709						0.233	0.797

***Model 1.2*: Full model testing how many individuals consoled**

Term	Estimate	SE	CI_{95}	$\chi2$	z	*P*-value	Min	Max
Fixed effects								
(Intercept)	***-0.688***	***0.244***	***-1.250 to 0.230***		***-2.814***	***.005***	***-0.995***	***-0.601***
Species^a	-0.031	0.319	-0.709 to 0.629	0.010	-0.098	.922	-0.192	0.321
Number of bystanders^b	0.177	0.150	-0.126 to 0.500	1.424	1.182	.233	0.094	0.271
Random effects								
Aggressor ID	0.404						0.253	0.449
Victim ID	0.367						0.282	0.439

^{a} *dummy coded and centred with bonobo as the reference category*

^{b} *z-transformed to a mean of 0 and a standard deviation of 1*

4.4.2 Dyad-level results: Which within-species factors drive consolation tendencies?

For both species, there were significant main effects of kinship (bonobos: estimate ± SE = -2.673 ± 1.220, z = -2.190, *P* = .022; chimpanzees: estimate ± SE = -0.897 ± 0.438, z = -2.048, *P* = .049), indicating that bystanders consoled kin more than nonkin. In both species, there were non-significant main effects of bystander gregariousness (bonobos: estimate ± SE = 0.168 ± 0.420, z = -0.399, *P* = .688; chimpanzees: estimate ± SE = -0.245 ± 0.208, z = -1.178, *P* = .238).

There were a number of between-species differences. Dyadic affiliation level significantly predicted chimpanzee consolation tendencies (estimate ± SE = 0.175 ± 0.089, z = 1.970, *P* = .044), but not for bonobos (estimate ± SE = 0.160 ± 0.166, z = 0.963, *P* = .327). Younger bonobos were consoled more than older bonobos (estimate ± SE = -1.170 ± 0.516, z = -2.268, *P* = .006), but not in chimpanzees (estimate ± SE = -0.102 ± 0.216, z = -0.471, *P* =

.633). Conversely, for chimpanzees, I found a significant main effect of victim sex, where female chimpanzees were consoled more than males (estimate ± SE = -1.128 ± 0.574, z = -1.965, *P* = .039). Bonobos did not show a significant main effect of victim sex (estimate ± SE = 0.008 ± 0.528, z = 0.014, *P* = .988). Whilst bystander age and bystander sex did not interact for bonobos (estimate ± SE = 0.017 ± 0.687, z = 0.024, *P* = .932), bystander age was a significant main effect (estimate ± SE = -1.113 ± 0.452, z = -2.462, *P* = .014; see *Figure 4.3*) with younger bystanders more likely to console. However, for chimpanzees there was a significant interaction between bystander age and bystander sex (estimate ± SE = -1.355 ± 0.692, z = -1.959, *P* = .039). This result indicates that younger male chimpanzees were most likely to console and older females and males were the least likely to console (see *Figure 4.4*). Finally, for bonobos I found a significant effect of group, where consolation was more likely to occur in group 1 compared to group 2 (estimate ± SE = -1.179 ± 0.566, z = -2.083, *P* = .026; see *Figure 4.5*). *Model 2.1* and *Model 2.2* featured *N* = 10.42 and *N* = 39.45 observations per estimated term respectively, indicating, alongside stability checks (see *Table 4.6*), that model overcomplexity was not a significant issue. A full table of the output for bonobos (*Model 2.1*) and chimpanzees (*Model 2.2*) can be seen in *Table 4.6*. A summary of effects across both species can be seen in *Table 4.7*.

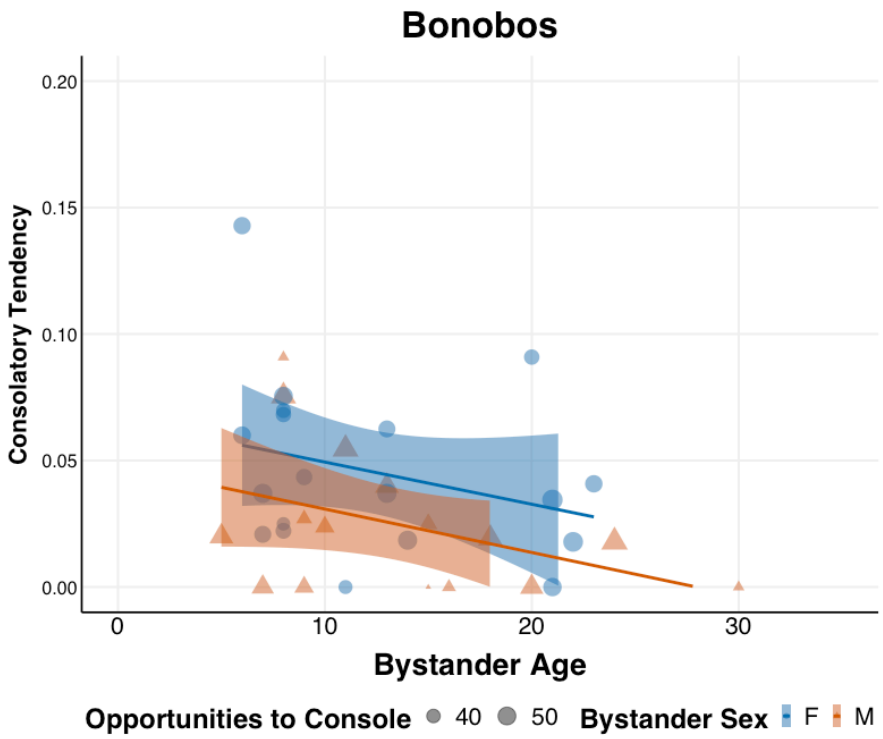

Figure 4.3. Scatterplot showing the significant main effect of bystander age from *Model 2.1* in bonobos, where young individuals tend to offer more consolation than older individuals. X-axis = age in years. Y-axis = total number of consolatory approaches divided by total number of opportunities. Females = blue points; males = red points. Point size corresponds to number of events the individual was present as a bystander (range = 31–58; *M* = 46.66; *SD* = 7.21). Shaded area corresponds to confidence limits for model estimates at 95% level.

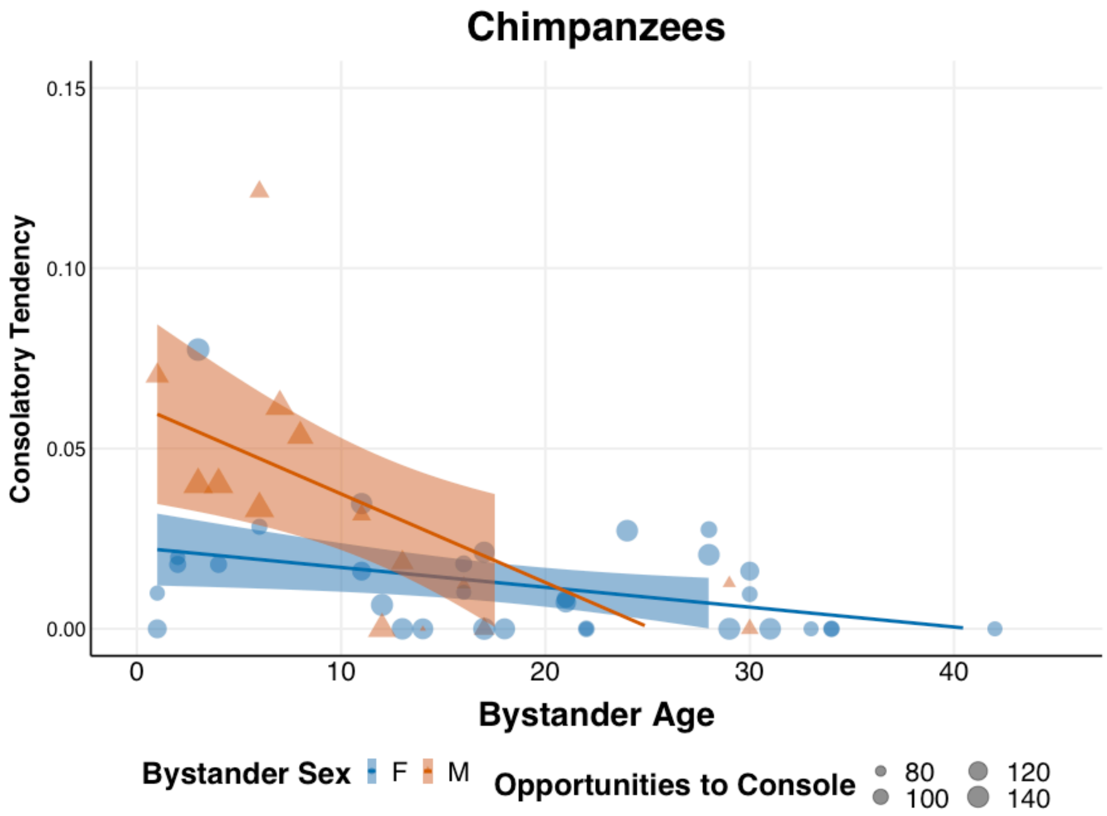

Figure 4.4. Scatterplot showing the significant interaction from *Model 2.2* between bystander age and bystander sex in chimpanzees, where young males tend to offer more consolation than other individuals. X-axis = age in years. Y-axis = total number of consolatory approaches divided by total number of opportunities. Females = blue points; males = red points. Point size corresponds to number of events the individual was present as a bystander (range = 72–155; *M* = 120.60; *SD* = 23.04). Shaded areas correspond to confidence limits for model estimates at 95% level.

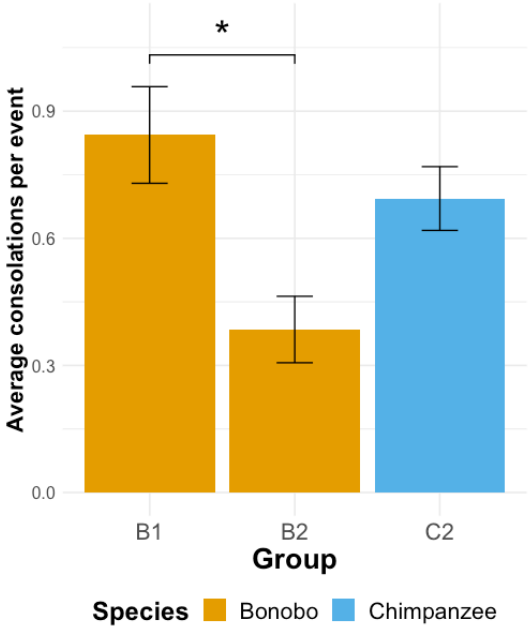

Figure 4.5. Barplot showing significant difference between group B1 and B2 for bonobos, where more consolatory interactions occurred in group B1 compared to group B2. Plot includes result for group C2 for visual comparison. Results obtained from *Model 2.1*. Whiskers show one standard error above and below mean. Asterisk shows significant difference between B1 and B2 at the $P < .05$ level.

Table 4.6. Results for *Model 2.1* and *Model 2.2*: Individual and social factors in bonobos and chimpanzees respectively. Results of each binomial matrix dyad model (estimates and standard errors, together with confidence intervals, results of likelihood ratio tests, and the range of estimates obtained when dropping levels of random effects one at a time). Significant *P* values (< 0.05) are shown in ***italicised bold***. Random effect output is provided in *Appendix B*.

Model 2.1: **Full model testing within-species trends in bonobos**

Fixed effects	Estimate	SE	CI_{95}	$\chi2$	z	*P*	Min	Max
(Intercept)	***-2.050***	***0.790***	***-3.380 to -0.447***		***-2.595***	***.009***	***-2.544***	***-1.630***
Group[a]	***-1.010***	***0.440***	***-2.822 to -0.064***	***4.932***	***-2.297***	***.026***	***-1.226***	***-0.797***
B. sex[b]	-0.356	0.454	-1.556 to 1.373		-0.784	.214	-0.709	-0.010
B. age[c]	***-0.693***	***0.294***	***-2.453 to -0.222***		***-2.360***	***.014***	***-0.902***	***-0.573***
B. rank				0.571		.752		
Low[d]	-0.979	0.603	-2.713 to 1.446		-1.623	.105	-1.329	-0.562
Medium[d]	-0.240	0.468	-2.642 to 1.192		-0.513	.608	-0.476	-0.056
B-V kinship[e]	***-1.566***	***0.815***	***-3.294 to -0.088***	***5.219***	***-1.922***	***.022***	***-2.103***	***-1.039***
B-V aff.[c]	0.225	0.131	-0.440 to 0.636	0.960	1.716	.327	0.144	0.269
B. greg.[c]	-0.009	0.290	-0.819 to 1.290	0.161	-0.030	.688	-0.224	0.228
V. sex[f]	0.177	0.389	-1.304 to 1.274	0.000	0.454	.988	-0.045	0.329
V. age[c]	***-0.515***	***0.282***	***-1.440 to -0.221***	***7.665***	***-1.826***	***.006***	***-0.703***	***-0.407***
B. age * B. sex	-0.310	0.507	-2.283 to 1.481	0.007	-0.611	.932	-0.711	-0.086

Model 2.2: **Full model testing within-species trends in chimpanzees**

Fixed effects	Estimate	SE	CI_{95}	$\chi2$	z	*P*	Min	Max
(Intercept)	***-3.942***	***0.707***	***-5.888 to -2.955***		***-5.797***	***.003***	***-4.612***	***-3.617***
B. sex[b]	-0.322	0.701	-2.292 to 0.828		-0.647	(—)[g]	-0.892	-0.142
B. age[c]	-0.619	0.368	-1.775 to -0.203		-2.312	(—)[g]	-0.741	-0.357
B. rank				0.495		.781		
Low[d]	-0.592	0.559	-1.441 to 1.101		-0.458	.275	-0.918	-0.228
Medium[d]	-0.554	0.527	-1.561 to 0.974		-0.712	.258	-0.784	-0.328
B-V kinship[e]	***-0.710***	***0.438***	***-1.737 to -0.002***	***3.891***	***-2.048***	***.049***	***-1.104***	***-0.678***
B-V aff.[c]	***0.215***	***0.089***	***-0.005 to 0.336***	***4.045***	***1.970***	***.044***	***0.159***	***0.310***
B. greg.[c]	-0.136	0.208	-0.697 to 0.179	1.393	-1.178	.238	-0.206	-0.011
V. sex[f]	***-0.553***	***0.574***	***-1.916 to -0.041***	***4.260***	***-1.965***	***.039***	***-1.253***	***-0.800***
V. age[c]	0.158	0.216	-0.462 to 0.384	0.228	-0.471	.633	0.065	0.278
B. age * B. sex	***-0.842***	***0.692***	***-2.202 to -0.108***	***4.247***	***-1.959***	***.039***	***-1.521***	***-1.052***

[a] *Dummy coded and centred with B1 as the reference category*

[b] *Dummy coded and centred with female as the reference category*

[c] *Z-transformed to a mean of 0 and a standard deviation of 1*

[d] *Dummy coded and centred with high as the reference category*

[e] *Dummy coded and centred with kin as the reference category*

[f] *Dummy coded and centred with female as the reference category*

[g] *P-values not provided due to limited interpretation as interaction is significant*

Table 4.7. Summary of within-species trends found across sanctuary-living bonobos and chimpanzees in *Models 2.1* and *Model 2.2*.

Predictor	Bonobos	Chimpanzees
Group	Y	—[a]
Bystander Age	Y	—[b]
Bystander Sex	N	—[b]
Bystander Age*Bystander Sex	N	Y
Bystander Rank	N	N
Bystander Gregariousness	N	N
Victim Age	Y	N
Victim Sex	N	Y
Kinship	Y	Y
Dyadic Affiliation Strength	N	Y

[a] *Not tested in chimpanzees*

[b] *Not interpretable due to significance of interaction*

4.5 Discussion

Systematic cross-species comparisons are vital for elucidating the evolutionary origins for complex socio-emotional behaviours, including empathy. Human research has revealed substantial individual and cultural variation in emotional responding and this study indicates that this may be the case for our closest living relatives. Due to apparent increased emotional sensitivity, reduced aggressivity, and potentially higher levels of social tolerance (Gruber & Clay, 2016; Hare et al., 2012), it has been suggested that bonobos may be more likely to offer consolation—considered a behavioural expression of empathy—than chimpanzees. In this study, I systematically addressed this question using a direct comparison of sanctuary-living chimpanzees and bonobos. My results indicate that, unlike such a prediction, chimpanzees and bonobos do not significantly differ in their consolation tendencies, both in terms of overall occurrence and the number of consolers that responded per event. There was, however, a significant effect of group in the bonobos, where consolation occurred more between dyads in group B1 than group B2. The present study could not test for group differences in chimpanzees as I only observed one group. However, expressions of empathy and other emotion-related behaviour are known to vary in wild chimpanzee communities of the same subspecies (Arnold & Whiten, 2001; Kutsukake & Castles, 2004), which parallels findings across diverse human cultures (Chopik et al., 2017; Vreden et al., in prep). The presence of intraspecies group variation in consolation in the sanctuary bonobos complements this literature and suggests that empathic tendencies may be shaped by broader socio-environmental circumstances.

My findings complement previous consolation research in *Pan* by showing that bystander age is an important predictor of consolation in bonobo and chimpanzee communities (Clay & de Waal, 2013; Webb et al., 2017). Although underlying mechanisms cannot be detected in an observational study, it is possible that young individuals may console more than older individuals as they are typically afforded more social tolerance before they become fully embedded into their respective group's dominance dynamics (de Waal, 1986). Furthermore, younger individuals may be less inhibitive with their responses in these contexts. I did not measure individual's capacity for inhibition in this study. However, an interesting follow-up would be to compare these two species on inhibition, such as through delayed gratification tasks (Beran et al., 1999), and investigate if this measure predicts an individual's relative tendency to console.

Consistent with the theory that social closeness predicts empathic responses (Anderson & Keltner, 2002; Preston & de Waal, 2002), kinship predicted consolation in both species. However, I only found an influence of dyadic affiliation level in chimpanzees. It is important to note that previous investigations on these bonobo groups revealed strong influences of social relationship on consolation occurrences (Clay & de Waal, 2013). However, since 2011 when these data were collected, the social groups have changed considerably. Some bonobos from Lola ya Bonobo have been released into a wild reserve in the Democratic Republic of the Congo, some have been migrated into different groups, and some have died. The change in composition over time is likely to have impacted on social relationships, and consequently how individuals orient towards others in terms of consolation. Temporal variation in consolatory efforts may reflect empathy as a phenomenon that emerge flexibly when conditions permit (Brooker et al., 2022).

It is possible that consolation may serve different functions in bonobo and chimpanzee societies. Chimpanzees may be more selective in their responses as wild and captive communities have been well-documented to exhibit political social lives, centred around strong adult male-male alliances and displays of dominance and subordinacy (Gruber & Clay, 2016). This may be further evidenced by the presence of an age-sex interaction in chimpanzees, whereby young males were the most consolatory and old males were the least consolatory. Enhanced responsiveness in young male chimpanzees may represent a drive to form and reinforce strong social bonds with their close peers and older individuals they will spend their lives with (Mitani, 2009). Furthermore, adult male chimpanzees were much less likely to be followed as distressed focals in my study (*N* = 17/160) compared to adult females (*N* = 103/160). Therefore, opportunities for adult male chimpanzees to console their closest social partners were respectively low in my sample and may additionally explain the direction of the age-sex interaction whereby older males were the least likely to console. In the Kanyawara community at Kibale Chimpanzee Project in Uganda, young male chimpanzees are typically more likely to be victims of aggression, which appears to be due to their tendencies to elicit the most aggression themselves (Sabbi et al., 2021). Regardless, social bonds formed during male chimpanzee development predict dominance trajectories (Bray et al., 2021). Thus, this effect at a young age in chimpanzees may be caused by younger males watching their peers being aggressed often during a period when they are building foundational relationships for later life (Sandel et al., 2020). In addition, the imbalances in my sample may also explain the presence of a victim sex effect, whereby females were consoled more than males. This effect may be driven by low power from my victim sex distribution.

In contrast, in bonobos, males typically only form strong relationships with their mothers (Surbeck et al., 2011) and occasionally other females for mating and alliance formation (Surbeck et al., 2012). Despite males being the philopatric sex for both species, only chimpanzee communities tend to feature strong male-male relationships (Gruber & Clay, 2016). Furthermore, the political dynamics in bonobo societies appear to be relatively more subtle, and thus difficult to study (Furuichi, 2011), Instead, bonobos may be less selective and respond out of care and emotional sensitivity towards others (Clay & de Waal, 2013; Kret et al., 2016). Bonobos tended to console victims of both sexes evenly. Furthermore, bonobo consolation was not biased towards non-kin close social partners. However, in line with recent findings that paedomorphic signalling increases likelihood of receiving consolation (Heesen et al., 2022), younger bonobo victims were generally more likely to be consoled in my study.

In this study, I imposed strict criteria of inclusion for consolation, where any behaviour following a solicitation from the victim was not counted. For example, if a victim immediately approached a bystander and solicited an interaction with them, any subsequent interactions initiated by the bystander during the 5-minute PC/PD period were not coded as consolatory approaches. This criterion was imposed as consolation is associated with empathy, however if bystanders are not the party to solicit contact then it is not possible to determine that they were motivated by the victim's distress to respond (de Waal & Aureli, 1996; de Waal & Preston, 2017). Therefore, there is also a possibility that victim-initiated interactions provided reassurance and comfort to the victim, yet these encounters were not counted in my analyses. A wider investigation into bystander-victim interactions following distress could reveal whether the intraspecies trends found in this study are associated with empathic tendencies, or wider conflict management responses in general (Clay et al., 2016).

Intraspecies variation is vital for comparative research across taxa (Kaufhold & van Leeuwen, 2019). Studies of primates have revealed substantial intergroup behavioural variation, such as bartering in long-tailed macaques (*Macaca fascicularis*; Brotcorne et al., 2017), activity and ranging in guerezas (*Colobus guereza*; Fashing, 2001), and even the connectedness of social networks in vervets (*Chlorocebus pygerythrus*; Borgeaud et al., 2016). The *Pan* apes similarly can vary between groups regarding expressions of various social and ecological behaviours. Examples include, but are by no means limited to, grooming traditions (van Leeuwen et al., 2012) and communication in chimpanzees (Crockford et al., 2004), and hunting behaviour and tool use in bonobos (Hohmann & Fruth, 2003). In addition, bonobos and chimpanzees also show marked intraspecies variation in levels of social tolerance (Cronin et al., 2014, 2015; van Leeuwen et al., under review), a factor considered to facilitate empathy (de Waal & Aureli, 1996; Palagi et al., 2014).

Whilst there were no overall species differences between the bonobos and chimpanzees in this sample, the two bonobo groups varied significantly. Intriguingly, and in contradiction of the *Social Constraints Hypothesis* (de Waal & Aureli, 1996), supported by analyses from within our research team (van Leeuwen et al., under review), the more despotic group (B1) had higher consolation tendencies than the more tolerant group (B2; also see *Chapters 5-6* for more details on the relative social tolerance of my study groups, measured during the same field season as consolation observations). Furthermore, my results show that bonobos and chimpanzees in this sample appeared to vary in which within-species factors influenced their tendencies to console. In bonobos, younger victims were consoled more than older victims, whereas in chimpanzees victim age was not significant but female victims were more likely to be consoled than males.

Similar to these within-species factors, variation in social tolerance may also influence empathy differently between *Pan* groups. Chimpanzee aggression is generally more common and more dangerous than in bonobos (Wilson et al., 2014); in this regard, approaching a victim in a more despotic group may bring greater risk of injury and escalating tension. For chimpanzees, consolatory approaches may function to not only reassure a distressed individual, but also to reduce social tension and the risk of escalation (Palagi et al., 2006). Although this may also be the case in bonobos, the risk of serious injury may generally be lower, even in a despotic group (Hare et al., 2012). Thus, consoling distressed individuals may be less important in a tolerant group, if there is lower risk of spontaneous or retaliative aggression. In this study, consolation may however be influenced by factors unrelated to social tolerance. For example, detected group variation may also be driven by differences in group composition, where the despotic group B1 had a higher number of infants and juveniles, who were shown to console more than adults. However, the effect is significant when controlling for all other factors, suggesting that tendencies may generally be higher in some groups compared to others. To decipher the association of social tolerance with primate empathy (de Waal & Aureli, 1996; Palagi et al., 2014), future research should assess tolerance levels and risk of aggression of multiple groups and compare these group-specific factors with relative tendencies to console.

In sum, this study supports the notion that within-species community variation among *Pan* behavioural tendencies may be more significant than between-species differences (Gruber & Clay, 2016; McGrew et al., 2001). Both bonobos and chimpanzees are highly flexible and adaptable species, and under particular conditions and pressures may exhibit greater or reduced tendencies to express empathy-related behaviours like consolation. In humans, we see cultural variation in behaviours such as communication, prosociality, conformity, and empathy and other socio-emotional responses that may be facilitated by certain social dynamics and cultural norms (Chopik et al., 2017; House et al., 2013; Hua et al., 2019; van Leeuwen et al., 2018; Vreden et al., in prep). The same appears to be true in our closest living relatives. Further research into species comparisons should always integrate group-level differences (e.g., composition, collective temperaments) that may promote or hinder empathic expressions such as consolation. Comparing more groups of the same species and investigating within-group drivers of various empathy-related behaviours may reveal a deep ancestral history of such cultural flexibility in emotional responsiveness, and what features promote or hinder the expression of empathy.

Chapter 5: Sanctuary-living bonobos and chimpanzees manage social tension with affiliative body contact

This chapter constitutes an empirical article to be submitted for publication with the following authorship:

Brooker, J. S., Goldsborough, Z., van Leeuwen, E. J. C., Kordon, S., Webb, C. E., de Waal, F. B. M., & Clay, Z. Sanctuary-living bonobos and chimpanzees manage social tension with affiliative body contact.

Abstract

The role of reassurance in human and primate societies is well documented regarding its purported functions to reduce social tension, arousal, and reduce aggressive tendencies in the target. In the great apes, studies of reassurance have mostly focused on post-conflict contexts, such as reconciliation and consolation. However, the same behavioural forms of contact-affiliation also regularly occur in other socially tense contexts, such as prior to intra- and intergroup competition. Our closest living relatives, bonobos and chimpanzees, have extensive overlapping affiliative behavioural repertoires and have been documented engaging in many tactile behaviours during tense periods. If affiliative social contact can be used by these species to resolve conflict, then use of these behaviours during competitive circumstances may reflect a strategy to manage social tension and prevent conflict. In this chapter, I directly compare tendencies of sanctuary-living bonobo and chimpanzee groups to engage in contact-affiliation, non-contact-affiliation, and conflict behaviour during a controlled period of social tension, initiated by use of a feeding experiment known as the 'peanut swing'. I compare observations from $N = 5$ sanctuary-living bonobo and chimpanzee groups with a total study population of $N = 124$. Both species and all groups generally overlapped in their tendencies to engage in contact-affiliation prior to competitive feeding. However, bonobo female-female pairs and chimpanzee male-male pairs engaged in more contact affiliation than other sex pairings. At the group-level, these trends were only clear for the most socially tolerant groups of bonobos and chimpanzees. Across groups, contact-affiliation was more common than non-contact-affiliation and conflict behaviour during the pre-feeding periods. Furthermore, vulnerable mouth-to-body behaviour in chimpanzees was more common in the tolerant chimpanzee group compared to the despotic group. Despite apparent species differences in aggressivity, social attentiveness, and emotional sensitivity, bonobos in these populations engaged in pre-feeding contact affiliation at similar tendencies to those of chimpanzees. The group-level variation indicates a possible function for pre-feeding affiliation, or 'celebration' behaviour, that can be encouraged or dampened by collective temperaments and within-group dynamics.

5.1 Introduction

5.1.1 The significance of reassuring touch

Purported as the earliest form of human communication (Kertay & Reviere, 1998), touch is one of the first senses to develop and reach maturity in our species (Gallace & Spence, 2010). Although the role of touch in human societies varies considerably, not only by culture but by setting, age, and gender (see Gallace & Spence, 2010 for a review), touch appears to be vital for physical and emotional development (Barnett, 2005; Feldman et al., 2010; Field, 2001). Deprivation from touch has been associated with impaired physical and cognitive development (Ardiel & Rankin, 2010) and increased handling can reduce behavioural markers of anxiety and increase scores on developmental assessments (Casler, 1965; Hopper & Pinneau, 1957).

Regardless of form or intention, physical contact can have powerful communicative properties and elicit diverse emotional responses (Jones & Yarbrough, 1985; McIntyre et al., 2022). In the human literature, a contextual analysis of naturally occurring touch identified 12 distinct meanings, such as support, affection, appreciation, compliance, and attention-getting (Jones & Yarbrough, 1985). Humans have even performed above chance at identifying emotions through touch alone (Hertenstein et al., 2006). When pairs were separated by a curtain and instructed to communicate an emotion to their partner through touch, participants could reliably identify anger, fear, disgust, love, gratitude, and sympathy.

Social touch appears to have several functions, for example to increase one's authenticity and affirmation of a social bond (Rose, 1990; Patterson et al., 1986), and to buffer stress (see Morrison, 2016 for a review). Known to have therapeutic qualities (Meehan, 1998; Sahi et al., 2021; Weekes et al., 1993), self- and mutual reassurance through touching represents an especially important function of tactile social behaviour in humans. Touch therapy has often been applied in healthcare contexts as a form of reassurance for patients and is associated with improved feelings of subjective distress from physical pain and activation in neural regions associated with threat responses (Coan et al., 2013; Coan et al., 2006; Johnson et al., 2013; López-Solà et al., 2018; Reddan et al., 2020). Furthermore, gentle reassuring touch is effective at reducing physical pain and improving mental wellbeing during medical treatment (Weze et al., 2006; Monroe, 2009). These effects appear to be amplified if the pair is a romantic couple. These findings indicate that a close social connection may make forms of touching more effective as reassurance.

Tactile communication forms a key component of social interactions for many other animals, with possible reassuring functions. For example, dolphins have been shown to affiliate through flipper-rubbing, which appears to help repair social bonds and reduce post-conflict group tension (Tamaki et al., 2006). Akin to humans, touch also appears to be vital for nonhuman animal development (Ardiel & Rankin, 2010; Barnett, 2005) with physiological implications. Reduced markers of stress following tactile communication has been seen in rats (Liu et al., 1997) and non-human primates, generally observed in studies of post-conflict consolation, a specific form of reassurance spontaneously offered to distressed conspecifics (e.g., Fraser et al., 2008; Palagi et al., 2014; Palagi & Norscia, 2013). Whilst extensively documented in humans (Davidov et al., 2013, 2021; Fujisawa et al., 2006; Roth-Hanania et al., 2011; Zahn-Waxler et al., 1992), consolation appears to be rare in the animal kingdom (Adriaense et al., 2020) and potentially emerges flexibly due to particular socio-ecological circumstances and abilities.

Two species known to actively use consolation are our closest living relatives, bonobos (*Pan paniscus*; Clay & de Waal, 2013; Palagi et al., 2013) and chimpanzees (*Pan troglodytes*; de Waal & Aureli, 1996; Romero et al., 2010). The presence of consolation in our closest living relatives, and not in other more distantly-related primates living in relatively similar socio-ecological environments (with the exception of *Macaca tonkeana* in Palagi et al., 2014; see Brooker et al., 2022 for a review), indicates a possible ancestral origin for this behaviour in our last common ancestor. However, evidence of consolation in birds (Fraser & Bugnyar, 2010) and absence in certain groups of chimpanzees (Arnold & Whiten, 2001; Fuentes et al., 2002), further supports the notion that types of reassurance may emerge and sustain flexibly.

A broader investigation, beyond the post-conflict context, is needed to fully understand the role of affiliative body contact in social communication and reassurance. Conflicts can destabilise primate groups and effective conflict management strategies are required to facilitate group cohesion and maintain harmony (Flack et al., 2005; Flack et al., 2006). Bonobos and chimpanzees are reported to perform many forms of social reassurance (de Waal, 1992), thus represent ideal candidates to investigate the role and possible trends of contact affiliation during social tension as a potential conflict management strategy.

5.1.2 Reassurance in *Pan* and other primates

In nonhuman primates, reassurance was functionally defined as the use of affiliative gestures to reduce aggressive tendencies or fear in a target (de Waal, 1989). Typically, reassurance has been considered as a reconciliation when directed to subordinates from dominances, and as appeasement from subordinates towards dominants. However, in non-conflict contexts of social tension, such as intergroup encounters or intragroup competition, specific forms of affiliative contact also occur in bonobos and chimpanzees (wild: Hohmann & Fruth, 2000; Samuni et al., 2019; semi-wild: Clay & de Waal, 2015; captivity: Paoli et al., 2007), which have not been systematically investigated.

When associated with feedings, the elevated occurrence of affiliative contact is also sometimes referred to as “celebration” (de Waal, 1992), implying an expression of positive excitement or anticipation. The role and trends of specific forms of reassurance as conflict management behaviours, such as consolation and reconciliation, are well documented in bonobos and chimpanzees. Examining the use of affiliative body contact in other contexts of social tension would provide further depth to elucidate how these two species manage their individual and collective temperaments and conflict prevention. For the purposes of this paper, I define 'reassurance behaviour' broadly as *the use of contact affiliation during socially tense contexts with the aim of preventing aggression and reducing anxiety*.

Forms of reassurance in bonobos and chimpanzees are well documented. Bonobos use genito-genital rubbing and other sexual behaviours for reassurance (Clay & de Waal, 2015; Hohmann & Fruth, 2000) and are reported to have more peaceful cofeeding experiences when preceded by sexual contacts (Wobber et al., 2010). Similarly, the use of reassurance has been shown to reduce aggression during cofeeding contexts in captive chimpanzees (de Waal, 1992). Chimpanzees are thought to use mouth-to-body contacts as a species-typical forms of reassurance, such as body kissing and placing fingers/hands in a partner's mouth (de Waal & van Roosmalen, 1979; Goodall, 1986). Genital contacts are also observed in wild and captive chimpanzees groups during periods of tension (Anestis, 2004; Sandel & Reddy, 2021; Savage & Malick, 1977), including genital touches, mounting, and rump-rump touching—akin to bonobo genito-genital rubbing—where individuals face away from one another and press their ano-genitals together, typically without rubbing (Goodall, 1989; also see Anestis, 2004 for an example of bonobo-like genito-genital rubbing in captive female chimpanzees).

Both *Pan* species also engage in touching and embracing during periods of social tension (de Waal, 1988, 1992; Goodall, 1989), as well as grooming and play. Social grooming functions as an affiliative network-building behaviour in many animal societies (Kutsukake & Clutton-Brock, 2010), and an experimental study showed grooming and food sharing were proximately linked in three *Pan* groups (Judge et al., 2006), however this effect dissipated when controlling for long-term reciprocity in the chimpanzee dyads. Grooming is purported to reduce social tension and/or individual anxiety in a variety of primates, including long-tailed macaques (*Macaca fascicularis*; Schino et al., 1988), crested black macaques (*Macaca nigra*; Aureli & Yates, 2010), pig-tailed macaques (*Macaca nemestrina*; Boccia et al., 1989), and Barbary macaques (*Macaca sylvanus*; Shutt et al., 2007). Play may serve similar functions among immature zoo-living chimpanzees, who engaged in more social play during pre-feeding periods compared to other times of day (Palagi et al., 2004).

Specific functions of tactile reassurance have been studied across primates and other animals in terms of reconciliation (i.e., aggressor-victim pairs) and post-conflict affiliation (i.e., bystander-victim pairs); this includes consolation where bystanders spontaneously offer reassuring body contact to distressed victims (de Waal & van Roosemalen, 1979). Although *Pan* species use various forms of post-conflict affiliation (see *Chapter 2* and *Chapter*

4), the broader use of reassurance during other periods of social tension, such as intragroup competition, has not been systematically compared in *Pan* or other primate species. Studying the broader contexts and functions of reassurance behaviour will help our understanding of how reassurance originally emerged, including specific forms like reconciliation and consolation. Using a controlled period of social tension—achieved through systematic deployment of the *peanut swing*, a cofeeding experiment typically applied to measure cofeeding social tolerance (Cronin et al., 2014, 2015; van Leeuwen et al., 2021)—in the present study, I compared instances of dyadic contact- and non-contact-affiliation in sanctuary-living bonobos and chimpanzees. I also documented instances of conflict behaviour to assess how affiliation and conflict temporally vary pre- and post-feeding. This study thus represents the first direct systematic comparison of the use of affiliation and conflict behaviour during a context of social tension in multiple *Pan* groups. I examined the prevalence of affiliation, conflict, and specific forms of affiliative contact during this context and how these behaviours are associated with dyadic and group-level trends. By observing affiliation and conflict on a collective scale, it was not possible to clearly test whether these forms of affiliative contact and particular interactions are directly associated with a reduced likelihood of aggression or reduced anxiety. Thus, to not infer that these social encounters function as reassurance, I use the term *contact-affiliation* to refer to these behaviours and interactions occurring prior to competitive feeding.

Reassurance is purported to reduce aggressive tendencies in primates (van Hooff, 1967; de Waal, 1992). Chimpanzees have been reported as more aggressive than bonobos, with greater risk of conflict and injury (Wilson et al., 2014) as well as a greater focus on linear dominance relationships, reaffirmed regularly through greetings and appeasement gestures (Boesch, 2009; Nishida, 2011). Therefore, I tested the hypothesis that chimpanzees will engage in more reassurance behaviour than bonobos. This resulted in my prediction that chimpanzees would show greater tendencies to perform contact affiliation during the pre-feeding period, and enhanced contact affiliation for all groups would be associated with reduced aggression. In addition, despite male philopatry in both *Pan* species, bonobo societies are typically characterised by strong female-female bonds that supports coalitionary relationships and greater female social power in competitive contexts, such as feeding (Parish, 1996; White & Wood, 2007). In contrast, males and male-male bonds generally occupy these roles in chimpanzees (Boesch, 2009; Mitani, 2009; Nishida, 2011). Therefore, I tested the hypothesis that there would be sex-based differences in reassurance behaviour according to species. I predicted that contact affiliation would be higher among bonded sex-pairs—female-female in bonobos, and male-male in chimpanzees—compared to other sex-pairs in both species.

Increased crowding in artificial living environments, compared to the wild, has been shown to influence social relationships of primates and other animals (de Waal et al., 2000). When forced into close proximity, pairs of equally familiar female common vampire bats (*Desmodus rotundus*) developed longer-lasting cooperative partnerships than control pairs (Razik et al., 2022). Furthermore, affiliative behaviour, including female grooming of the harem male, increased in Hamadryas baboons (*Papio hamadryas hamadryas*) when kept in crowded conditions (Judge et al., 2006). This was reported as social affiliation being used as a possible tension reduction strategy. Among great apes, although wild orangutans are largely solitary, a zoo-living group were shown to develop conflict mitigation strategies, including reconciliation, indicating a capacity to adapt to changes in living conditions (Kopp & Liebal, 2018). Whilst previously thought to foster greater conflict, there is evidence in both *Pan* species that increased population density may also foster increased affiliation, such as grooming (Nieuwenhuijsen & de Waal, 1982; Paoli et al., 2007). Furthermore, socio-sexual behaviours in a captive group of bonobos have also been shown to peak during short-term crowded feedings, whilst anxiety markers and aggression rates remained stable (Paoli et al., 2007).

This results in the hypothesis that affiliation serves to reduce aggression in contexts of physical crowding. As the *peanut swing* experiment introduces a crowded feeding context, I could test for species-specific and group-specific trends in affiliation and conflict behaviour. In addition, I deployed this paradigm in a sanctuary environment, which provides the benefits of large sample groups living in semi-naturalistic conditions as well as a systematically controlled arena across sites to observe spontaneous social interactions during the application of a cofeeding experiment. I did not seek to explicitly compare reassurance against population densities; however I used this paradigm to investigate how affiliation and conflict behaviour fluctuate during a period of social tension. As well as contact behaviours, such as touching and embracing, bonobos and chimpanzees use non-contact behaviours, such as sexual invitations and holding out their hands to others, during periods of social tension with purported appeasement functions to reduce aggressive tendencies in others (de Waal, 1988, 1992; Goodall, 1986; Kano, 1992; Nishida et al., 2010; Romero & de Waal, 2010; van Hooff, 1967). Thus, where the use of pre-feeding contact-affiliation may reinforce social bonds prior to competition, the reaffirmation of dominance status through appeasement behaviours may reduce the likelihood for aggression during competitive contexts. I predicted that, during the pre-feeding period, increased contact-affiliation and increased non-contact affiliation would be associated with decreased levels of conflict in both species. I also predicted that periods of increased conflict at the onset of competition—when the feeding starts—would be followed by increased contact-affiliation and increased non-contact affiliation as a means to diffuse tension and prevent conflict escalation.

Finally, I compared individual strategies of reassurance for specific behaviours in chimpanzees. Mouth-to-body behaviours—body kissing and placing a finger or hand in a partner's mouth—are common forms of reassurance in chimpanzees (Goodall, 1986; Nishida et al., 2010). Vulnerable tactile affiliative behaviour has been purported to promote trust between potential competitors (Palmer & Pomianek, 2007), and appear to be used to test social bonds in other mammals, including capuchin monkeys (*Cebus*; Perry, 2011) and hyenas (*Crocuta crocuta*; East et al., 1993). Where these behaviours place one party at risk of serious injury, I tested the hypothesis that vulnerable tactile behaviours would be fostered by social tolerance. I predicted that mouth-to-body behaviours would be more likely to occur in a tolerant group of chimpanzees, compared to a relatively more despotic group. In addition, sexual behaviour is a key reassurance strategy for both species, but particularly bonobos. Thus, I predicted that both individuals from all groups of both species would engage in pre-feeding sexual behaviour, but that tendencies would be higher in bonobo groups than chimpanzee groups. These comparisons of pre-feeding sexual behaviour can be seen in *Chapter 7*.

5.2 Methods

5.2.1 Study sites and subjects

I analysed data collected from *N* = 5 groups of sanctuary-living apes across two African sanctuaries, totalling *N* = 129 individuals. Three groups of bonobos (*N*: B1 = 22; B2 = 18; B3 = 14) were observed at Lola ya Bonobo Sanctuary in the Democratic Republic of the Congo between July and September 2019. Two further groups of chimpanzees (*N*: C1 = 25; C2 = 50) were studied at Chimfunshi Wildlife Orphanage in Zambia between March and August 2019 (see *Section 3.1* for more information about these field sites). Due to mother-dependence, only apes aged 3 years and older are considered when assessing cofeeding tolerance using the *peanut swing*. As this study purely focused on social interactions, I included individuals of all ages that were regularly seen interacting with individuals beyond their mother and maternal family. Furthermore, the total possible population for each session varied, as some individuals were absent due to veterinary care. These absences resulted in a total sample range of *N* = 124 (B1 = 22; B2 = 16; B3 = 14; C1 = 25; C2 = 47). The sample groups were fairly balanced regarding age and sex, and a summary can be seen in *Table 5.1*.

Table 5.1. Social compositions[a] of groups that took part in the peanut swing experiment. Number of individuals of each sex within each age class. Bonobos were observed at Lola ya Bonobo Sanctuary in the Democratic Republic of the Congo and chimpanzees were observed at Chimfunshi Wildlife Orphanage Trust in Zambia.

Species	Group	Total	Infants[b] F / M[c]	Juveniles[b] F / M[c]	Adults[b] F / M[c]
Bonobo (*Pan paniscus*)	1 (B1)	22	0 / 1	5 / 5	7 / 4
	2 (B2)	16	0 / 0	7 / 4	1 / 4
	3 (B3)	14	0 / 0	4 / 2	4 / 4
Chimpanzee (*Pan troglodytes*)	1 (C1)	25	0 / 2	5 / 1	11/ 6
	2 (C2)	47	4 / 1	5 / 7	23 / 7
Total	5	124	4 / 4	26 / 19	46 / 25

[a] *Values reflect individuals that were eligible for at least one session. This excludes Eleke (B2), Kodoro (B2), Masya (C2), Mikey (C2), and Mumba (C2)*

[b] *Age in years: Infants = 0–2; Juveniles = 3–11; Adults = 12+ (based on Cronin et al., 2014)*

[c] *F = Number of females; M = Number of males*

5.2.2 The "peanut swing" experiment

To systematically compare pre-feeding reassurance behaviour in sanctuary-living apes, I applied an established experimental measure of cofeeding tolerance—the *peanut swing*—to create a controlled arena of social tension (Cronin et al., 2014, 2015; van Leeuwen et al., 2021). Full details on the *peanut swing* paradigm is deployed to assess group-level social tolerance can be read in Cronin et al. (2014) and *Section 3.2.2.1*. *Section 3.2.2.1* also provides a detailed explanation of how I adapted this experiment to measure pre-feeding social affiliation and conflict patterns. The cofeeding tolerance of these groups in 2019, as measured by these sessions is compared in van Leeuwen et al. (under review), in which I am a coauthor. We found that, relative to each other, B1 and C1 shared similarly despotic climates, whereas B2, B3, and C2 shared similarly tolerant climates. For the present study, I solely focused on affiliative and conflict social interactions and use these tolerance assessments for context.

Increased social arousal is associated with reassurance behaviours in bonobos and chimpanzees (de Waal, 1992), and has been observed in past implementations of the *peanut swing*. Therefore, I introduced a standardised five-minute pre-feeding window, initiated by vocal alerts from the researchers towards the apes to indicate feeding. The time between the first alerts to the apes and the distribution of the peanuts averaged across all swings as 5min6s, but for the purposes of all analyses, I only considered social behaviours occurring within exactly five immediate minutes prior to distribution. When the peanuts hit the ground—referred to as "T0"—the pre-feeding period ended, and researchers continued to film for another 5-minutes. Each session was filmed from multiple angles and camera operators annotated the sessions from start to finish by highlighting when individuals arrived, their identities, and what behaviours occurred.

Figure 5.1. Example of a peanut swing session with a chimpanzee group (C2) at Chimfunshi Wildlife Orphanage, Zambia. *Left*: Researchers holding the bamboo trough pre-T0 whilst another researcher is filming the chimpanzees. *Right*: Researchers have collided the bamboo trough into the fence and the peanuts have entered the enclosure.

At Chimfunshi Wildlife Orphanage, I led 12 peanut-swing sessions at C1 and 11 sessions at C2 in July-August 2019 between 1030 and 1115 or 1330 and 1415 hours. At Lola ya Bonobo, SK led 12 sessions at B1, 12 sessions at B2, and 13 sessions at B3 in August-September 2019 between 0800 and 1230 or 1400 and 1615 hours, to coincide with more sporadic feeding protocols. Sessions were balanced between morning and afternoon across all groups. Unlike the original design, we were unable to wait for all members of the groups to be present, due to the inclusion of the pre-feeding window. For these analyses, I excluded data from sessions with less than 80% of the group seen prior to T0 and some where equipment failed. This resulted in a total session *N* per group of: B1 = 8; B2 = 10; B3 = 10; C1 = 9; C2 = 8). Details of session data can be seen in *Table 5.2*.

Table 5.2. Summary of the session data for the peanut swing experiment across all groups. Includes: range and average pre-T0 group size per experiment, which fluctuated due to absences; total number of sessions I analysed for each group in this study; the range and average number of dyads that could potentially be recorded engaging in pre-feeding affiliation; and the relative tolerance status for each of these groups in comparison to each other (van Leeuwen et al., under review).

Species	Group	Pre-T0 group size[a]	Sessions[b]	Dyads per session[c]	Relative tolerance status
Bonobo (*Pan paniscus*)	1 (B1)	18–22 (*M* = 20.6)	8	153–231 (*M* = 203.6)	Despotic
	2 (B2)	14–16 (*M* = 14.9)	10	91–120 (*M* = 103.8)	Tolerant
	3 (B3)	12–14 (*M* = 13.6)	10	66–91 (*M* = 85.9)	Tolerant
Chimpanzee (*Pan troglodytes*)	1 (C1)	19–25 (*M* = 21.1)	9	171–253 (*M* = 213.1)	Despotic
	2 (C2)	41–47 (*M* = 43.0)	8	820–946 (*M* = 903.5)	Tolerant

[a] *Range of eligible individuals across all sessions. Mean in ( )*

[b] *Total number of sessions where 80%+ of the group was seen prior to T0*

[c] *Range of possible dyads per session that could have affiliated prior to T0. Mean in ( )*

5.2.3 Reassurance observations and behavioural coding

All social interactions were coded using the video software ELAN (2019; Wittenburg et al., 2006). I was thus able to code for each individual every social, agonistic, and self-directed behaviour they engaged in. This coding method enabled the compilation of datasets comprising individual- and dyad-level pre-feeding reassurance tendencies. Individuals who were not observed at all prior to T0 were excluded. Social interactions were coded once per dyad with the initiator's identity for each behaviour and the recipient's response. Durations were not coded due to the intensity of the coding programme, however, new bouts were coded per behaviour if there was a latency of at least 15 seconds between the same behaviour types.

I applied an extensive ethogram to account for the myriad behaviours either species may use to affiliate prior to feeding (*Appendix A*; de Waal, 1988; Kano, 1992; Goodall, 1986; Nishida et al., 2010). Bonobos and chimpanzees each use rich repertoires of communicative gestures and tactile behaviour, including during periods of social tension. Forms of tactile affiliation have been shown to have reassuring effects on stress markers (Clay & de Waal, 2013; Fraser et al., 2008), and forms of non-tactile affiliation have generally been associated with appeasement functions in *Pan* (de Waal, 1988, 1992; Goodall, 1989). Therefore, I assigned each affiliative social behaviour into one of two categories: 'contact-affiliation' for tactile social behaviours typically used as reassurance; and 'non-contact-affiliation' for non-tactile communicative social behaviours that may be used as appeasement. In addition, I also coded all instances of social 'conflict' behaviours to compare how levels of affiliation and conflict associate during the pre-feeding and cofeeding periods.

For the purposes of this study, *contact affiliation* incorporates all tactile forms of social affiliative behaviour. This includes: embrace, mount, pat, touch, genital touch, mount walk, and genito-genital contact (coded as rump-rump touch in chimpanzees). A full ethogram for contact-affiliation recorded in this study is shown in *Appendix A.1*. These behaviours have been previously described to have reassuring functions during periods of social tension (Aureli & Yates, 2010; Boccia et al., 1989; de Waal, 1992; Judge et al., 2006; Palagi et al., 2006; Schino et al., 1988; Shutt et al., 2007). Some contact behaviours only occurred in chimpanzee groups, including body kiss, mouth kiss, grasp hand, and finger/hand in mouth. Social state behaviours were also coded, including social play, contact-sit, and groom, if they lasted for five seconds or longer, with new bouts coded after 30 second latencies.).

Non-contact affiliation represents other social behaviour that does not involve physical contact, including behaviours previously described as having appeasement functions in the *Pan* apes (de Waal, 1988, 1992; Goodall, 1986; Kano, 1992; Nishida et al., 2010). This includes sexual invitation, hold out hand (i.e., palm up), hold out hand bent (i.e., palm down), and peer. I also included bob, bow/crouch, and submissive greeting (i.e., clear directional 'pant grunts' vocalisations), however these were generally only seen in chimpanzees. Sexual invitations were coded separately from genital contact as they constitute separate behaviours that do not necessarily preclude contact. Distinction of these behaviours was checked for and reported in *Section 5.4.3*. A full ethogram for non-contact-affiliation recorded in this study is shown in *Appendix A.2*.

Conflict represents all forms of dyadic social agonism behaviour, which is distinct from reassurance and appeasement (Goodall, 1986; Kano, 1992; Nishida et al., 2010). This includes high-contact aggression (hit, slap, kick, trample, bite), low-contact aggression (poke, push, push away, brush aside), chase, threat (threat bark, swagger, display, flail arm, stamp), and bluff display. Conflict behaviours were only included when an agonistic behaviour involved two clear parties. Bluffing behaviour, defined in *Table 5*, frequently occurred without a clear target. Thus, undirected bluff displays and withdraws were not included in this analysis. A full ethogram for conflict behaviour recorded in this study is shown in *Appendix A.3*.

To assess inter-coder reliability (ICR), 8% of bonobo sessions (N = 3) and 13% of chimpanzee sessions (N = 3) were coded twice. The ICR results for dyad social interactions—including all contact-affiliation, non-contact-affiliation, and conflict behaviours—indicated almost perfect agreement (bonobo $\kappa = 0.96$, chimpanzee $\kappa = 0.95$). Of all agreed behaviours, reliability of coded behaviour type was also high (bonobo $\kappa > 0.9$, chimpanzee $\kappa > 0.8$).

5.3 Analysis

5.3.1 Overview of statistical approach

In this study, I used a combination of Bayesian mixed models to test my predictions. The Bayesian approach provides allowance of including prior knowledge into the model, a reduction of a risk of type 1, and a smoother method of quantifying model uncertainty (Kruschke et al., 2012; McElreath, 2020; van de Schoot et al., 2015), especially when using narrow credibility intervals. The Frequentist approach offers the probability of observing the data under the null hypothesis, whereas the Bayesian method informs about the reliability of the data of the parameters used, given the data observed (McElreath, 2020). For these reasons, I took the Bayesian approach for these analyses, in particular as it allows us to gather information that we can apply as prior knowledge into future studies of this new subject of investigation.

All models were fitted using the Stan computational framework (http://mc-stan.org/), accessed through the 'brms' package (v 2.9.0; Bürkner, 2017) in RStudio (v. 1.3.1093; RStudio Team, 2020). For comparisons of pre-feeding contact-affiliation prevalence among species, groups, and particular sex-dyads, I fitted Bayesian Generalized Linear Mixed Models (GLMMs; see *Section 5.3.2*). To compare temporal variation in the use of contact-affiliation behaviours across sessions, relative to non-contact-affiliation gestures and conflict behaviour, I fitted Bayesian Generalized Additive Models (GAMs; see *Section 5.3.3*). For comparisons of mouth-to-body behaviours in chimpanzees (see *Section 5.3.4*), I fitted Bayesian GLMMs.

Each model included four Markov chain Monte Carlo (MCMC) chains, with 10,000 iterations per chain, of which I specified 2,000 iterations as warm-up to ensure sampling calibration. This resulted in 40,000 posterior samples in total for each model. The model diagnostics revealed an accurate reflection of the original response values by the posterior distributions, as R-hat statistics were < 1.01, the numbers of effective samples >100, and MCMC chains generally had no divergent transitions (Bürkner, 2017; see *Model 1*). I used default priors (weakly informative with a student's t-distribution of 3 degrees of freedom and a scale parameter of 2.5). For all models, I characterised uncertainty by two-sided credible intervals (95% CrI), denoting the range of probable values in which the true value could fall (Kruschke, 2014). Evidence of an effect in a positive or negative direction was thus present if posterior distributions shifted away substantially from zero in either direction. Centring on zero would imply the null expectation of posterior distributions.

Pairwise comparisons on interactions and factor main effects with more than two levels were computed using the hpd.summary function of the package emmeans (Lenth et al., 2022). I used this function to obtain estimates for means, standard deviations, and lower and upper highest posterior distribution (HPD) intervals of all factor and interaction combinations in my GLMMs. Evidence of an effect was interpreted as 95% HPD intervals not including zero in either direction.

I checked for model convergence by visually inspecting the trace plots of MCMC chains and posterior distributions of all models (Depaoli & van de Schoot, 2017), which are shown in *Appendix C*. Density estimates of the observed, empirical data set with density estimates for 1000 simulated data sets drawn from the posterior predictive distribution for all models are shown in *Appendix C*.

5.3.2 Species and group differences in pre-feeding contact-affiliation (GLMMs)

I fitted two Bayesian GLMMs to test how pre-feeding contact-affiliation varied across bonobo and chimpanzee groups. I collapsed my data into a dyad-level dataframe, with each observation row corresponding to a dyad within a session, resulting in N = 12694 observation rows. Using a dyad-level dataframe allowed me to control for variable group size by taking into account all possible combinations of individuals who could affiliate.

For these GLMMs, I used a binary dependent variable of *pre-feeding contact* (e.g., did the dyad engage in pre-feeding contact affiliation, Y/N), fitted with a Bernoulli distribution. The first model (*Model 1*) included a fixed effects structure comprising a main effect of species, an interaction of species and sex-dyad (i.e., FF = Female-Female; FM = Female-Male; MM = Male-Male), and a main effect of kinship. Dyads were classed as 'kin' if they shared a maternal genetic relationship, therefore including all mother-infant, sibling-sibling, and grandparent-grandchild pairs. Some dyads at Chimfunshi represented a genetic uncle-nephew dynamic and were also included as 'kin'. Full paternity data is currently unavailable at both field sites, and thus I was unable to consider paternal kin relationships. The random effects included dyad, group, and session number to control for repeated observations of dyads and groups, as well as repeated exposure to the experimental paradigm. Individuals at both sanctuary sites can and have been migrated between groups in the past. Thus, I used a crossed random effects structure as individual identities are not necessarily fixed to group identities. The second Bernoulli model (*Model 2*) included a fixed effects structure comprising a main effect of group, an interaction of group and sex-dyad, and a main effect of kinship. The random effects structure included dyad and session number.

During initial model set-up, I included random slopes of kinship and sex-dyad within group (only in *Model 1*) and session number (in *Model 1* and *Model 2*). In early versions of these models with two MCMC chains and up to 2,000 iterations on each chain, the random slopes returned a prior distribution around 0, indicating that they were not making a credible contribution to the model. Attempts to run a full model including all fixed effects, random effects, and random slopes, with four MCMC chains and 10,000 iterations on each chain were unable to converge, indicating that we did not have enough data to account for the variation with this parametrisation. As dyad was included a random effect, which had a fixed sex-dyad and kinship value for each level, I decided to proceed without random slopes in these models to reduce unnecessary complexity.

My species model (*Model 1*) converged successfully with all five sample groups included. However, for the group model (*Model 2*), I noticed substantial uncertainty in predictions for one fixed effect interaction parameter involving group B3-MM dyads compared to the reference category of B1-FF. These issues were likely caused by a lack of observations of MM dyads interacting at all in B3 (despite the presence of MM dyads), and thus the model was unable to predict when they might interact. The removal of B3 did not influence inference of the effect of group or its interaction with sex-dyad, however due to this uncertainty I only present output here from a reduced model with group B3 removed. Output from the original group model with B3 included can be seen in *Appendix C.1*. All pairwise estimates are displayed with 95% highest posterior density (HPD) intervals obtained through the hpd.summary function of the package emmeans (Lenth et al., 2022). HPD intervals indicates the points of a distribution that are most credible, covering most of the distribution (Kruschke, 2015). Values within the HPD intervals have higher credibility (i.e., probability density) than values outside the range (Kruschke, 2015).

5.3.3 Temporal variation in behaviour occurrences (GAMs)

I fitted two GAMs to test how affiliation and conflict varied across the full 10-minutes of *peanut swing* sessions. GAMs are an extension of GLMMs, with relaxed assumptions on linearity, thereby allowing one to check for nonlinear relationships that may otherwise be missed (Pedersen et al., 2019). Thus, I used GAMs to check for linear and nonlinear patterns of species (*Model 3.1*) and group differences (*Model 3.2*) in the use of affiliative (contact and non-contact) and conflict behaviour across the 10-minute session periods. I used a categorical response variable of behaviour type, comprising three levels; contact-affiliation, non-contact-affiliation, and conflict. I assigned conflict as the reference category. For *Model 3.1*, the fixed effects structure comprised species (*Model 3.1*) as a linear term and two splines to look for smooths of behaviour latency from session onset—one for general patterns and one for species patterns. For *Model 3.2*, the fixed effects structure comprised group as a linear term and two splines to look for smooths of behaviour latency from session onset—one for general patterns and one for group patterns. Both *Model 3.1* and *Model 3.2* included a random effect of swingID, with each level corresponding to a unique session within a group (e.g., bg1s1: b = bonobo; g1 = group B1; s1 = session 1).

5.3.4 Pre-feeding use of mouth-to-body behaviours in chimpanzees

I also fitted four GLMMs to test how body kissing and finger/hand in mouth varied between chimpanzee groups. I collapsed my data into an individual-level dataframe with each observation row corresponding to an individual within a session, resulting in 863 observation rows comprising $N = 124$ individuals appearing in 1–10 sessions ($M = 6.96$) each. For the first two GLMMs, I used a Poisson count response variable corresponding to the number of body kiss bouts an individual offered (*Model 4.1.1*) and received (*Model 4.1.2*), respectively during each session. For the next two GLMMs, I used a Poisson count response variable corresponding to the number of finger/hand in mouth bouts an individual offered (*Model 4.2.1*) and received (*Model 4.2.2*), respectively. All models featured the same fixed and random effects structures. For fixed effects, group, age, and sex of the initiator were included. Initiator ID and session number were included as random effects.

5.4 Results

5.4.1 Descriptive: Overview of contact-affiliation

Across 45 sessions, I coded the occurrence of 2236 contact-affiliation behaviours, 1041 non-contact-affiliation behaviours, and 246 conflict behaviours. Prior to T0, bonobos engaged in $M = 1.46$ ($SD = 2.65$) contact-affiliation behaviours per session, and chimpanzees engaged in $M = 2.33$ ($SD = 3.23$). Controlling for variable group sizes by taking a dyadic perspective, bonobo dyads engaged in $M = 0.14$ ($SD = 0.72$) contact-affiliation behaviours prior to T0 versus $M = 0.12$ ($SD = 0.58$) in chimpanzees.

In the chimpanzee groups, 153 mouth-to-body behaviours were coded, consisting of 107 instances of body kiss (*M* per individual per session [*SD*]: C1 = 0.09 [0.38]; C2 = 0.28 [0.58]) and 46 instances of finger/hand in mouth (*M* per individual per session [*SD*]: C1 = 0.02 [0.15]; C2 = 0.13 [0.49]). As expected, neither body kiss nor finger/hand in mouth were seen in bonobos. Summaries of the average rate of behaviour counts for each individual per session across all groups are depicted in *Figures 5.2-5.4*.

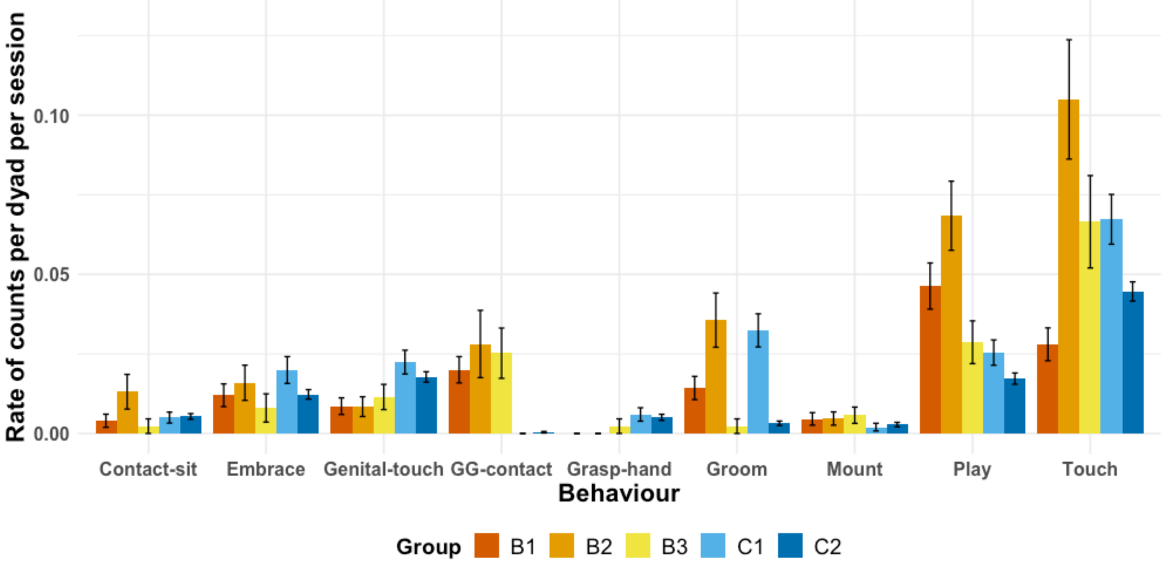

Figure 5.2a. Descriptive plot showing the average prevalence of contact-affiliation behaviours per group member across all peanut swing sessions (excluding mouth-to-body behaviours, which are shown in *Figure 5.2b*). X-axis = behaviour; Y-axis = rate of counts per individual per session. Whiskers show one standard error above and below mean. Abbreviations: GG-contact = genito-genital contact.

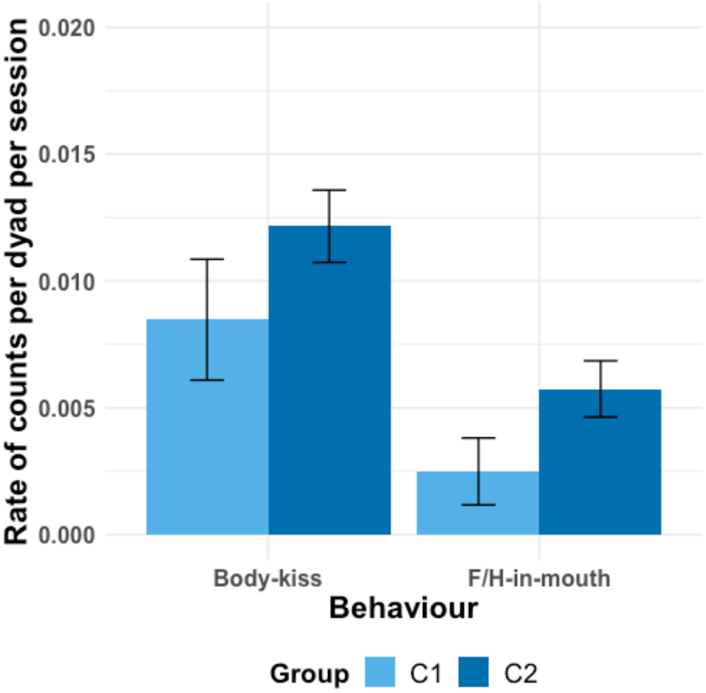

Figure 5.2b. Descriptive plot showing the average prevalence of pre-feeding mouth-to-body contact-affiliation behaviours per group member across all peanut swing sessions in the chimpanzee groups. X-axis = behaviour; Y-axis = rate of counts per individual per session. Whiskers show one standard error above and below mean. Abbreviations: F/H-in-mouth = finger/hand in mouth.

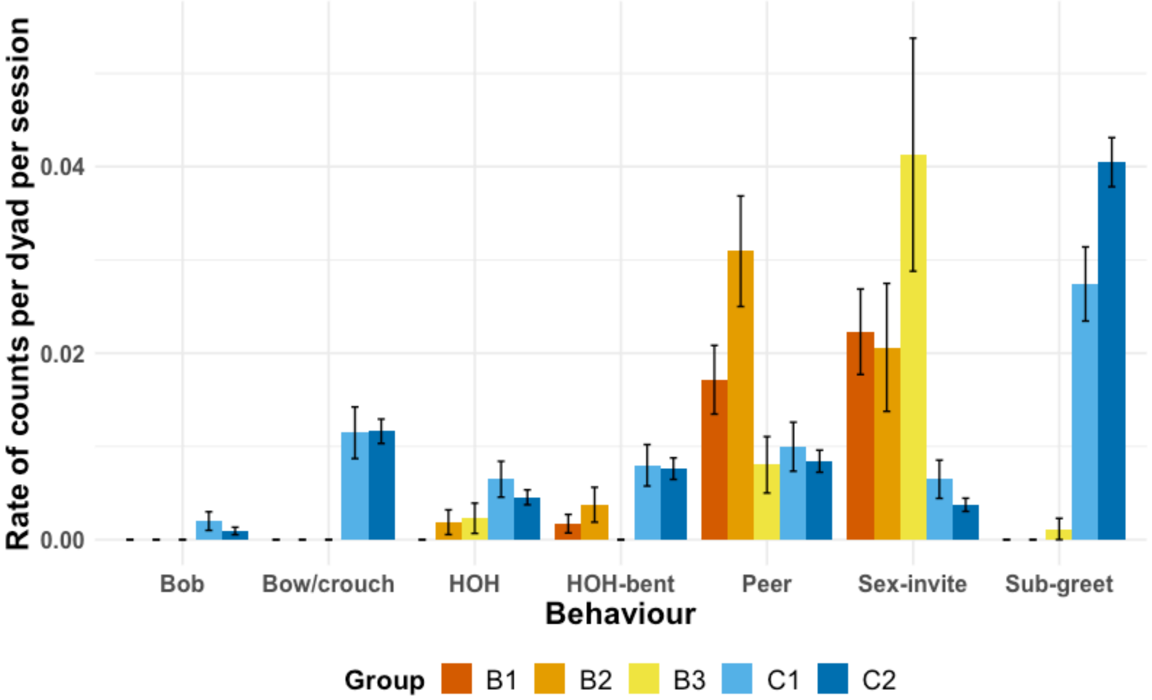

Figure 5.3. Descriptive plot showing the average prevalence of non-contact-affiliation behaviours per group member across all peanut swing sessions. x-axis = behaviour; y-axis = rate of counts per individual per session. Whiskers show one standard error above and below mean. Abbreviations: HOH = "Hold out hand".

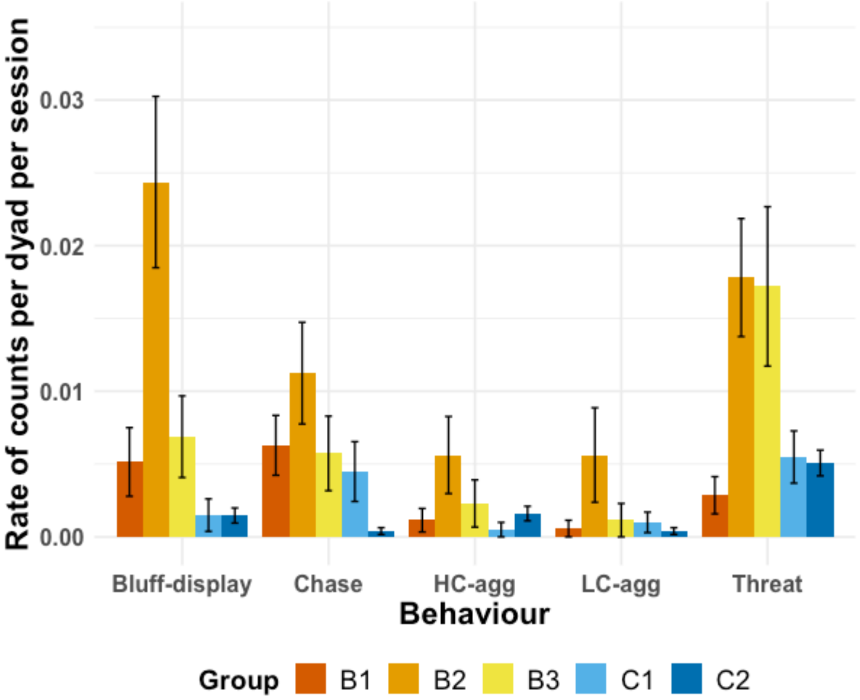

Figure 5.4. Descriptive plot showing the average prevalence of conflict behaviours per group member across all peanut swing sessions. X-axis = behaviour; Y-axis = rate of counts per individual per session. Whiskers show one standard error above and below mean. Abbreviations: HC-agg = high-contact aggression; LC-agg = low-contact aggression.

5.4.2 Pre-feeding contact-affiliation tendencies

5.4.2.1 Species differences

In the species model (*Model 1*), bonobo dyads were not more likely to engage in pre-feeding contact affiliation than chimpanzees (*b* = -1.10, *SD* = 0.05, 95% credible interval (CrI) [-2.45, 0.51]). Instead, pairwise comparisons revealed that sex-dyads (FF = Female-Female; FM = Female-Male; MM = Male-Male) hypothesized as socially-bonded were more likely to have at least one pre-feeding affiliative contact than other sex-dyads in both bonobos (FF-FM: *b* = 0.85, *SD* = 0.29, 95% CrI [0.29, 1.43]; FF-MM: *b* = 1.18, *SD* = 0.41, 95% CrI [0.37, 1.95]) and in chimpanzees (FM-MM: *b* = -0.84, *SD* = 0.23, 95% CrI [-1.30, -0.38]; FF-MM: *b* = -1.66, *SD* = 0.25, 95% CrI [-2.15, -1.19]). In addition, female-male dyads in chimpanzees were also more likely to affiliate than female-female dyads (FM-FM: *b* = -0.82, *SD* = 0.17, 95% CrI [-1.16, -0.49]). The species:sex-dyad interaction pairwise effects are visualised in *Figure 5.5*. There was also a credible effect of kinship, where kin dyads were more likely to affiliate than non-kin dyads (*b* = -1.14, *SD* = 0.10, 95% CrI [-1.57, -0.71]). Full statistical output for *Model 1* can be seen in *Table 5.3a* and the pairwise comparisons can be seen in *Table 5.3b*. Trace plots, posterior predictive checks, and MCMC plots for *Model 1* are shown in *Appendix C.2*.

Table 5.3a. Summary of *Model 1*; a Bayesian generalised linear mixed model for species comparisons of pre-feeding contact affiliation in bonobos and chimpanzees. All parameter estimates are on the logit scale. Robust effects of predictors (i.e., in the frequentist approach, "significant" effects) are highlighted in italic-bold font. Dependent variables listed in header line. Abbreviations: B = Bonobo; C = Chimpanzee; F-F = Female-Female; F-M = Female-Male; M-M = Male-Male; *eff. N* = Effective Sample Size; *b* = estimate.

Model 1: Species differences in pre-feeding contact-affiliation tendencies (observations N = 12694), binary variable (0 = no contact, 1 = 1+ contacts)

	eff. N	*b*	*S.D.*	*2.50%*	*97.50%*
Intercept	8,710	-2.13	0.09	-3.15	-1.05
Species [C][a]	7,979	-1.10	0.05	-2.45	0.51
Kinship [Non-Kin][b]	***13,565***	***-1.14***	***0.10***	***-1.57***	***-0.71***
Species [B] x Sex-dyad [F-M][c]	***15,300***	***-0.85***	***0.55***	***-1.43***	***-0.29***
Species [C] x Sex-dyad [F-M][c]	***17,697***	***0.82***	***0.73***	***0.49***	***1.15***
Species [B] x Sex-dyad [M-M][c]	***17,485***	***-1.18***	***0.22***	***-1.99***	***-0.39***
Species [C] x Sex-dyad [M-M][c]	***14,626***	***1.66***	***0.29***	***1.18***	***2.14***
Dyad Intercept	10,262	1.74	0.17	1.58	1.91
Group Intercept	5,233	0.58	0.40	0.05	1.97
Session Intercept	11,677	0.23	0.24	0.10	0.43

[a] *Reference level = Bonobo*

[b] *Reference level = Kin*

[c] *Reference level = Bonobo Female-Female*

Table 5.3b. Summary of pairwise contrasts for *Model 1*, comparing pre-feeding contact-affiliation tendencies across sex-dyads within- and between-species. Parameter estimates are on the logit scale and were obtained through the hpd.summary function of the package emmeans. Abbreviations: HPD = Highest Posterior Density (defined in *Section 5.3.2*); F-F = Female-Female; F-M = Female-Male; M-M = Male-Male.

***Model 1*: Pairwise comparisons for species:sexdyad**

Contrasts	*Mean*	*S.D.*	Lower HPD	Upper HPD
(Bonobo F-F) - (Chimpanzee F-F)	1.10	0.73	-0.28	2.65
(Bonobo F-F) - (Bonobo F-M)	***0.85***	***0.29***	***0.29***	***1.43***
(Bonobo F-F) - (Chimpanzee F-M)	0.28	0.73	-1.18	1.73
(Bonobo F-F) - (Bonobo M-M)	***1.18***	***0.41***	***0.37***	***1.95***
(Bonobo F-F) - (Chimpanzee M-M)	-0.56	0.75	-2.06	0.91
(Chimpanzee F-F) - (Bonobo F-M)	-0.25	0.72	-1.66	1.20
(Chimpanzee F-F) - (Chimpanzee F-M)	***-0.82***	***0.17***	***-1.16***	***-0.49***
(Chimpanzee F-F) - (Bonobo M-M)	0.08	0.78	-1.43	1.61
(Chimpanzee F-F) - (Chimpanzee M-M)	***-1.66***	***0.25***	***-2.15***	***-1.19***
(Bonobo F-M) - (Chimpanzee F-M)	-0.58	0.72	-2.09	0.77
(Bonobo F-M) - (Bonobo M-M)	0.33	0.39	-0.45	1.07
(Bonobo F-M) - (Chimpanzee M-M)	***-1.42***	***0.74***	***-2.94***	***-0.01***
(Chimpanzee F-M) - (Bonobo M-M)	0.90	0.77	-0.55	2.49
(Chimpanzee F-M) - (Chimpanzee M-M)	**-0.84**	**0.23**	**-1.30**	**-0.38**
(Bonobo M-M) - (Chimpanzee M-M)	***-1.74***	***0.79***	***-3.34***	***-0.25***

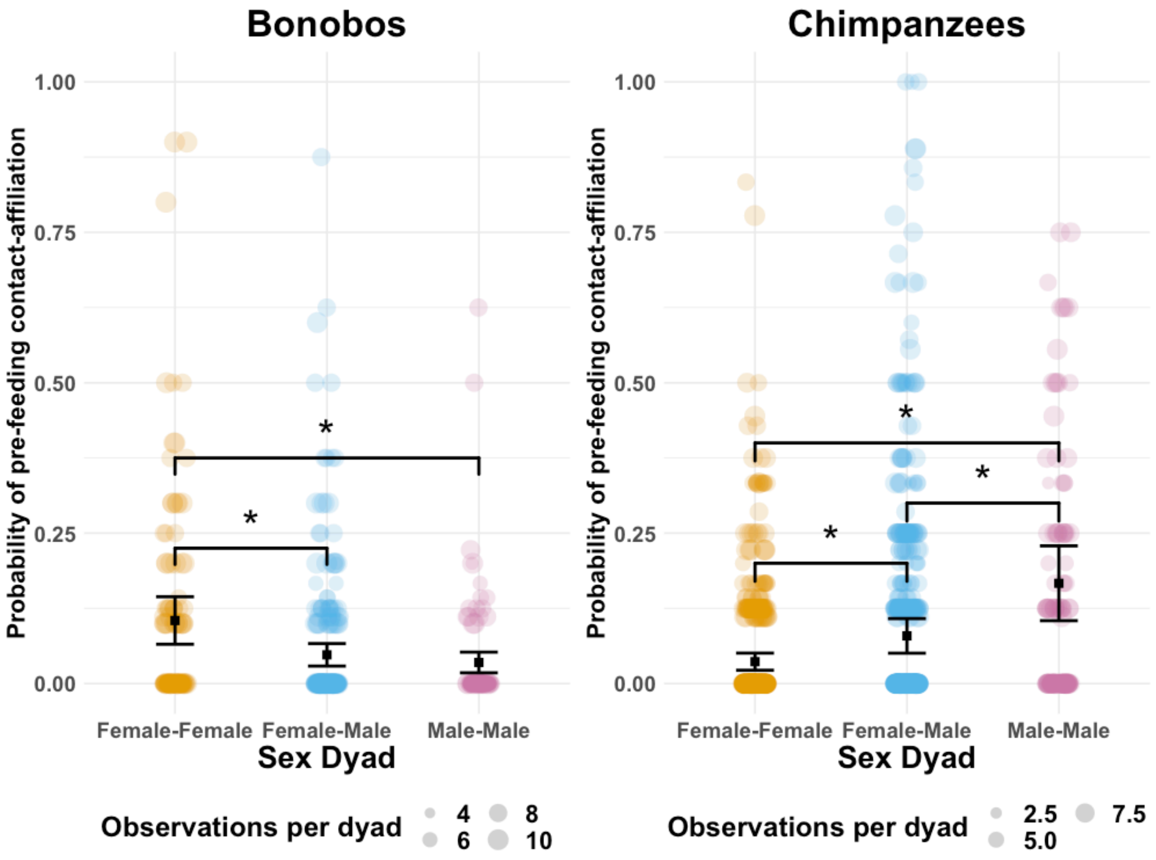

Figure 5.5. Variation in tendencies to engage in contact-affiliation during pre-feeding periods across sex-pairings in bonobos and chimpanzees. Data plots depict predicted probability of contact-affiliation for the interaction term 'species x sex-dyad' for *Model 1*, a Bayesian generalised linear mixed model. Square points and error bars correspond to posterior means and the upper and lower 95% credible intervals, respectively. Each circle corresponds to an individual data point from a sampled dyad observed within at least one peanut swing session and their tendency to affiliate prior to feeding. The size of the circles corresponds to the number of sessions that dyad could have affiliated in. Credible differences between within-species dyads are denoted by [*].

5.4.2.2 Group differences

In the group model (*Model 2*), there were credible pairwise contrasts between sex-dyads in multiple groups. In B2, female-female dyads were more likely to affiliate than female-male dyads (FF-FM: *b* = 1.32, *SD* = 0.53, 95% CrI [0.28, 2.37]) and male-male dyads (FF-MM: *b* = 1.50, *SD* = 0.68, 95% CrI [0.17, 2.85]). In C1, the only credible difference between sex-dyads was that female-female dyads were more likely to affiliate than female-male dyads (FF-FM: *b* = -0.76, *SD* = 0.34, 95% CrI [-1.43, -0.08]). In C2, all sex-dyads varied, where female-female dyads were less likely to affiliate than female-male dyads (FF-FM: *b* = -0.84, *SD* = 0.19, 95% CrI [-1.21, -0.45]) and male-male dyads (FF-MM: *b* = -1.86, *SD* = 0.28, 95% CrI [-2.42, -1.32]), and female-male dyads were less likely to affiliate than male-male dyads (FM-MM: *b* = -

1.02, *SD* = 0.27, 95% CrI [-1.54, -0.49]). The group:sex-dyad interaction is depicted in *Figure 5.6*. I also found a credible effect of kinship, where kin dyads were more likely to affiliate and have higher contact counts than nonkin dyads (*b* = -1.10, *SD* = 0.22, 95% CrI [-1.53, -0.66]). Full output for *Model 2* can be seen in *Table 5.4* and the pairwise comparisons can be seen in *Appendix C.3*. Trace plots, posterior predictive checks, and MCMC plots for *Model 2* are also shown in *Appendix C.3*.

Table 5.4. Summary of *Model 2*, Bayesian regression models for group comparisons (showing comparisons between models with and without group b3). Robust effects of predictors (i.e., in the frequentist approach, "significant" effects) are highlighted in italic-bold font. Dependent variables listed in header lines. Summary of pairwise contrasts for all group:sexdyad combinations are also shown. For legibility, within-group comparisons are shown in the first table and between-group comparisons are shown in the second table. A version Abbreviations: F-F = Female-Female; F-M = Female-Male; MM = Male-Male; *eff. N* = Effective Sample Size; *b* = estimate.

***Model 2*: Group differences in pre-feeding contact-affiliation tendencies [excluding group B3] (observations *N* = 11835), binary variable (0 = no contact, 1 = 1+ contacts)**

	eff. N	*b*	*S.D.*	*2.50%*	*97.50%*
Intercept	8,681	-2.88	0.42	-3.73	-2.07
Group[a]					
[B2]	***7,170***	***1.48***	***0.54***	***0.42***	***2.54***
[C1]	8,989	-0.19	0.43	-1.03	0.67
[C2]	8,483	-0.64	0.38	-1.37	0.10
Kinship [Nonkin][b]	***11,846***	***-1.10***	***0.22***	***-1.53***	***-0.66***
Group [B1] x Sex-dyad [F-M][c]	9,379	-0.07	0.44	-0.91	0.79
Group [B2] x Sex-dyad [F-M][c]	***8,411***	***-1.32***	***0.53***	***-2.37***	***-0.27***
Group [C1] x Sex-dyad [F-M][c]	***13,222***	***0.76***	***0.34***	***0.08***	***1.43***
Group [C2] x Sex-dyad [F-M][c]	***15,106***	***0.84***	***0.19***	***0.46***	***1.23***
Group [B1] x Sex-dyad [M-M][c]	11,666	-0.25	0.57	-1.39	0.85
Group [B2] x Sex-dyad [M-M][c]	***10,885***	***-1.50***	***0.68***	***-2.85***	***-0.18***
Group [C1] x Sex-dyad [M-M][c]	12,915	0.86	0.55	-0.22	1.91
Group [C2] x Sex-dyad [M-M][c]	***11,229***	***1.86***	***0.28***	***1.31***	***2.42***
Dyad Intercept	9,322	1.75	0.09	1.58	1.93
Session Intercept	10,898	0.26	0.09	0.12	0.47

[a] *Reference level = B1*

[b] *Reference level = Kin*

[c] *Reference level = B1 Female-Female*

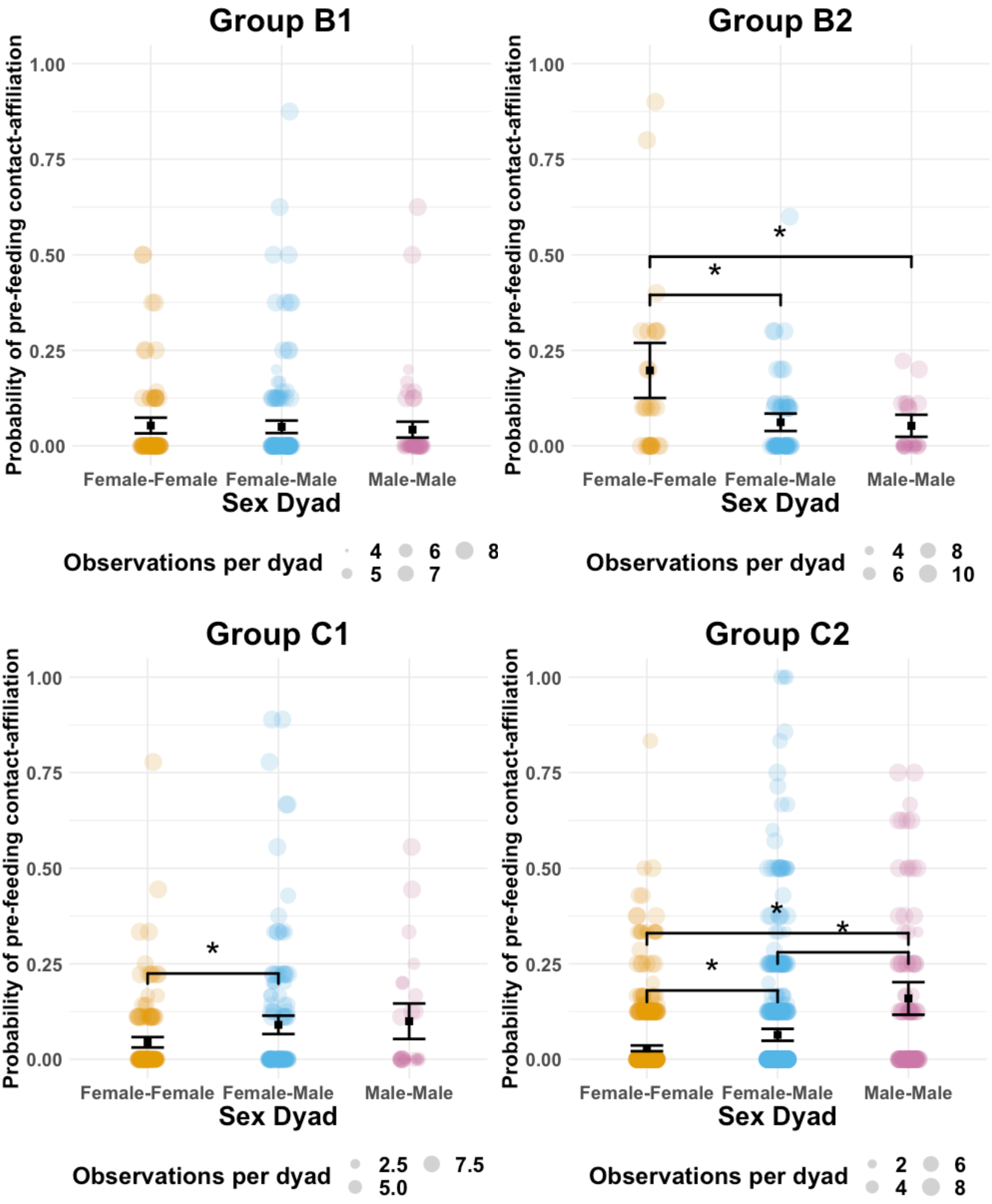

Figure 5.6. Variation in tendencies to engage in contact-affiliation during pre-feeding periods across sex-pairings in groups of bonobos (B1, B2) and chimpanzees (C1, C2). Data plots depict predicted probability of contact-affiliation for the interaction term 'group x sex-dyad' for *Model 2*, a Bayesian GLMM. Square points and error bars correspond to posterior means and the upper and lower 95% credible intervals, respectively. Each circle corresponds to an individual data point from a sampled dyad observed within at least one peanut swing session and their tendency to affiliate prior to feeding. Circle size corresponds to number of sessions that dyad could have affiliated in. Credible differences between within-species dyads are denoted by [*].

5.4.3 Temporal variation in contact-affiliation, non-contact-affiliation, and conflict

All means (*M*) represent an average rate for each eligible group member per session. Across the full 10-minute observation period for *N* = 28 peanut swing sessions, *N* = 665 contact-affiliation behaviours occurred in bonobos (group *N*: B1 = 239 [*M* = 1.45]; B2 = 293 [*M* = 1.97]; B3 = 133 [*M* = 0.98]). In chimpanzees, across *N* = 17 peanut swing sessions, *N* = 1340 contact-affiliation behaviours occurred (group *N*: C1 = 386 [*M* = 2.03]; C2 = 954 [*M* = 2.77]).

In addition, *N* = 179 non-contact-affiliation behaviours occurred in bonobos (group *N*: B1 = 72 [*M* = 0.44]; B2 = 61 [*M* = 0.41]; B3 = 46 [*M* = 0.34]). In chimpanzees, *N* = 723 non-contact-affiliation behaviours occurred (group *N*: C1 = 144 [*M* = 0.76]; C2 = 579 [*M* = 1.68]). I coded sexual invitations as a non-contact-affiliation behaviour separately from genital contact as they constitute separate behaviours that do not necessarily preclude contact. This was reflected in my data as only 50.43% of coded sexual invitations were followed by a genital contact. Furthermore, only 8.26% of genital touches, 21.43% of mounts, and 48.91% of GG-contacts were preceded by sexual invitations.

Outside of affiliation, *N* = 126 conflict behaviours occurred in bonobo peanut swing sessions (group *N*: B1 = 28 [*M* = 0.17]; B2 = 69 [*M* = 0.46]; B3 = 29 [*M* = 0.21]). In chimpanzees, *N* = 93 conflict behaviours occurred (group *N*: C1 = 26 [*M* = 0.14]; C2 = 67 [*M* = 0.19]).

5.4.3.1 Comparing temporal variation in pre-feeding affiliation and conflict across species

Model 3.1 revealed robust effects for behaviour type across an average peanut swing session in both bonobos and chimpanzees (see *Appendix C.4*). Contact-affiliation and non-contact-affiliation varied across the 10-minute observation period in accordance with conflict, the reference category for behaviour type. Looking at *Figure 5.7*, it appears that contact-affiliation for bonobos starts as the most likely behaviour and generally maintains until the end of the feedings at 600s. At the onset of feeding (T0) at 300s, conflict increases slightly and decreases slowly towards 600s. Non-contact-affiliation starts on a par with conflict in terms of likelihood and only increases slightly as conflict increases post-T0. Chimpanzees follow a similar pattern for contact-affiliation, however non-contact-affiliation starts high and increases sharply post-T0 when conflict increases after the feeding commences. The peak for post-T0 conflict likelihood reaches a similar level to bonobos, however the decline appears to be sharper as affiliation increases. Relative to levels of affiliation, pre-feeding conflict behaviour appears less likely in chimpanzees than bonobos. The statistical output from *Model 3.1* is shown in *Appendix C.4* along with trace plots, posterior predictive checks, and MCMC plots.

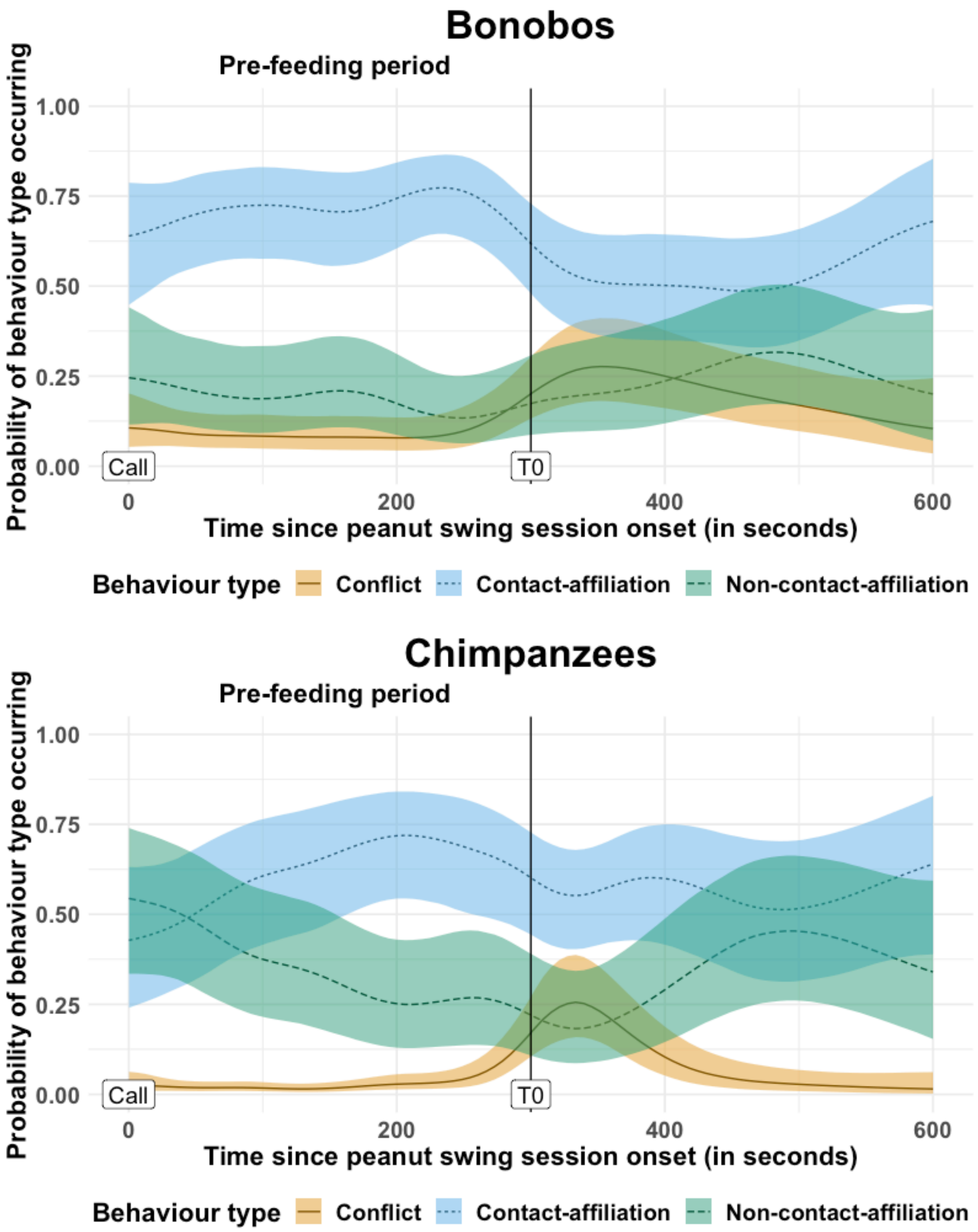

Figure 5.7. Temporal line plot for Model 3.1 showing how average expressions of each behaviour type vary across the 10-minute session period for both bonobos and chimpanzees. The groups are alerted at 0 seconds (Call) and feedings start at 300 seconds (T0). Observations end at 600 seconds. Each line refers to the relative posterior probability of each behaviour type across time: yellow = conflict; blue = contact-affiliation; and green = non-contact-affiliation. The shaded areas reflect 95% credibility intervals for each behaviour type.

5.4.3.2 Comparing temporal variation in pre-feeding affiliation and conflict across group

Model 3.2 revealed robust effects for behaviour type across an average peanut swing session for all groups of bonobos and chimpanzees. As is visualised in *Figure 5.8a* and *Figure 5.8b*, there were robust effects for nonlinear patterns of behaviour type in each group. All groups follow similar patterns, whereby contact-affiliation is highest during the pre-feeding period compared to non-contact-affiliation and conflict. Non-contact-affiliation also appears to be higher than conflict in all groups prior to feeding, apart from B2. At 300s when the feeding starts, all groups show a rise and subsequent fall in conflict behaviour. In the bonobo groups, the rise in conflict peaks at a lower point for B1 than the other groups as non-contact-affiliation increases. In contrast, the peaks in conflict for B2 and B3 are followed by sharp increases in contact-affiliation. For the chimpanzee groups, the peaks in conflict are followed by sharp increases in contact-affiliation for C1 and non-contact-affiliation for C2. However, it is notable that contact-affiliation stays relatively high in C2 after the end of the pre-feeding period and increases again halfway through the post-feeding period. An increase in contact-affiliation during the post-feeding period also occurs in group C1. The output from *Model 3.2* is shown in *Appendix C.4* along with trace plots, posterior predictive checks, and MCMC plots.

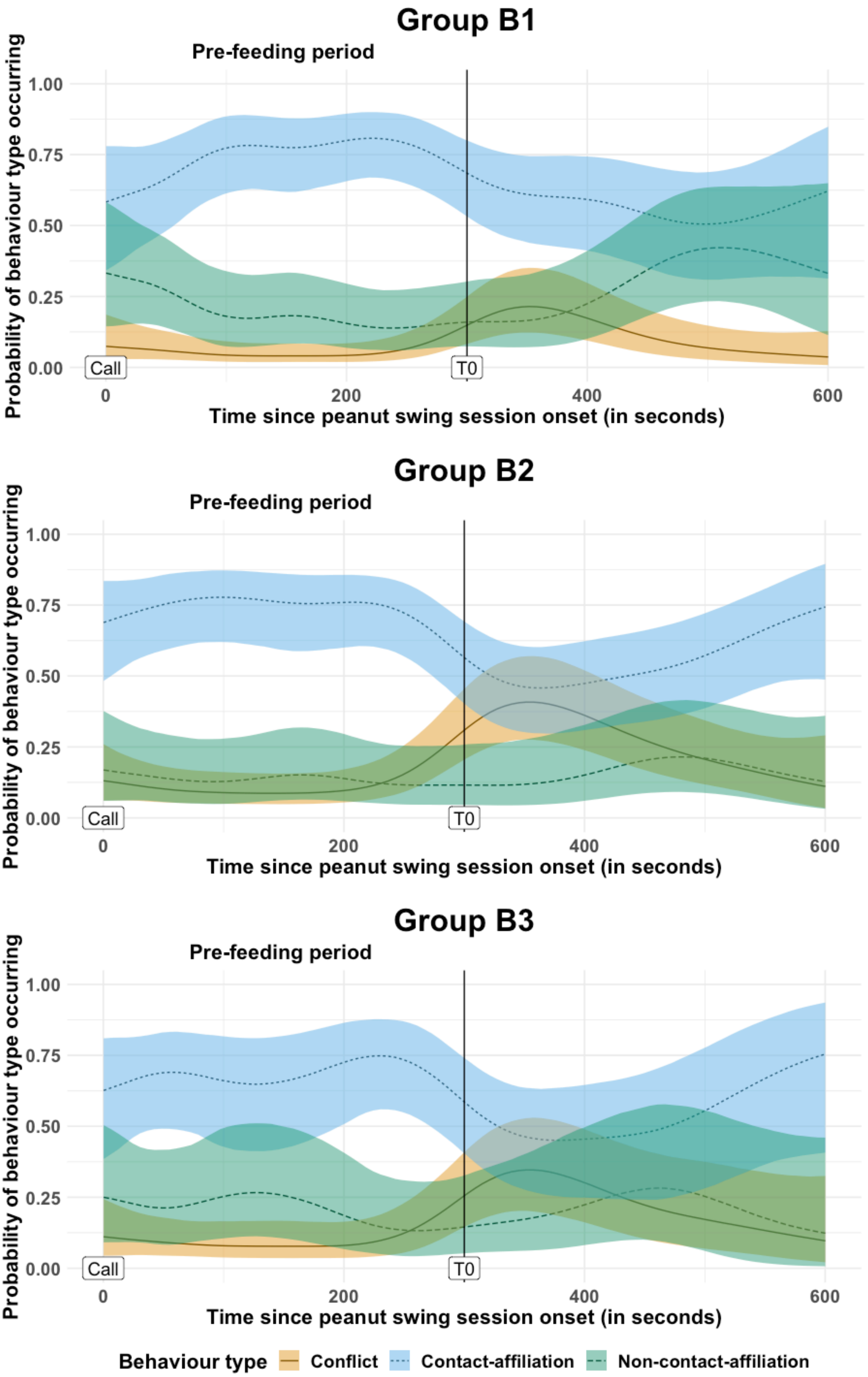

Figure 5.8a. Temporal line plot for Model 3.2 showing how average expressions of each behaviour type vary across the 10-minute session period for all bonobo groups. The groups are alerted at 0 seconds (Call) and feedings start at 300 seconds (T0). Observations end at 600 seconds. Each line refers to the relative posterior probability of each behaviour type across time: yellow = conflict; blue = contact-affiliation; and green = non-contact-affiliation. The shaded areas reflect 95% credibility intervals for each behaviour type.

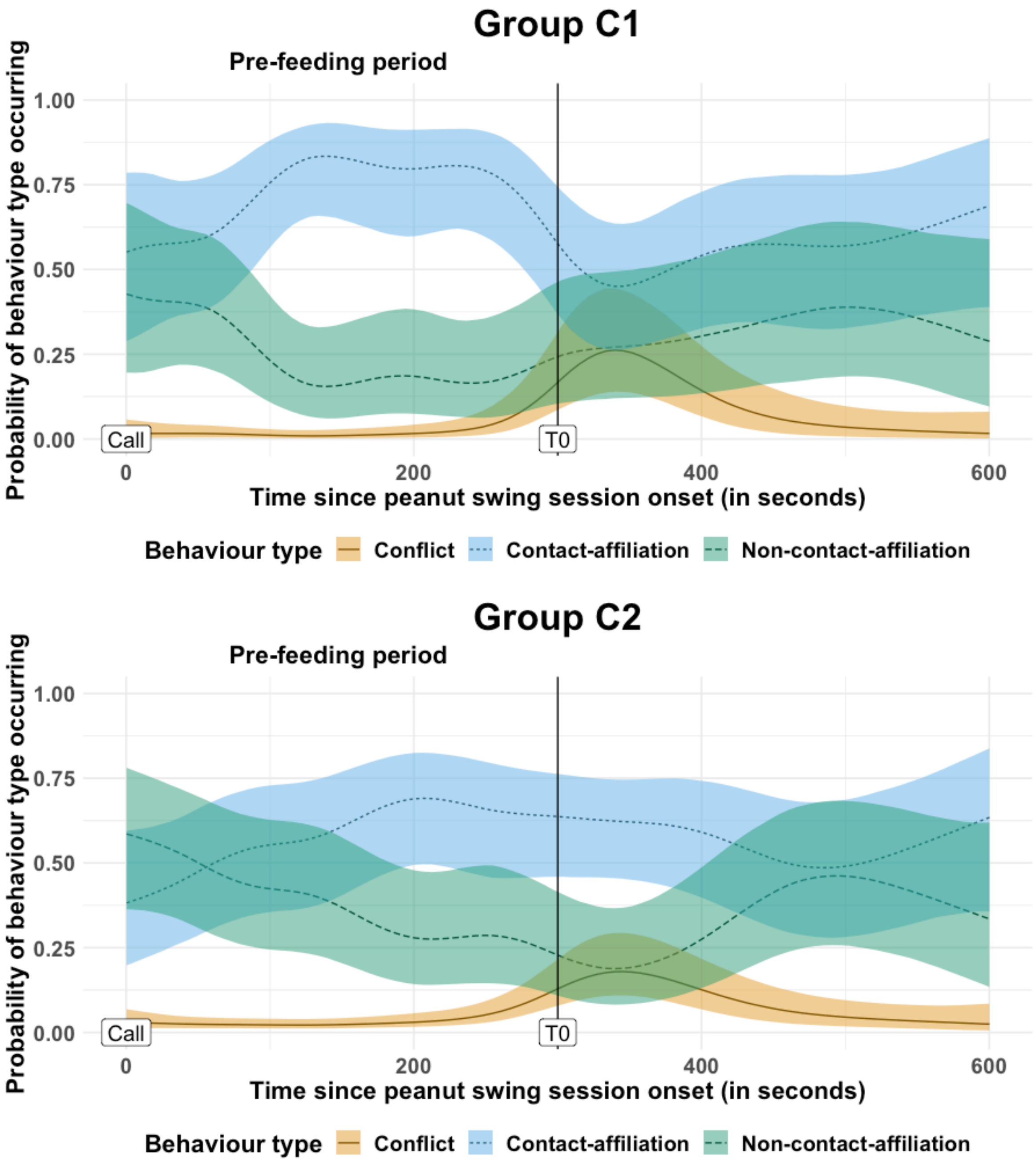

Figure 5.8b. Temporal line plot for Model 3.2 showing how average expressions of each behaviour type vary across the 10-minute session period for all chimpanzee groups. The groups are alerted at 0 seconds (Call) and feedings start at 300 seconds (T0). Observations end at 600 seconds. Each line refers to the relative posterior probability of each behaviour type across time: yellow = conflict; blue = contact-affiliation; and green = non-contact-affiliation. The shaded areas reflect 95% credibility intervals for each behaviour type.

5.4.4 Mouth-to-body behaviours in chimpanzees

5.4.4.1 Body kiss

All means (*M*) represent an average rate for each eligible group member per session. Across *N* = 17 sessions, a total of *N* = 107 counts of body kiss occurred (group *N*: C1 = 17 [*M* = 0.09]; C2 = 90 [*M* = 0.28]). In C1, *N* = 10 body kisses were offered by females (*M* = 0.08) and *N* = 7 were offered by males (*M* = 0.13). In C2, *N* = 48 body kisses were offered by females (*M* = 0.23) and *N* = 42 were offered by males (*M* = 0.38). In C1, *N* = 7 body kisses were received by females (*M* = 0.06), and *N* = 10 were received by males (*M* = 0.18). In C2, *N* = 30 body kisses were received by females (*M* = 0.14), and *N* = 60 were received by males (*M* = 0.54). Individual tendencies to offer and receive body kiss are displayed in *Figure 5.9*.

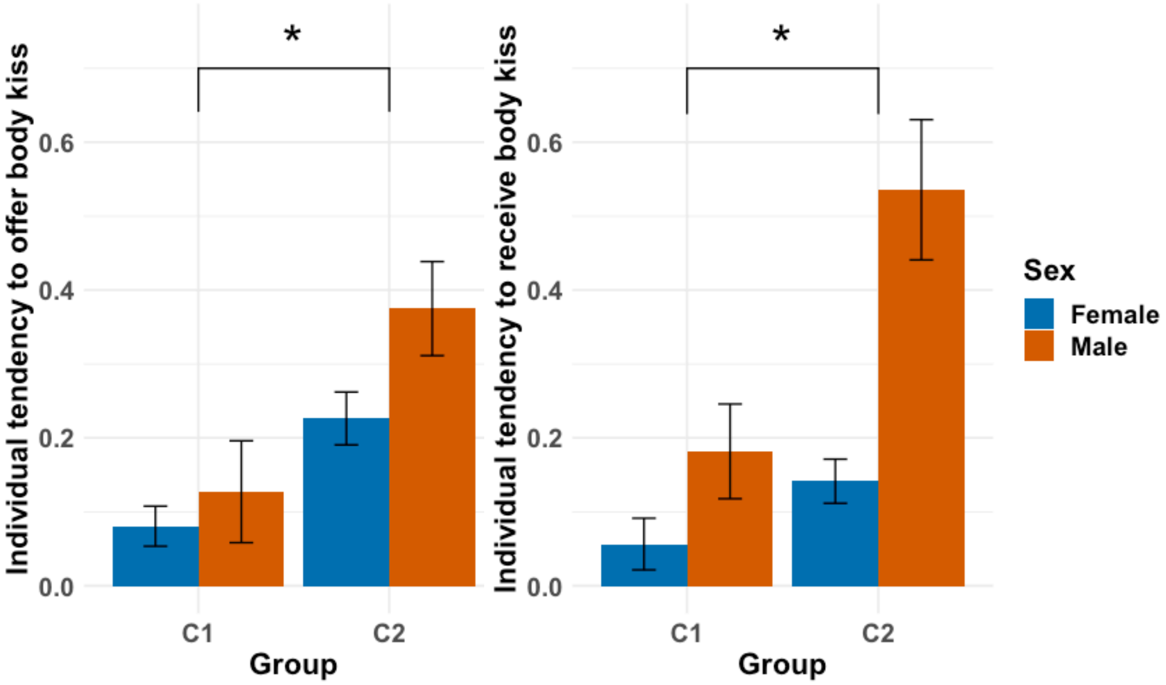

Figure 5.9. Bar plots displaying group and sex differences in the use of body kiss during pre-feeding periods in two chimpanzee groups. Left plot depicts tendencies to offer body kiss and right plot depicts tendencies to receive body kiss. Tendencies to offer and receive body kiss were higher in group C2 and more likely to be offered or received by male chimpanzees. Bars depict posterior means and standard errors from a Bayesian generalised linear mixed model. Abbreviations: F = Female; M = Male.

Both Poisson models comparing the use of body kissing in the chimpanzee groups revealed that individuals from C2 were more likely to offer (*Model 4.1.1*: *b* = 1.43, *SD* = 0.57, 95% CrI [0.38, 2.64]) and receive (*Model 4.1.2*: *b* = 1.27, *SD* = 0.70, 95% CrI [-0.01, 2.73]) body kissing during the pre-feeding period than group C1. Post-hoc hypothesis testing for *Model 4.1.2* revealed over 95% [-9.53, -4.67] of the posterior probability for sex lies beyond 0. Males were credibly observed to offer (*b* = 0.85, *SD* = 0.50, 95% CrI [-0.15, 1.85]) and receive body kissing than females (*b* = 1.71, *SD* = 0.63, 95% CrI [0.50, 3.00]). Post-hoc hypothesis testing for *Model 4.1.1* revealed over 95% [-7.86, -4.25] of the posterior probability for sex lies beyond 0. The likelihood of offering (*b* = 0.07, *SD* = 0.02, 95% CrI [0.02, 0.11]) and receiving (*b* = 0.05, *SD* = 0.03, 95% CrI [0.00, 0.11]) increases in older individuals. Full output for *Models 4.1.1* and *4.1.2* can be seen in *Table 5.5*. Trace plots, posterior predictive checks, and MCMC plots for these models are shown in *Appendix C.5*.

Table 5.5. Summary of *Model 4.1.1* and *Model 4.1.2*; Bayesian generalised linear mixed models for group comparisons of body kiss in chimpanzees. Robust effects of predictors (i.e., in the frequentist approach, "significant" effects) are highlighted in italic-bold font. Dependent variables are listed in bold font in header lines. Abbreviations: *eff. N* = Effective Sample Size; *b* = estimate.

***Model 4.1.1*: Group differences in body kiss offered (observations *N* = 503), Poisson variable (number of initiations as counts)**

	eff. N	*b*	*S.D.*	*2.50%*	*97.50%*
Intercept	11,278	-5.09	0.80	-6.85	-3.68
Group [C2][a]	***12,919***	***1.43***	***0.57***	***0.38***	***2.64***
Age	***13,235***	***0.07***	***0.02***	***0.02***	***0.11***
Sex [Male][b-c]	**12,303**	**0.85**	**0.50**	**-0.15**	**1.85**
Individual Intercept	8,095	1.37	0.31	0.86	2.06
Session Intercept	13,245	0.22	0.16	0.01	0.60

***Model 4.1.2*: Group differences in body kiss received (observations *N* = 503), Poisson variable (number of initiations as counts)**

	eff. N	*b*	*S.D.*	*2.50%*	*97.50%*
Intercept	12,454	-5.63	0.96	-7.72	-3.98
Group [C2][a, c]	***14,111***	***1.27***	***0.70***	***-0.01***	***2.73***
Age	***15,861***	***0.05***	***0.03***	***0.00***	***0.11***
Sex [Male][b]	***11,792***	***1.71***	***0.63***	***0.50***	***3.00***
Individual Intercept	9,281	1.77	0.37	1.18	2.62
Session Intercept	19,807	0.15	0.13	0.01	0.47

[a] *Reference level = C1*

[b] *Reference level = Female*

[c] *Post-hoc hypothesis testing revealed over 95% of the posterior probability lies beyond 0*

5.4.4.2 Finger/hand in mouth

All means (*M*) represent an average rate for each eligible group member per session. Across *N* = 17 sessions, a total of *N* = 46 counts of finger/hand in mouth occurred (group *N*: C1 = 4 [*M* = 0.09]; C2 = 42 [*M* = 0.28]). In C1, *N* = 1 count of finger/hand in mouth was offered by a female (*M* = 0.01) and *N* = 3 were offered by males (*M* = 0.05). In C2, *N* = 18 counts of finger/hand in mouth were offered by females (*M* = 0.08) and *N* = 42 were offered by males (*M* = 0.21). In C1, *N* = 3 counts of finger/hand in mouth were received by females (*M* = 0.02), and *N* = 1 were received by males (*M* = 0.02). In C2, *N* = 12 counts of finger/hand in mouth were received by females (*M* = 0.06), and *N* = 30 were received by males (*M* = 0.27). Individual tendencies to offer and receive finger/hand in mouth are displayed in *Figure 5.10*.

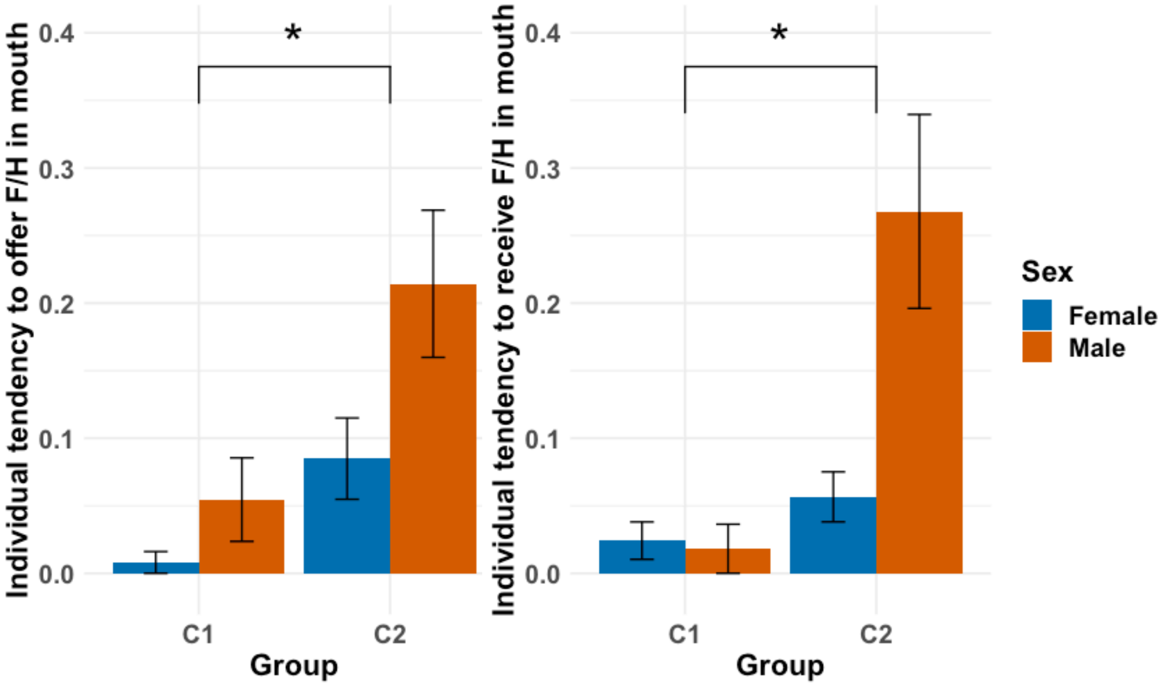

Figure 5.10. Bar plot displaying group and sex differences in the use of finger/hand in mouth during pre-feeding periods in two chimpanzee groups. Left plot depicts tendencies to offer finger/hand in mouth and right plot depicts tendencies to receive finger/hand in mouth. Bars depict posterior means and standard errors from a Bayesian generalised linear mixed model. Abbreviations: F = Female; M = Male; F/H in mouth = finger/hand in mouth.

The Poisson models, comparing the use of finger/hand in mouth in the chimpanzee groups, revealed that individuals from C2 were more likely to offer (*Model 4.2.1*: *b* = 2.25, *SD* = 0.90, 95% CrI [0.66, 4.22]) and receive (*Model 4.2.2*: *b* = 2.24, *SD* = 1.32, 95% CrI [-0.09, 5.11]) finger/hand in mouth during the pre-feeding period than group C1. Males were more likely to both offer (*b* = 1.87, *SD* = 0.67, 95% CrI [0.64, 3.29]) and receive (*b* = 2.23, *SD* = 1.13, 95% CrI [0.21, 4.69]) finger/hand in mouth than females. The likelihood of offering (*b* = 0.08, *SD* = 0.03, 95% CrI [0.02, 0.14]) and receiving (*b* = 0.13, *SD* = 0.05, 95% CrI [0.04, 0.25]) finger/hand in mouth also increases in older individuals. Full output for *Models 4.2.1* and *4.2.2* can be seen in *Table 5.6*. Diagnostics and additional figures for these models can be seen in the *Appendix C.6*.

Table 5.6. Summary of *Model 4.2.1* and *Model 4.2.2*; Bayesian generalised linear mixed models for group comparisons of finger/hand in mouth in chimpanzees. Robust effects of predictors (i.e., in the frequentist approach, "significant" effects) are highlighted in ***italic-bold font***. Dependent variables are listed in bold font in header lines. Abbreviation: *eff. N* = Effective Sample Size; *b* = estimate.

Model 4.2.1 Group differences in finger/hand in mouth offered (observations *N* = 503), Poisson variable (number of initiations as counts)

	eff. N	*b*	*S.D.*	*2.50%*	*97.50%*
Intercept	14,504	-7.74	1.38	-10.86	-5.42
Group [C2][a]	***20,302***	***2.25***	***0.90***	***0.66***	***4.22***
Age	***20,546***	***0.08***	***0.03***	***0.02***	***0.14***
Sex [Male][b]	***16,647***	***1.87***	***0.67***	***0.64***	***3.29***
Individual Intercept	9,713	1.42	0.43	0.74	2.40
Session Intercept	12,184	1.06	0.48	0.38	2.23

Model 4.2.2 Group differences in finger/hand in mouth received (observations *N* = 503), Poisson variable (number of initiations as counts)

	eff. N	*b*	*S.D.*	*2.50%*	*97.50%*
Intercept	8,895	-10.35	2.38	-15.93	-6.63
Group [C2][a]	15,654	2.24	1.32	-0.09	5.11
Age	***12,507***	***0.13***	***0.05***	***0.04***	***0.25***
Sex [Male][b]	***11,853***	***2.23***	***1.13***	***0.21***	***4.69***
Individual Intercept	9,322	2.45	0.7	1.40	4.11
Session Intercept	12,175	1.10	0.49	0.41	2.30

[a] *Reference level = C1*

[b] *Reference level = Female*

5.5 Discussion

The use of contact-affiliation as a means to reassure oneself and others is prevalent in primate societies, including our own, and appears to be effective at managing social tension and conflict. This study is the first to systematically compare the use of contact-affiliation during a controlled pre-feeding period in bonobos and chimpanzees and how it relates to conflict behaviour. Here, I demonstrate that sanctuary-living groups of our closest living relatives, bonobos and chimpanzees, use rich and diverse forms of tactile affiliation during periods of social tension. Contrary to my prediction that chimpanzees would engage in more pre-feeding contact-affiliation than bonobos, in terms of general tendencies, neither species in my sample engaged more than the other during this controlled period of social tension, nor did any groups stand out as being the most likely to engage. Instead, these findings reveal species-specific trends, related to forms of contact affiliation and prevalence among particular sex-pairings. However, there was notable variation in social affiliation performed at the group-level, supporting the notion that intergroup variation is vital for understanding the extent of *Pan* behavioural diversity (Kaufhold & van Leeuwen, 2019), including for reassurance.

Both species and groups overlapped regarding general tendencies to engage in contact-affiliation and used a wide repertoire of contact behaviours during the pre-feeding periods, including touching, embracing, and various genital contacts. There were, however, species differences regarding affiliation. As predicted, in bonobos, female-female pairs were more likely to engage in contact affiliation prior to feeding than both female-male pairs and male-male pairs. As also predicted, in chimpanzees, male-male pairs were more likely to engage in contact affiliation prior to feeding than female-female pairs, but not female-male pairs. However, when looking at the individual groups, there appear to be group-specific differences that appear to match differences in social tolerance, as measured by van Leeuwen et al. (under review). In a separate investigation of within-species variation in cofeeding tolerance, we found that groups B1 and C1 shared similarly despotic climates, where individuals tended to crowd in lower densities in the cofeeding zone. In contrast, groups B2, B3, and C2 shared similarly socially tolerant climates, where individuals tended to crowd at similar higher densities than the despotic groups. Male-male pairs in the more socially-tolerant chimpanzee group (C2) engaged in contact affiliation more than both other sex-pairings. In the socially-despotic chimpanzee group (C1), there are no credible differences between tendencies for male-male pairings to affiliate compared to other sex pairings. Additionally, in bonobos there was a similar discrepancy where there are no differences between any of the sex-pairings in the despotic group (B1). In contrast, female-female pairs affiliated more than other sex pairings in the tolerant group (B2).

Mixed sex relationships appear to be important for bonobo and chimpanzee social dynamics—especially mother-son bonds in bonobos (Furuichi, 1989; Kano, 1992; Schubert et al., 2013)—however, female-female relationships in bonobos and male-male relationships in chimpanzees have typically been described as those with the strongest bonds (Boesch, 2009; Furuichi, 2011; Mitani, 2009; Nishida, 2011; Parish, 1996; White & Wood, 2007). In bonobos, coalitions of adult females typically dominate over other group members (Furuichi, 2011; Surbeck et al., 2012; Vervaecke et al., 2000; White & Wood, 2007). By contrast, in chimpanzees an alpha male and his close male allies typically dominate over others (Boesch, 2009; Nishida, 2011). Strong female-female bonds in bonobos have been shown to support coalitionary relationships and greater female social power in competitive contexts, such as feeding (Parish, 1996; White & Wood, 2007). In addition, stronger social bonds appear to facilitate cooperation, resource-sharing, and tolerance for inequity in chimpanzees (Brosnan et al., 2005; Samuni et al., 2018). For this study, I was unable to collect sufficient data to compare the relative bonding between the sexes across all groups. However, it may be reasonable to expect that strong bonds between the most socially central sex in each species (i.e., individuals occupying the highest ranks) would facilitate more crowded, peaceful feedings, especially when reinforced through tactile affiliation prior to competition. At the species-level, my findings reflect these proposed species differences. However, at the group-level, this was only apparent in the socially tolerant groups.

Intergroup variation in *Pan* social tolerance is well documented (Cronin et al., 2014; DeTroy et al., 2021; van Leeuwen et al., 2021), however the proximate and ultimate mechanisms determining this variation is still unclear. There are indications that certain social compositional features can influence cofeeding tolerance, for example chimpanzee groups with more females carrying dependent offspring have been demonstrated to show lower levels of tolerance (DeTroy et al., 2021). Adult female chimpanzees are often victims of aggression from males (Nishida, 2003; Sabbi et al., 2021) and those carrying vulnerable offspring may thus be more hesitant towards approaching a competitive feeding arena. However, this study of pre-feeding affiliation may point towards a more proximate determinant of *Pan* social tolerance, namely the strength of bonds between the most dominant individuals within the respective community.

As predicted, the data revealed relatively consistent trends across species and groups regarding the use of contact-affiliation prior to feeding corresponding with low levels of conflict (de Waal, 1992). Whilst more direct testing is necessary to determine whether affiliative contact during social tension has a reassuring function of reducing aggression, my findings support my prediction that increased probability of contact-affiliation corresponded with reduced probability of conflict. In further support, conflict peaked after the onset of feeding in all groups and broadly decreased in line with increased probability of affiliative behaviours. The potential association of social tolerance with pre-feeding affiliation may also be seen in the role of non-contact-affiliative gestures performed prior to feeding. These behaviours, such as sexual invitation, hold-out-hand, and submissive pant-grunting have previously been indicated as appeasement towards dominant individuals (de Waal, 1988, 1992; Goodall, 1986; Kano, 1992; Nishida et al., 2010; van Hooff, 1967). In the chimpanzee groups in this study, these behaviours seemed to be more pronounced in the tolerant chimpanzee group (C2) compared to the despotic chimpanzee group (C1) prior to feeding and during the cofeeding period. Appeasement in chimpanzees has been purported to serve similar functions to reassurance, to reduce aggressive tendencies (de Waal, 1992; Romero & de Waal, 2010; van Hooff, 1967). Thus, similar to the possible role of reinforcing social bonds prior to competition, reaffirming of dominance status through appeasement behaviours may reduce the likelihood for aggression during a competitive context. This seemed apparent in the tolerant chimpanzee group (C2), where non-contact-affiliation increased sharply when conflict peaked, whilst contact-affiliation remained high. More direct testing on whether lower probability of aggression is associated with high levels of affiliation could reveal whether these contacts have a clear function of conflict prevention.

There were also some species-specific reassurance markers across study groups. Firstly, as expected, body kiss and finger/hand in mouth were only seen in chimpanzees. These mouth-to-body behaviours are commonly used during periods of social tension in chimpanzees, including consolatory and reconciliatory contexts (de Waal & van Roosemalen, 1979; de Waal, 1989b; Nishida et al., 1999; Wittig & Boesch, 2003). Engagement in mouth-to-body behaviours during social tension seems paradoxical due to their vulnerable nature, especially by chimpanzees who engage in lethal conflicts (Wilson et al., 2014). Chimpanzees have even been observed to bite fingers and hands off of competitors (de Waal, 1986; Wilson et al., 2004). Yet, chimpanzees, but not bonobos, consistently offer themselves up to risk of puncture wounds, permanent disfiguration, and even maiming as a form of social reassurance. Interestingly, these behaviours were observed in both a relatively despotic group (C1) and a relatively socially tolerant group (C2). However, prevalence varied considerably for each behaviour at the group-level, where both body kiss and finger/hand in mouth were more likely to occur in the tolerant group (C2), in support of my prediction. Furthermore, males were more likely to both offer and receive both types of mouth-to-body behaviour.

Group-specific and species differences in the tendency to use vulnerable tactile affiliative behaviour during a competitive context may function to promote trust between potential competitors (Palmer & Pomianek, 2007). The link between exposing vulnerable body parts, bond testing, and signalling theory has been documented in capuchins (Perry, 2011) and hyenas (East et al., 1993). In chimpanzees, vulnerable behaviours appear to reflect similar 'rituals of trust' (Palmer & Pomianek, 2007), where there is assumed confidence between the two parties that there is no agonistic intent. The next step would be to directly test the functions of pre-feeding affiliative contact, include mouth-to-body behaviours, and whether they function to communicate social trust and reduce social tension. More direct observations and comparisons across groups on the tendencies to use mouth-to-body behaviours could shed light on whether increased social tolerance facilitates greater tendencies to use these behaviours or vice versa.

In sum, despite apparently lower levels of aggressivity (Wilson et al., 2014), increased social attentiveness (Kano et al., 2015), and sensitivity towards conspecific emotions (Kret et al., 2016), results from this study indicate that bonobos engage in pre-feeding contact affiliation at similar tendencies to chimpanzees. This result complements recent findings that the *Pan* apes do not differ substantially at the species-level regarding social characteristics such as tolerance in the *Pan* apes (Cronin et al., 2014; Cronin et al., 2015; van Leeuwen et al., under review). Nevertheless, the results highlight substantial species and group differences in the forms of tactile affiliation in these contexts, and the individuals they are directed towards. In fact, the observed group-level variation and its potential role in proximately driving social tolerance suggest that pre-feeding contact behaviours are strongly influenced by within-group social dynamics. More systematic comparisons, such as these contexts in wider samples of groups could help to elucidate how ubiquitous reassurance is among *Pan*, and what group-signatures of reassurance exist across different communities.

Chapter 6: Pre-feeding reassuring body contacts facilitate cofeeding tolerance in sanctuary-living bonobos and chimpanzees

This chapter constitutes an empirical article to be submitted for publication with the following authorship:

Brooker, J. S., van Leeuwen, E. J. C., Goldsborough, Z., Kordon, S., Webb, C. E., de Waal, F. B. M., & Clay, Z. Pre-feeding reassuring body contacts facilitate cofeeding tolerance in sanctuary-living bonobos and chimpanzees

Abstract

Social tolerance—the propensity to gather in close proximity to conspecifics without aggression—represents a key contributor towards social group functioning. Although humans are generally characterized as a tolerant species, levels can vary across individuals, groups and populations. Similarly, levels of social tolerance are known to vary considerably among great ape communities. Specifically, variation in cofeeding tolerance among our closest living relatives, bonobos and chimpanzees, has been shown to be greater at the group-level than the species-level, despite species differences in aggressivity and dominance style. There are indications that varying social composition can lead to differences in group cofeeding tolerance, however the proximate drivers shaping social tolerance in our closest living relatives remain relatively opaque. Both bonobos and chimpanzees use reassuring body contact during periods of social tension, such as intergroup encounters, competitive feeding contexts and for conflict management. Here, using a cofeeding paradigm that assesses social tolerance across $N = 5$ semi-wild *Pan* groups consisting of $N = 116$ individuals, I show that increased engagement in reassuring body contact prior to competitive feeding increases an individual's likelihood of access to the food resource. Both the number of affiliative contact partners and absolute number of affiliative contacts is associated with increased presence within the cofeeding zone. These trends were seen in both species but were most pronounced in both a tolerant and despotic chimpanzee group and one tolerant bonobo group. Despite evidence of within-group differences aggression and dominance style, my results show that engaging in reassuring body contact facilitates increased cofeeding tolerance in both chimpanzees and bonobos.

6.1 Introduction

Among primates and other animals, social tolerance is considered to be a pre-requisite for prosocial and cooperative phenomena, such as empathy and social learning (see DeTroy et al., 2022 for a review). When initially discussed in the primate literature, social tolerance was identified by recording dominant individuals refraining from monopolising resources over their subordinate counterparts, expressed in behaviours including "dyadic codrinking" and "resource-proximity" (de Waal, 1986a). Broadly, social tolerance is thought to represent tendencies for conspecifics to gather in close proximity around valuable resources with little to no aggression (Cronin & Sánchez, 2012), facilitating information transmission and effective cooperation (Chen et al., 2009; Hare et al., 2007; Martin et al., 2021; Melis et al., 2006).

Compared to other species, humans appear to be exceptional in their potential for both extreme tolerance and extreme aggression (Hill et al., 2014; Wrangham & Glowacki, 2012; Zefferman & Mathew, 2015). Our tolerant nature has facilitated between-group cooperation and the growth of ultra-connected societies that stretch the planet. Our apparent tendencies for xenophilia have been suggested to be shared with one of our closest living relatives, the bonobos (*Pan paniscus*; Hare et al., 2012). Some wild bonobo communities regularly mingle affiliatively with other groups, sometimes for weeks or months at a time (Lucchesi et al., 2020), with such intergroup encounters including food sharing as well as the exchange of sex and play (Fruth & Hohmann, 2018; Furuichi, 2020; Sakamaki et al., 2018). In contrast, our other closest living relatives, the chimpanzees (*Pan troglodytes*) appear to be comparatively xenophobic and engage in boundary patrols to monitor and protect their territories (Boesch et al., 2002; Goodall, 1986). When chimpanzees encounter another group, typically, they respond aggressively, sometimes lethally (Boesch et al., 2007; Watts et al., 2006). Outgroup threat appears to enhance chimpanzee ingroup social cohesion (Brooks et al., 2021; Samuni et al., 2020), which may explain why killings are often conducted by cooperative coalitions. Bonobos do not appear to patrol and defend their home ranges and, whilst some are hostile, intergroup encounters generally do not result in physical aggression (Hohmann & Fruth, 2002; Pisor & Surbeck, 2019).

Whilst aggressivity and expressions of dominance are more common in chimpanzees than bonobos (Gruber & Clay, 2016), recent measures of *Pan* intragroup social tolerance indicate that the two species may overlap considerably. A study of captive and semi-wild *Pan* groups revealed that differences in expressions of cofeeding social tolerance are more substantial at the group-level, compared to the species-level, whereby some bonobo groups exceeded some chimpanzee groups and vice versa (van Leeuwen et al., under review; also see Cronin et al., 2014 and Cronin et al., 2015). Thus, akin to humans where levels of xenophilia and xenophobia can vary at the community-level and according to context (Cieri et al., 2014; Pisor & Surbeck, 2019), social tolerance in *Pan* does not appear to be fixed at the species-level as had previously been assumed (Hare et al., 2007). However, even within communities, social tolerance appears to vary substantially over time. A longitudinal investigation of semi-wild chimpanzees has shown that tolerance varied within groups substantially across a period of eight years (DeTroy et al., 2021). Whilst group size did not seem to influence cofeeding tolerance in these chimpanzees, social composition appeared to contribute. Groups with higher numbers of mothers with dependent offspring and lower numbers of adolescent females typically showed lower degrees of social tolerance (DeTroy et al., 2021). Mothers with young offspring were particularly less likely to enter the cofeeding zone when adolescent and adult males were present, suggesting hesitation due to their—and likely their offspring's—increased vulnerability.

However, the proximate mechanisms driving within-species variation in social tolerance remain relatively opaque. Within the context of feeding, one potential driver may be how groups members associate prior to feeding. It is well-established that bonobos and chimpanzees engage in pre-feeding "celebration" behaviours, where they engage in affiliative body contact—also termed reassurance, or appeasement when directed towards higher-ranking conspecifics (de Waal, 1992; van Hooff, 1967; see *Chapter 5*). In *Pan*, typical reassurance behaviours can include embracing, touching, and genital contact, with sexual behaviours common in bonobos (de Waal, 1988, 1992; Goodall, 1989; Kano, 1992). Body kissing and placing hands or fingers in the mouth of conspecifics are typical forms of reassurance in chimpanzees but not apparently in bonobos (de Waal, 1992; Goodall, 1989).

Reassuring body contact occurs in wild and non-wild *Pan* populations and is purported to reduce aggressivity and reaffirm social bonds at periods that threaten group stability (de Waal, 1992; van Hooff, 1967). *Pan* reassurance also seems to have alliance forming and social bond testing functions (de Waal, 1986b). In bonobos, socio-sexual contacts increase during periods where conflicts are likely, including during intragroup competition over resources or intergroup encounters (Clay & de Waal, 2015; Palagi et al., 2006). Furthermore, there are indications that increased play in the hours lead up to feeding may function as a means to prevent tension in some captive bonobos (Palagi et al., 2006).

Using an established cofeeding paradigm designed to assess group-level social tolerance (Cronin et al., 2014), I investigated whether pre-feeding contact affiliation predicts an individual's access to a limited food resource during a competitive period of social tension. By measuring individual performance on the task (i.e., respective presence or absence within the cofeeding zone), I tested whether increased engagement in pre-feeding contact affiliation with fellow group members predicts greater access to a restricted cofeeding zone. I expected that individuals of either species who had more contact-affiliation partners prior to feeding would spend more time in the cofeeding zone. Similarly, I predicted that increased numbers of absolute affiliative contacts (i.e., the total volume of affiliative contact behaviours) an individual engaged in would predict increased presence in the cofeeding zone.

Risk of aggression, particularly severe aggression, is higher in chimpanzee communities than bonobos (Wilson et al., 2014), suggesting that social reassurance may be riskier but more important for chimpanzees during competitive contexts than bonobos. In addition, chimpanzees appear to have a stricter linear hierarchical structure headed by an alpha male and his closest allies where dominance status is often affirmed through greeting and appeasement gestures, particularly during periods of social tension (Boesch, 2009; Nishida, 2011). In contrast, hierarchies are more flexible and less formal in bonobo societies (Paoli & Palagi, 2008; Stevens et al., 2007; Vervaecke et al., 2000). Thus, I tested the hypothesis that there would be between-species differences in the strength of the positive association between pre-feeding contact affiliation and cofeeding tolerance, specifically that chimpanzee groups should show stronger effects compared to bonobos groups.

6.2 Methods

6.2.1 Study sites and subjects

The study took place at two sanctuary study sites in Africa. I compare data collected from $N = 5$ *Pan* groups (bonobo $N = 3$; chimpanzee $N = 2$) totalling $N = 129$ individuals (bonobo $N = 54$; chimpanzee $N = 75$) at two independent sanctuary sites in Africa (see *Table 6.1* for a summary of the social compositions of these groups). Bonobos were observed between July and September 2019 at Lola ya Bonobo Sanctuary in the Democratic Republic of the Congo. Chimpanzees were observed between March and August 2019 at Chimfunshi Wildlife Orphanage in Zambia. For more details on these sanctuary sites, see *Section 3.1*.

Table 6.1. Social compositions of the study populations tested under the *peanut swing* paradigm. Excluding all infants due to ineligibility for tolerance coding. Also excluding absentees due to long-term veterinary care. Relative tolerance status as scored by van Leeuwen et al. (under review).

Species	Group	Total	Juveniles[b] F / M[c]	Adults[b] F / M[c]	Relative tolerance status
Bonobo (*Pan paniscus*)	1 (B1)	21	5 / 5	7 / 4	Despotic
	2 (B2)	16	7 / 4	1 / 4	Tolerant
	3 (B3)	14	4 / 2	4 / 4	Tolerant
Chimpanzee (*Pan troglodytes*)	1 (C1)	23	5 / 1	11/ 6	Despotic
	2 (C2)	42	5 / 7	23 / 7	Tolerant
Total	5	116	26 / 19	46 / 25	

[a] *Values reflect individuals that were eligible for at least one session. This excludes Eleke (B2), Kodoro (B2), Masya (C2), Mikey (C2), and Mumba (C2)*

[b] *Age in years: Juveniles = 3–11; Adults = 12+ (based on Cronin et al., 2014)*

[c] *F = Number of females; M = Number of males*

At Lola ya Bonobo, 12 experiments were conducted at group 1 (hereafter: B1) and group 2 (hereafter: B2), and 13 experiments at group 3 (hereafter: B3) in August-September 2019 between 0800 and 1230 or 1400 and 1615 hours, to coincide with non-fixed feeding protocols. At Chimfunshi Wildlife Orphanage, 12 experiments were conducted at group 1 (hereafter: C1) and 11 at group 2 (hereafter: C2) between 1030 and 1115 or 1330 and 1415 hours, to avoid clashing with regular feeding protocols. Sessions were balanced between morning and afternoon across all groups at both field sites.

6.2.2 The peanut swing experiment and tolerance measure

To investigate whether pre-feeding social reassurance increases cofeeding tolerance in sanctuary-living *Pan* populations, we applied a modified version of an established experimental measure to assess social tolerance; the "*peanut swing*" (Cronin et al., 2014, 2015; DeTroy et al., 2021; van Leeuwen et al., 2021). More details on the experimental deployment of the peanut swing paradigm and its conventional application as a measure to record group-level social tolerance can be found in Cronin et al. (2014). I applied the peanut swing experiment to systematically record both contact affiliative interactions that occurred prior to feeding, as well as individual access to a valuable food resource during a competitive period. See *Section 3.2.2* for a comprehensive overview of the peanut swing experimental protocol and see *Sections 6.2.2.1–6.2.2.2* for further details about how these videos were coded regarding pre-feeding affiliation and cofeeding tolerance.

Due to mother-dependence, only apes aged 3 years and older were considered when constructing the peanut swing and subsequent analyses of cofeeding tolerance.

Furthermore, the total peanut volume for each session varied, as some individuals were absent due to veterinary care. These restrictions resulted in a total sample range of N = 116 individuals (B1 = 21; B2 = 16; B3 = 14; C1 = 23; C2 = 42). We completed a total of 60 sessions across the five groups (B1 = 12; B2 = 12; B3 = 13; C1 = 12; C2 = 11). Full group attendance for each session was not always possible due to the semi-wild conditions under which the apes are housed and the restriction of a 5-minute pre-feeding window. However, full attendance is also not guaranteed during regulated feedings in these sanctuaries. In order to assess the most naturalistic representations of the group's climates, I excluded sessions where less than 80% of the group were confirmed to be present prior to deployment of the swing. This criterion would ensure that a fair balance of individuals across ages, sexes, and rank classes would be present. Some further sessions were excluded due to equipment errors, such as incorrect camera angling. This resulted in N = 45 swings being eligible for inclusion (B1 = 8; B2 = 10; B3 = 10; C1 = 9; C2 = 8).

6.2.2.1 Pre-feeding affiliation observations and coding

Reassurance interactions were all-occurrence coded using the video software ELAN (Wittenburg et al., 2006, see *Chapter 3*). I was thus able to code for each individual every social, agonistic, and self-directed behaviour they engaged in. This enabled the compilation of datasets comprising individual- and dyad-level pre-feeding affiliation tendencies. In some sessions, the swing was deployed after 5-minutes had passed. For all cases, I only included pre-feeding affiliation that occurred in the immediate 5-minutes before T0. Individuals who were not observed at all prior to T0 were excluded.

Social interactions were coded once per dyad alongside the initiator's identity for each behaviour and the recipient's response. Due to the intensity of the coding programme, occurrence but not duration of each behaviour was recorded. However, new bouts were coded if there was a latency of at least 15 seconds between contact of the same behaviour type. The affiliative behaviour ethogram was developed for each species' contact affiliative behaviours (see *Appendix A.1*). Pre-feeding contact affiliation behaviours included embrace, mount, pat, touch, genital touch, and genito-genital contact (coded as rump-rump touch in chimpanzees). All contact behaviours were checked for in every group, however, some reassurance contact behaviours, such as finger/hand in mouth, grasp hand, and body kiss, were virtually absent in bonobo groups. Other behaviours, including social play, contact-sit, and groom, were coded if they lasted for five seconds or longer. As these behaviours have been associated with reassuring functions (Aureli & Yates, 2010; Boccia et al., 1989; de Waal, 1992; Judge et al., 2006; Palagi et al., 2006; Schino et al., 1988; Shutt et al., 2007), they were included as contact-affiliation in these analyses. As an initial investigation into a possible function of reassurance to facilitate social tolerance, I excluded non-contact social behaviours and focused on contact behaviours that appear to have alliance forming, social bond testing, and possible tension management functions when used during periods of social tension (Clay & de Waal, 2015; de Waal, 1986b; Palagi et al., 2006).

6.2.2.2 Tolerance data coding

This application of the peanut swing as an assay to score individual access to a valuable, depleting resource. Previous studies using the *peanut swing* have measured cofeeding tolerance by recording the total sum of individuals present within 1-metre of the ground area where the peanuts landed—referred to as the "cofeeding zone"—at 15-second scan points post-deployment up to 2-minutes, for a total of eight scans. For this study, I coded each individual's presence within the cofeeding zone at the same 15-second scan points. Tolerance coding was conducted in conjunction with pre-feeding affiliation coding. I followed each individual to code social interactions up to T0, after which I coded presence within the zone (1 = in the zone; 0 = outside of the zone). These values were totalled into a value constituting the total number of scans present within the cofeeding zone for each individual for each session.

6.3 Analysis

6.3.1 Summary of statistical approaches

I used a mixed models approach to assess whether pre-feeding reassurance predicted an individual's subsequent presence within the cofeeding zone. Cofeeding tolerance was modelled at the individual-level using Generalised Linear Mixed Models (GLMMs) with logit link functions and Poisson error distributions. I collapsed observations into an individual-level dataset, whereby each observation row corresponded to a summary of an individual's reassurance behaviour in the 5-minutes prior to the swing as well as their presence in the cofeeding zone. The sample for these models consisted of N = 810 observations of N = 116 individuals in N = 45 swings across N = 5 groups. The response variable was a Poisson count of the number of scans that individual spent within the cofeeding zone. I used separate models to test two measures of reassurance—number of contact partners and number of absolute contacts (described in *Section 6.3.2*). As I expected reassurance to have a greater influence in chimpanzee groups than bonobos groups, I included interactions of reassurance and species/group in separate models for each measure of reassurance.

All models were fitted in RStudio (version 1.3.1093; RStudio Team, 2020) using the R package lme4 (Bates et al., 2015). To avoid models being overconfident regarding precision of fixed effects estimates and prevent a type I error, I adopted a maximal model approach (Barr et al., 2013) and included all theoretically identifiable random slope components and their correlations with the intercepts. Theoretical identifiability was defined as at least three unique values per level of a random effect for covariate fixed effects and at least two levels with at least two observations per level of a random effect for factor fixed effects. As in *Chapter 4*, model stabilities were assessed using a function provided by

Roger Mundry[2], comparing estimates obtained from the model based on all data with those obtained from models with the levels of the random effects excluded one at a time. I checked for collinearity of fixed effects using variance inflation factors for a standard linear model with the car package (Fox & Weisberg, 2019). Confidence intervals were derived using the function bootMer of the package lme4 using 1,000 parametric bootstraps and bootstrapping over the random effects too. To acquire accurate *P*-values for each fixed effect, I used likelihood ratio tests (LRT; Dobson et al., 2018) via the drop1 function of the package lme4 (Bates et al., 2015) in R to compare full models with respective null models lacking each fixed effect whilst retaining the rest of the model structure, including all random effects and random slopes. As in *Chapter 4* (see *Section 4.3.1*), model complexity was checked by calculating the number of observations per estimated term. Totals exceeding $N = 10$ were deemed sufficient for avoiding overcomplexity.

6.3.2 Does pre-feeding contact affiliation predict cofeeding tolerance?

I tested if pre-feeding contact affiliation increased tolerance, and whether this increase was greater or lower in either species, and/or varied between groups. To do this, I ran two sets of GLMMs in which I operationalized pre-feeding contact affiliation either as the total number of partners the individual had contact affiliation with (given and received) during the 5-minute pre-feeding window (*Model 1.1* and *Model 2.1*) or the total number of individual contact behaviours an ape gave or received during the pre-feeding window, regardless of social partner (*Model 1.2* and *Model 2.2*). Due to the discrepancy in population size across the study groups, I divided the number of affiliative partners and contacts by the total number of possible partners present during the given session (i.e., the total number of individuals from the group that were present during the prefeeding period).

To test for species variation, I included the interaction between species and pre-feeding contact affiliation (*Model 1.1* and *Model 2.1*). To test for group variation, I included the interaction between group and pre-feeding contact affiliation (*Model 1.2* and *Model 2.2*). I also included control variables of sex and age of the individual. I included random effects of individual identity, session number, and group (only for *Model 1.1* and *Model 2.1*), as well as all theoretically identifiable random slope components and their correlations with the intercepts (age, sex, and pre-feeding contact affiliation within session and group, and contact affiliation partners within individual). As in *Chapter 5*, I used a crossed random effects structure as individual identities are not necessarily fixed to group identities due to managed migrations between groups. To assess the effect of the interactions, I compared full models with respective reduced models lacking the interaction as a fixed effect but

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[2] Not publicly available. For enquiries, contact Roger Mundry directly.

retaining the main respective main effects alongside the same control variables and random effects structure (Baayen et al., 2008; Dobson & Barnett, 2018). In case the interaction did not significantly (i.e., $P < 0.05$) improve model fit, I used the reduced model to interpret the respective main effects (Bates et al., 2015).

6.4 Results

6.4.1 Summary of pre-feeding contact affiliation

Across our observations, bonobos had contact reassurance with an average of $M = 1.26$ social partners during the pre-feeding window, compared to chimpanzees who had an average of $M = 2.67$ social partners. However, corrected as a proportion of group size, individuals from each species interacted with an almost identical proportion of their group (M: bonobos = 0.082; chimpanzees = 0.081). Furthermore, bonobos engaged in an average of $M = 2.78$ contact reassurance behaviours per session compared to $M = 4.86$ in chimpanzees. Corrected for group size, this amounted to $M = 0.186$ behaviours per possible partner in bonobos and $M = 0.150$ in chimpanzees.

6.4.2 Does increased pre-feeding affiliative partners increase cofeeding tolerance?

The full model (*Model 1.1*) was a better fit than a null model lacking the interaction (LRT: $\chi2 = 9.780$, $P = .021$; see *Appendix D.1*). However, the full-reduced comparison revealed that including the interaction term did not result in a better fit than the reduced model comprising just main effects (LRT: $\chi2 = 3.141$, $P = .076$; see *Table 6.2*). Therefore, I present results for the reduced model comprising only main effects. *Model 1.1* revealed that the number of pre-feeding contact affiliation partners as a proportion of group size positively predicted cofeeding tolerance (estimate ± SE = 0.124 ± 0.042, $\chi2 = 6.108$, $P = .013$; *Figure 6.1*). Model stability checks revealed this effect was robust (see *Table 6.3*). *Model 1.1* also shows no significant effects of species (estimate ± SE = 0.348 ± 0.372, $\chi2 = 0.325$, $P = .569$), sex (estimate ± SE = 0.018 ± 0.271, $\chi2 = 0.004$, $P = .948$), nor individual age (estimate ± SE = 0.176 ± 0.235, $\chi2 = 2.567$, $P = .109$). Checks of variance inflation factors revealed maximum collinearity between the fixed effects of 1.06, indicating no problem with collinearity. Dispersion parameter checks revealed a score of 1.23, indicating slight overdispersion but not enough to warrant corrective measures. *Model 1.1* featured $N = 24.58$ observations per estimated term, indicating, alongside stability checks (see *Table 6.3*), that model overcomplexity was not a significant issue. Statistical output for the reduced version of *Model 1.1* can be seen in *Table 6.3*. All estimates and stability for random slopes are included in *Appendix D.2*.

Table 6.2. Results for full-reduced comparison of *Model 1.1*. Full version included an interaction and respective main effects of species and pre-feeding contact affiliation partners, alongside control variables of sex and age of the individual, with random effects for the identities of the group, individual, and session number. Reduced model included the same structure, except only main effects and no interaction term.

***Model 1.1*: Species differences**

Model	**AIC**	**BIC**	**logLik**	**Deviance**	**Chi^2**	**Df**	***P*-value**
Reduced	3825.341	3980.384	-1879.671	3759.341			
Full	3824.200	3983.941	-1878.100	3756.200	3.141	1	.076

Table 6.3. Results for *Model 1.1*—do increased pre-feeding contact affiliation partners (corrected for group size) increase cofeeding tolerance? Estimates and standard errors, together with confidence intervals, results of likelihood ratio tests, and the range of estimates obtained when dropping levels of random effects one at a time. Significant *P* values (< 0.05) are shown in ***italicised bold***.

***Model 1.1*: Reduced model with main effects only**

Term	**Estimate**	**SE**	**CI$_{95}$**	**$\chi 2$**	**z**	***P*-value**	**Min**	**Max**
Fixed effects								
(Intercept)	***0.951***	***0.258***	***0.466 to 1.386***		***3.689***	***< .001***	***0.579***	***1.536***
Species^a	0.348	0.372	-0.269 to 1.003	0.325	0.936	.569	-0.864	0.819
N Partners^b	***0.124***	***0.042***	***0.048 to 0.195***	***6.108***	***2.959***	***.013***	***0.076***	***0.209***
Sex^c	0.018	0.271	-0.459 to 0.488	0.004	0.066	.948	-0.103	0.161
Age^b	0.176	0.235	-0.292 to 0.635	2.567	0.749	.109	-0.004	0.286
Random effects								
Group	0.233						0.000	0.521
Individual	0.812						0.700	0.940
Session	0.097						0.053	0.321

[a] *dummy coded and centred with Bonobo as the reference category*

[b] *z-transformed to a mean of 0 and a standard deviation of 1*

[c] *dummy coded and centred with Female as the reference category*

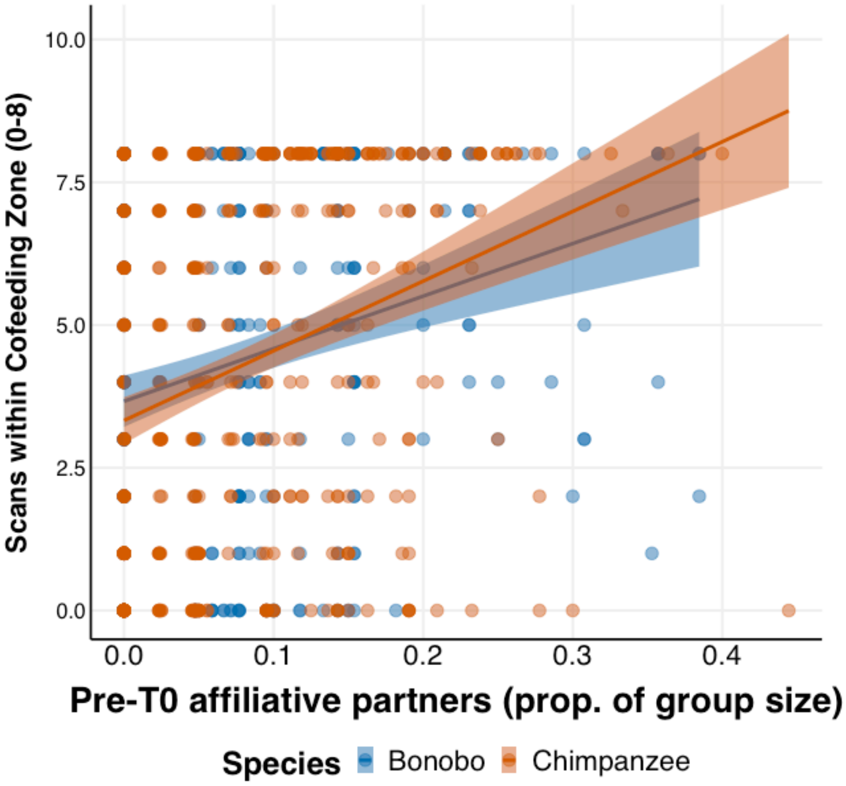

Figure 6.1. Scatterplot revealing a significant effect (*P* = .013) of pre-feeding affiliative partners on cofeeding tolerance in sanctuary-housed bonobos and chimpanzees (GLMM). X-axis = proportion of group individual had pre-feeding contact affiliation with; Y-axis = presence within cofeeding zone, measured by number of 15-seconds scans (up to 120-seconds, or eight scans) individual was in the cofeeding zone following the onset of feeding (T0). Fit line is straight to indicate positive linear relationship found in GLMM. Shaded areas correspond to confidence limits for model estimates at 95% level.

Similarly, at the group-level, the full model (*Model 1.2*) was a better fit than a null model lacking the interaction (LRT: χ2 = 30.502, *P* < .001; see *Appendix D.1*). However, the full-reduced comparison revealed that including the interaction term did not result in a better fit than the reduced model comprising just main effects (likelihood ratio test: χ2 = 8.276, *P* = .082; see *Table 6.4*). Therefore, here I present results for the reduced model consisting of only main effects. The number of pre-feeding contact affiliation partners as a proportion of group size positively predicted cofeeding tolerance (estimate ± SE = 0.130 ± 0.041, χ2 = 9.566, *P* = .002; *Figure 6.2*). *Figure 6.2* indicates that this positive influence of contact partners on cofeeding tolerance is only pronounced in three groups (B2, C1, C2). However, model stability checks revealed this effect was robust (see *Table 6.5*). *Model 1.2* shows a significant effect for group on cofeeding tolerance (see *Table 6.5* for estimates and standard errors, χ2 = 17.016, *P* = .002). Control predictors of sex and age were not significant (sex: estimate ± SE = 0.009 ± 0.165, χ2 = 0.003, *P* = .958; age: estimate ± SE = 0.062 ± 0.079, χ2 = 0.580, *P* = .446). Checks of variance inflation factors revealed maximum collinearity between the fixed effects of 1.11, indicating no problem with collinearity. Dispersion parameter checks revealed a score of 1.20, indicating slight overdispersion but not enough to warrant corrective measures. *Model 1.2* featured *N* = 17.26 observations per estimated term, indicating, alongside stability checks (see *Table 6.5*), that model overcomplexity was not a significant issue. Statistical output can be seen in *Table 6.5*. All estimates and stability for random slopes are included in *Appendix D.2*.

Table 6.4. Results for full-reduced comparison of *Model 1.2*. Full version included an interaction and respective main effects of group and pre-feeding contact affiliation partners, alongside control variables of sex and age of the individual, with random effects for the identities of the individual identity, and session number. Reduced model included the same structure, except only the main effects of group and pre-feeding contact affiliation partners without the interaction.

***Model 1.2*: Group differences**

Model	**AIC**	**BIC**	**logLik**	**Deviance**	**Chi^2**	**Df**	***P*-value**
Reduced	3821.980	4042.798	-1863.990	3727.980			
Full	3821.704	4061.316	-1859.852	3719.704	8.276	4	.082

Table 6.5. Results for *Model 1.2*—do increased pre-feeding contact affiliation partners (corrected for group size) increase cofeeding tolerance? Estimates and standard errors, together with confidence intervals, results of likelihood ratio tests, and the range of estimates obtained when dropping levels of random effects one at a time. Significant *P* values (< 0.05) are shown in ***italicised bold***.

***Model 1.2*: Reduced model with main effects only**

Term	Estimate	SE	CI$_{95}$	$\chi2$	z	*P*-value	Min	Max
(Intercept)	***0.799***	***0.232***	***0.361 to 1.211***		***3.451***	***.001***	***0.663***	***0.909***
Group[a]				***17.016***		***.002***		
B2	***0.845***	***0.299***	***0.275 to 1.419***		***2.829***	***.005***	***0.717***	***0.980***
B3	0.019	0.326	-0.619 to 0.638		0.058	.954	-0.106	0.143
C1	-0.165	0.282	-0.713 to 0.369		-0.585	.559	-0.293	-0.055
C2	***0.514***	***0.260***	***0.051 to 1.020***		***1.978***	***.048***	***0.408***	***0.634***
N Partners[b]	***0.130***	***0.041***	***0.055 to 0.203***	***9.566***	***3.182***	***.002***	***0.102***	***0.207***
Sex[c]	0.009	0.165	-0.298 to 0.321	0.003	0.057	.958	-0.035	0.193
Age[b]	0.062	0.079	-0.089 to 0.201	0.580	0.779	.446	0.037	0.117
Random effects								
Individual	0.858						0.786	0.933
Session	0.116						0.000	0.130

[a] *dummy coded and centred with B1 as the reference category*

[b] *z-transformed to a mean of 0 and a standard deviation of 1*

[c] *dummy coded and centred with Female as the reference category*

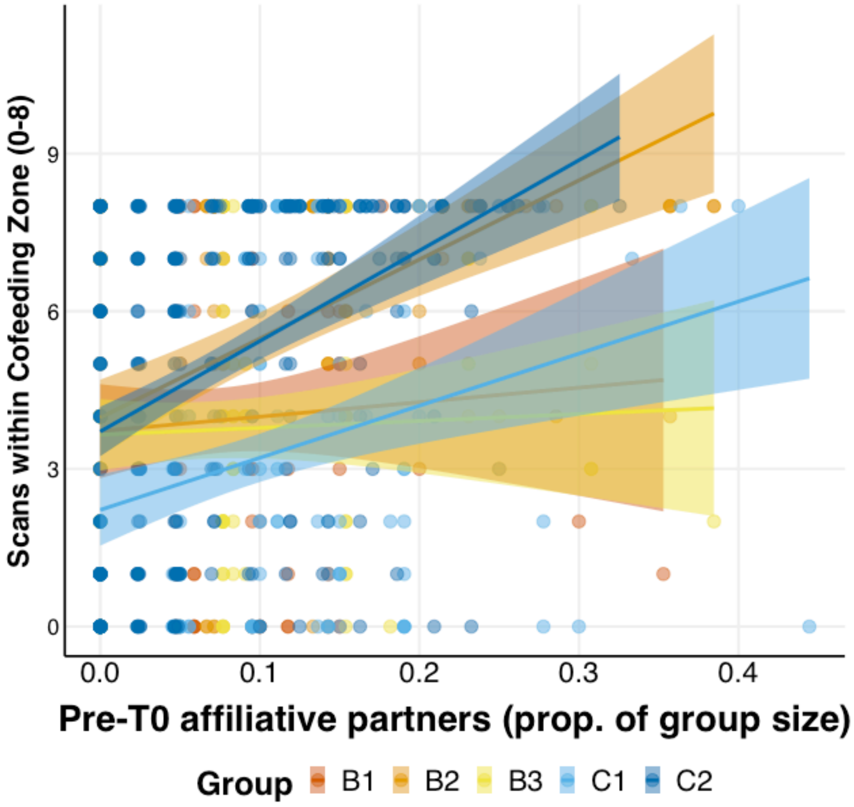

Figure 6.2. Scatterplot revealing a significant effect (*P* = .002) of pre-feeding affiliative partners on cofeeding tolerance across multiple sanctuary-living bonobo and chimpanzee groups (GLMM). X-axis = proportion of group individual had pre-feeding contact affiliation with; Y-axis = presence within cofeeding zone, measured by number of 15-seconds scans (up to 120-seconds, or eight scans) individual was in the cofeeding zone following the onset of feeding (T0). Fit line is straight to indicate positive linear relationship found in GLMM. Shaded areas correspond to confidence limits for model estimates at 95% level.

6.4.3 Does increased pre-feeding affiliative contacts increase cofeeding tolerance?

The full model (*Model 2.1*) was a better fit than a null model lacking the interaction (LRT: χ2 = 11.622, *P* = .009; see *Appendix D.1*). However, the full-reduced comparison revealed that including the interaction term did not result in a better fit than the reduced model comprising just main effects (LRT: χ2 = 2.097, *P* = .148; see *Table 6.6*). Therefore, I present results for the reduced model consisting of only main effects. *Model 2.1* revealed that the absolute volume of pre-feeding affiliative contacts as a proportion of group size positively predicted cofeeding tolerance (estimate ± SE = 0.189 ± 0.055, χ2 = 9.122, *P* = .001; *Figure 6.3*). Model stability checks revealed this effect was robust (see *Table 6.7*). There were no significant effects for species (estimate ± SE = -0.388 ± 0.302, χ2 = 1.414, *P* = .199), sex (estimate ± SE = 0.026 ± 0.220, χ2 = 2.712, *P* = .908), or age (estimate ± SE = 0.222 ± 0.172, χ2 = 5.214, *P* = .197). Checks of variance inflation factors revealed maximum collinearity between fixed effects of 1.06, indicating no problem with collinearity. Dispersion parameter checks revealed a score of 1.24, indicating slight overdispersion but not enough to warrant corrective measures. *Model 2.1* featured *N* = 24.58 observations per estimated term, indicating, alongside stability checks (see *Table 6.7*), that model overcomplexity was not a significant issue. Statistical output of *Model 2.1* can be seen in *Table 6.7*. All estimates and stability for random slopes are included in *Appendix D.2*.

Table 6.6. Results for full-reduced comparison of *Model 2.1*. Full version included an interaction and respective main effects of species and pre-feeding affiliative contacts, alongside control variables of sex and age of the individual, with random effects for the identities of the group, individual identity, and session number. Reduced model included the same structure, except only the main effects of species and pre-feeding affiliative contacts without the interaction.

***Model* 2.1: Species differences**

Model	AIC	BIC	logLik	Deviance	Chi^2	Df	*P*-value
Reduced	3829.022	3984.065	-1881.511	3763.022			
Full	3828.925	3988.666	-1880.463	3760.925	2.097	1	.148

Table 6.7. Results for *Model 2.1*—do increased pre-feeding affiliative contacts (corrected for group size) increase cofeeding tolerance in *Pan*? Estimates and standard errors, together with confidence intervals, results of likelihood ratio tests, and the range of estimates obtained when dropping levels of random effects one at a time. Significant *P* values (< 0.05) are shown in ***italicised bold***.

***Model* 2.1: Reduced model with main effects only**

Term	Estimate	SE	CI$_{95}$	$\chi 2$	z	*P*-value	Min	Max
Fixed effects								
(Intercept)	***1.244***	***0.206***	***0.802 to 1.534***		***6.032***	***< .001***	***0.638***	***1.442***
Species[a]	-0.388	0.302	-0.766 to 0.349	1.414	-1.284	.199	-0.761	0.650
N Contacts[b]	***0.189***	***0.055***	***0.130 to 0.277***	***9.122***	***3.427***	***.001***	***0.156***	***0.302***
Sex[c]	0.026	0.220	-0.347 to 0.429	2.712	0.116	.908	-0.115	0.230
Age[b]	0.222	0.172	-0.103 to 0.503	5.214	1.290	.197	0.041	0.308
Random effects								
Group	0.338						0.000	0.349
Individual	0.800						0.664	0.889
Session	0.084						0.052	0.295

[a] *dummy coded and centred with Bonobo as the reference category*

[b] *z-transformed to a mean of 0 and a standard deviation of 1*

[c] *dummy coded and centred with Female as the reference category*

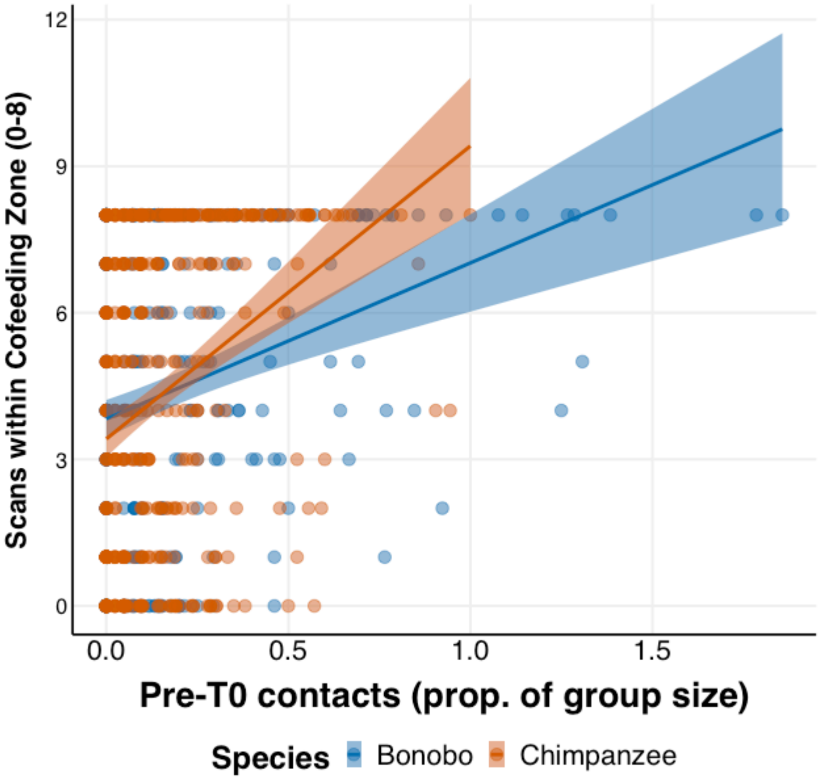

Figure 6.3. Significant effect (*P* = .001) of pre-feeding affiliative contacts on cofeeding tolerance in both bonobos and chimpanzees (GLMM). X-axis = absolute volume of pre-feeding affiliative contacts individual engaged in (corrected for group size); Y-axis = presence within cofeeding zone, measured by number of 15-seconds scans (up to 120-seconds, or eight scans) individual was in the cofeeding zone following the onset of feeding (T0). Fit line is straight to indicate positive linear relationship found in GLMM. Shaded areas correspond to confidence limits for model estimates at 95% level.

Similarly, at the group-level, the full model (*Model 2.2*) was a better fit than a null model lacking the interaction (LRT: χ2 = 35.919, *P* < .001; see *Appendix D.1*). However, the full-reduced comparison revealed that including the interaction term did not result in a better fit than the reduced model comprising just main effects (likelihood ratio test: χ2 = 4.057, *P* = .398; see *Table 6.8*). Therefore, here I present results for the reduced model consisting of only main effects. The absolute volume of pre-feeding affiliative contacts as a proportion of group size positively predicted cofeeding tolerance (estimate ± SE = 0.190 ± 0.045, χ2 = 19.718, *P* < .001; *Figure 6.4*). *Figure 6.4* indicates that this positive influence of contacts on cofeeding tolerance is only pronounced in three groups (B2, C1, C2). However, model stability checks revealed this effect was robust (see *Table 6.9*). *Model 2.2* shows a significant effect for group (see *Table 6.9* for estimates and standard errors, χ2 = 18.515, *P* = .001). Control predictors of sex and age of the individual were not significant (sex: estimate ± SE = 0.089 ± 0.142, χ2 = 0.372, *P* = .529; age: estimate ± SE = 0.063 ± 0.067, χ2 = 0.828, *P* = .351). Checks of variance inflation factors revealed maximum collinearity between the fixed effects of 1.13, indicating no problem with collinearity. Dispersion parameter checks revealed a score of 1.21, indicating slight overdispersion but not enough to warrant corrective measures. *Model 2.2* featured N = 17.26 observations per estimated term, indicating, alongside stability checks (see *Table 6.9*), that model overcomplexity was not a significant issue. Statistical output for the reduced version of *Model 2.2* can be seen in *Table 6.9*. All estimates and stability for random slopes are included in *Appendix D.2*.

Table 6.8. Results for full-reduced comparison of *Model 2.2*. Full version included an interaction and respective main effects of group and pre-feeding affiliative contacts, alongside control variables of sex and age of the individual, with random effects for the identities of the individual identity, and session number. Reduced model included the same structure, except only the main effects of group and pre-feeding affiliative contacts without the interaction.

***Model* 2.2: Group differences**

Model	**AIC**	**BIC**	**logLik**	**Deviance**	**Chi^2**	**Df**	***P*-value**
Reduced	3818.893	4039.712	-1862.446	3724.893			
Full	3822.836	4062.448	-1860.418	3720.836	4.057	4	.398

Table 6.9. Results for *Model 2.2*—do increased pre-feeding affiliative contacts (corrected for group size) increase cofeeding tolerance across *Pan* groups? Estimates and standard errors, together with confidence intervals, results of likelihood ratio tests, and the range of estimates obtained when dropping levels of random effects one at a time. Significant *P* values (< 0.05) are shown in ***italicised bold***.

***Model* 2.2: Reduced model with main effects only**

Term	**Estimate**	**SE**	**CI$_{95}$**	**χ2**	**z**	***P*-value**	**Min**	**Max**
(Intercept)	***0.824***	***0.210***	***0.380 to 1.215***		***3.915***	***< .001***	***0.705***	***0.939***
Group[a]				***18.515***		***.001***		
B2	***0.619***	***0.251***	***0.134 to 1.122***		***2.463***	***.014***	***0.619***	***0.749***
B3	-0.015	0.276	-0.594 to 0.539		-0.055	.956	-0.015	0.103
C1	-0.099	0.255	-0.576 to 0.434		-0.388	.698	-0.099	0.027
C2	***0.476***	***0.241***	***0.019 to 0.950***		***1.975***	***.048***	***0.476***	***0.582***
N Contacts[b]	***0.190***	***0.045***	***0.120 to 0.259***	***19.718***	***4.177***	***< .001***	***0.190***	***0.255***
Sex[c]	0.089	0.142	-0.206 to 0.345	0.372	0.629	.529	0.089	0.147
Age[b]	0.063	0.067	-0.069 to 0.192	0.828	0.932	.351	0.063	0.092
Random effects								
Individual	0.838						0.780	0906
Session	0.106						0.000	0.128

[a] *dummy coded and centred with B1 as the reference category*

[b] *z-transformed to a mean of 0 and a standard deviation of 1*

[c] *dummy coded and centred with Female as the reference category*

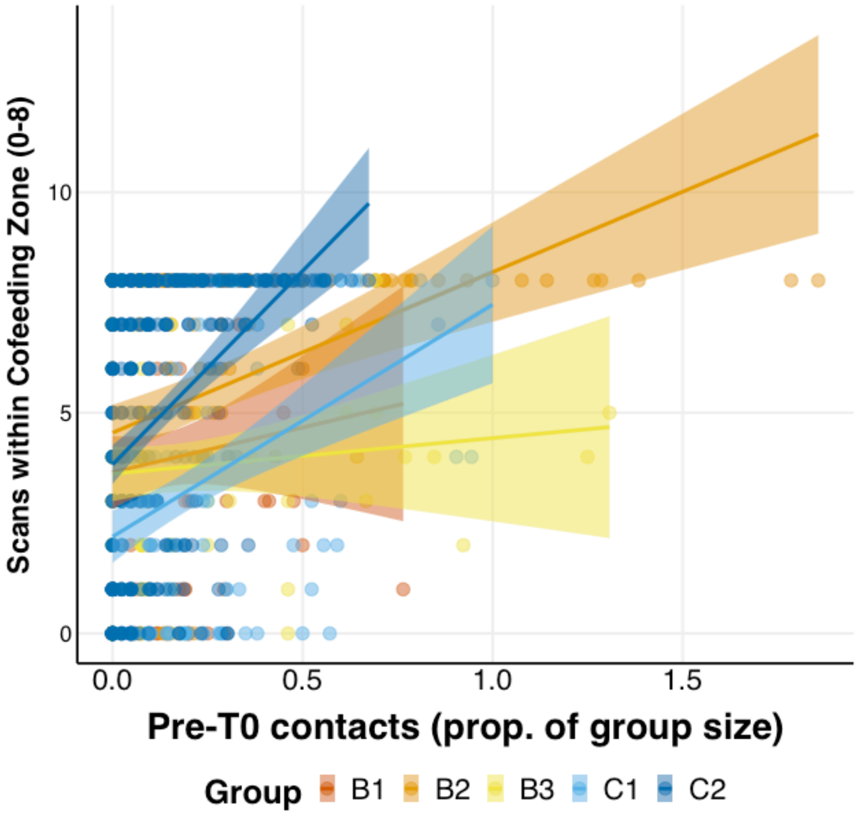

Figure 6.4. Significant effect ($P < .001$) of pre-feeding affiliative contacts on cofeeding tolerance across multiple bonobo and chimpanzee groups (GLMM). X-axis = absolute volume of pre-feeding affiliative contacts individual engaged in (corrected for group size); Y-axis = presence within cofeeding zone, measured by number of 15-seconds scans (up to 120-seconds, or eight scans) individual was in the cofeeding zone following the onset of feeding (T0). Fit line is straight to indicate positive linear relationship found in GLMM. Shaded areas correspond to confidence limits for model estimates at 95% level.

6.5 Discussion

In humans and other primates, social tolerance promotes more effective cooperation (Chen et al., 2009; Hare et al., 2007; Melis et al., 2006), communicative exchanges (Scopa & Palagi, 2016), and possibly empathy (de Waal & Aureli, 1996; Palagi et al., 2014; but see *Chapter 4*). Whilst humans appear to be extraordinarily tolerant in how we gather and cooperate, considerable between-group variation exists, as in our closest living relatives too (Kaufhold & van Leeuwen, 2019). Despite previous assumptions of stark species differences, recent assays of social tolerance indicate that groups of sanctuary- and zoo-living bonobos and chimpanzees vary more in cofeeding tolerance at the group-level than they do at the species-level (Cronin et al., 2014; DeTroy et al., 2021; van Leeuwen et al., 2021, under review). Moreover, these variations may fluctuate over time due to social compositional factors, such as typically reduced crowding during feeding when chimpanzee groups contain more females with dependent offspring (DeTroy et al., 2021). This may reflect hesitancy due to increased vulnerability on the part of the mother, and her offspring, yet cannot explain why non-caregiving individuals avoid competitive zones. Hence, as yet undetermined proximate mechanisms may encourage individuals to gather during these competitive periods. Here I show that increased contact affiliation—both in terms of engagement with partners and absolute volume of contact behaviour—may facilitate increased cofeeding density on a proximate level for semi-wild *Pan* groups. In bonobos and chimpanzees, individuals who shared more pre-feeding contact affiliation with social partners spent more time within a restricted cofeeding zone, having greater access to a limited, depleting food resource.

There are associations between increased social connectedness and increased social tolerance in primates (Balasubramaniam et al., 2017; Duboscq et al., 2013; Pasquaretta et al., 2014). However, both tolerant and despotic chimpanzee groups can feature strong reciprocal social bonds (Kaburu & Newton-Fisher, 2015). Furthermore, a study of four macaque species varying in social tolerance levels has indicated that access to food depends more on social integration and dominance rank than dominance style (Amici et al., 2020). Strong social bonds and alliances in bonobos and chimpanzees are associated with greater cooperation, resource sharing, and tolerance of inequity (Brosnan et al., 2005; Parish, 1996; Samuni et al., 2018; White & Wood, 2007).

Relatedly, reassurance behaviours—including those associated with increased vulnerability (Palmer & Pomianek, 2007)—serve possible aggression reducing, bond testing, and alliance forming functions (de Waal, 1992; van Hooff, 1967; see *Chapter 5*). Specific forms of reassurance are also purported to have other functions, such as reducing victim distress during consolation (Clay & de Waal, 2013; Romero et al., 2010). In pre-feeding contexts, reassurance may function to buffer social tension in the short-term when individuals anticipate competition, and potential group instability. Whilst I did not directly test whether pre-feeding affiliative contacts have a reassuring function, the results indicate that reassurance behaviours may serve to foster increased social tolerance on a proximate level in both chimpanzees and bonobos.

Engaging in affiliative contact during a competitive period of social tension is risky for species, like bonobos and chimpanzees, that are also known to engage in conflict around feeding times (Aureli et al., 2002; de Waal, 1992). In this sense, it is possible that this shared engagement in vulnerable behaviour may reflect 'rituals of trust' (Palmer & Pomianek, 2007), where there is assumed confidence between the two parties that there is no agonistic intent. Relatedly, in *Chapter 5*, I demonstrate that the use of vulnerable behaviours during periods of social tension may be more common in more socially tolerant groups. Akin to similar associations with vulnerable behaviours appearing to promote reciprocal trust in capuchins (*Cebus*; Perry, 2011) and hyenas (*Crocuta crocuta*; East et al., 1993), engagement in pre-feeding rituals of reassurance may foster a more peaceful, egalitarian cofeeding experience in *Pan*.

My study revealed within-species group variation. In both chimpanzee groups in this study (one socially despotic (C1) and one socially tolerant (C2)) increased pre-feeding contact affiliation positively influenced an individual's access to the cofeeding zone. Notably, and descriptively, individuals in the despotic group (C1) with no pre-feeding affiliation appeared to have a lower average baseline access to the cofeeding zone than individuals in the tolerant group (C2). I did not explicitly test group differences on this level. However, each individual in the despotic group (C1) appears to require more affiliative partners and contacts to access the feeding zone than a tolerant group (C2) counterpart. This suggests that, while social connectedness may facilitate greater social tolerance generally (Amici et al., 2020), it may require more effort in despotic chimpanzee communities to access resources. Pre-feeding affiliation itself may not be facilitated by tolerance, but rather that increased pre-feeding affiliation may suppress inter-individual intolerance. Further study with more populations varying in collective temperament would help reveal whether this trend is consistent.

For bonobos, the influence of pre-feeding affiliation on social tolerance is less clear. Broadly, both bonobos and chimpanzees showed a positive association of pre-feeding contact affiliation and access to the cofeeding zone. However, for bonobos at the group level, one tolerant group (B3) and one relatively despotic group (B1) appeared to lack a clear relationship between these variables. The nature of feeding competition appears to vary between bonobos and chimpanzees. Bonobos have also been observed to share food with other group members in the wild (Yamamoto, 2015) and even with strangers in sanctuary settings (Tan & Hare, 2013). Furthermore, bonobos often cofeed in the wild with outgroups (e.g., Lucchesi et al., 2020). Such intergroup tolerance around food is generally unheard of in chimpanzees (Gruber & Clay, 2016). Whilst the two species shared a general association between pre-competition contact and social tolerance, the mechanisms that drive peaceful feedings may also vary. Factors including the type of food, opportunity for mating, and even group size appear to influence intergroup tolerance in bonobos (Lucchesi et al., 2020; Lucchesi et al., 2021). If socio-ecological factors can influence intergroup tolerance, then they may also influence the need for reassurance during possibly competitive periods. Thus, future research should assess the relative stability and social climate—i.e., rates of aggression, hierarchical changes (Van Elsacker et al., 1999; Von Rohr et al., 2012)—prior to experimental sessions to investigate if fluctuating social dynamics influence the use of reassurance prior to competition. For example, if an individual has recently received more aggression or lost dominance status, they may seek more reassurance interactions to reaffirm their social trust and confidence during competition (de Waal, 1986a; Palmer & Pomianek, 2007). This possible group- and species-level variation in how much pre-feeding affiliation associates with cofeeding tolerance reveals further support for the inclusion of multiple groups when testing for species-level variation (Kaufhold & van Leeuwen, 2019).

There are some alternative explanations for individual and collective variation in both reassurance and tolerance across trials, such as motivation and latency since previous feedings. Associations between individuals of each species are known to vary in accordance with proximity to feeding periods (de Waal, 1992; Palagi et al., 2006). Furthermore, food motivation and competition may be influenced by temporal closeness to a recent feeding. I controlled for these influences by balancing trials across morning and afternoon sessions, and never conducting the swing within two hours following a feeding. However, captive bonobos and chimpanzees are known to have individual food preferences (Clay & Zuberbühler, 2009; Hopper et al., 2011; Shorland et al., 2019; Slocombe & Zuberbühler, 2006), and thus it is possible that individuals lacked motivation to compete over a limited food resource that they are less interested in. Broadly, peanuts appeared desirable to all study subjects, however, future research could assess individual food preferences prior to experimental sessions to control for personal preference.

Humans and *Pan* share behavioural flexibility and a capacity to adapt to changing social contexts (Boesch et al., 2002; Gruber et al., 2019; van Leeuwen et al., 2013). Hence, conditions can vary, and collective anxiety prior to competition may also vary from one day to the next (Aureli et al., 2002; Palagi et al., 2006). Thus, affiliative tendencies in these contexts may fluctuate, for example, if tension is particularly high due to other external social conditions, there may be a greater need for reassurance. By conducting multiple sessions for each group across different time points and over multiple weeks, I attempted to control for these random influences and gather a general depiction of how these groups associate during competitive periods.

In conclusion, engagement in pre-feeding affiliative contact may proximately facilitate social tolerance in sanctuary-living bonobos and chimpanzees. The two species remain distinct in their apparent differences towards tolerance of outgroups (Gruber & Clay, 2016). However, my findings and recent studies of *Pan* social tolerance (Jaeggi et al., 2010; van Leeuwen et al., under review) indicate considerable overlap between the two species, not only in levels of within-group social tolerance, but also potential proximate drivers of such tolerance. Deeper study may elucidate other proximate and ultimate mechanisms that influence *Pan* social tolerance, and whether their effectiveness fluctuates according to other social dynamics (Kaufhold & van Leeuwen, 2019). The apparent common function of reassurance as a means to foster tolerance parallels with human society, indicating a possible shared ancestry with our last common ancestor. To further investigate how great ape sociality informs our understanding of human evolution, we must continue to draw findings from multiple groups and study sites for the broadest and most nuanced picture.

Chapter 7: Sexual healing: Genital contacts during periods of social tension in sanctuary-living bonobos and chimpanzees

This chapter constitutes an empirical article to be submitted for publication with the following authorship:

Brooker, J. S., Webb, C. E., van Leeuwen, E. J. C., de Waal, F. B. M., & Clay, Z. Sexual healing: Genital contacts during periods of social tension in sanctuary-living bonobos and chimpanzees.

Abstract

The use of sexual behaviour during tense contexts has been documented extensively in mixed-sex and same-sex pairings of our closest living relatives, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). Bonobos have a reputation for being 'hypersexual', especially compared to chimpanzees. This reputation is largely driven by evidence that bonobos engage in habitual and heightened frequencies of sexual behaviour, especially during periods of social tension, where genital contacts between same-sex and mixed-sex dyads are purported to function to enhance cooperation, resolve conflicts and provide reassurance. Although chimpanzees also engage in sexual contacts and genital touching in these situations, the two species have yet to be compared systematically, which may have led to inaccuracies in knowledge about the extent of species variability. To address this, I recorded all instances of genital and non-genital contact affiliation among sanctuary-living bonobos and chimpanzees during two mutually exclusive socially tense contexts—part 1: post-conflict consolation; and part 2: pre-feeding reassurance. Results revealed that bonobos were more likely to use genital contacts during consolation than chimpanzees, but both species used genital contacts during pre-feeding affiliation at comparable levels. In bonobos, neither age nor sex of either party influenced tendency to use genital contact during consolation, however female bonobos were more likely to receive genital contact during pre-feeding affiliation than males. In chimpanzees, females were more likely to receive genital contact than males in both contexts, and older chimpanzees were more likely to initiate genital contacts during pre-feeding affiliation than younger conspecifics. For both species, non-kin pairs were more likely to engage in genital contact than kin pairs in both contexts. Contrary to expected species differences, these findings indicate significant overlaps in the role that genital contacts appear to play during periods of social tension in the *Pan* apes. These findings contribute to recent indications that affiliative genital contact supports management of social relationships and social tension across hominids.

7.1 Introduction

Sexual behaviour—conceptive and non-conceptive genital contact occurring within and between the sexes—is commonplace in human society, playing a significant role in the development of durable relationships across cultures (Heiman et al., 2011; Schmitt, 2005). As well as being a positive predictor of human social relationship quality and general wellbeing (Grøntvedt et al., 2020; Heiman et al., 2011), diverse forms of sexual behaviour are widespread throughout the animal kingdom (Orille, 2020; Sommer & Vasey, 2006), particularly among nonhuman primates (see Dixson, 2012 for a review of primates).

Among the primates, bonobos are most known for their rich and heightened sexual behaviour (Furuichi, 2011; Hohmann & Fruth, 2000; Gruber & Clay, 2016; Woods & Hare, 2011). Sexual behaviour plays a significant role in the social ontogeny of both female and male bonobos, emerging already during the first year of life (Furuichi et al., 2014). Initially, most bonobo sexual interactions begin between mother-infant pairings when either party are distressed or anxious (Clay et al., 2022; Hashimoto, 1997). Bonobos engage in genital contacts across a variety of contexts with their peers, including play (Enomoto, 1990), but predominantly during social tension and feeding (Clay et al., 2022; Clay & de Waal, 2015; de Waal, 1990; Hohmann & Fruth, 2000; Moscovice et al., 2019).

Genito-genital rubbing—when two individuals, most often females, embrace ventro-ventrally and swing their hips laterally with their vulvae or penises in contact (Hohmann & Fruth, 2000; Kuroda, 1980)—is a species-typical behaviour in bonobos that is thought to primarily function to enhance cooperation and social bonding (Moscovice et al., 2019). Genito-genital rubbing is linked with food sharing and closeness during feeding (Moscovice et al., 2017). These findings and observations of genito-genital rubbing between females during intergroup encounters (Furuichi, 2011; Idani, 1990) and within-group fusions (Moscovice et al., 2015) indicate that this sexual behaviour may also facilitate greater social tolerance.

Although much attention has been placed on bonobo sexuality, the significance of sexuality among chimpanzees is relatively understated despite its apparent prevalence. Genital touching and mounting are seen across ages in chimpanzees, in both mixed-sex and same-sex pairings (Sandel & Reddy, 2021). Genital contacts occur frequently during chimpanzee play (Savage & Malick, 1977) and genital touching is used often in greetings (Nishie, 2016) where it appears to represent a form of reassurance, occurring often during consolation and reconciliation too (Arnold & Whiten, 2001; de Waal & van Roosmalen, 1979; Romero et al., 2011). Similarly, rump-rump touching—where individuals face away from one another and place their rumps in contact, akin to bonobo genito-genital rubbing—occurs often during periods of social tension among chimpanzees (Sandel & Reddy, 2021) and has been purported to have a reassuring function (Goodall, 1989). Although more habitual in bonobos, same-sex genito-genital rubbing has been observed in one captive group of female chimpanzees and was associated with grooming relationships, indicating a social bonding function (Anestis, 2004). In addition, oral-genital contact has emerged in chimpanzees during contexts such as play (Savage & Malick, 1977) and social tension relief (Brooker et al., 2020). Sociosexuality therefore appears to be important part of bonobo and chimpanzee social life, and different forms may flexibly emerge according to context and population.

In bonobos, sociosexual behaviour has predominantly been studied regarding its tension relieving and social bonding function (Clay & de Waal, 2015; de Waal, 1990; Hohmann et al., 2009; Hohmann & Fruth, 2000). Genito-genital rubbing is common during periods of within-group tension, such as post-conflict periods (Clay & de Waal, 2013; Palagi et al., 2004) and during feeding, when there may be competition (Hohmann & Fruth, 2000; Paoli et al., 2007; see *Chapter 5*). Chimpanzees also appear to use sociosexual behaviour similarly: they often mount and touch genitals, including male-male testicle shaking, following conflicts and during intergroup and predator encounters (Arnold & Whiten, 2001; Goodall et al., 1979; Herbinger et al., 2009; Romero et al., 2011). Sandel & Reddy (2021) found that genital contacts in wild chimpanzees were most common during socially-tense contexts, including subgroup fusions and territorial behaviour. Whilst grooming and rank relationships did not predict sociosexual patterns, individuals of all ages and sexes were seen to mount and touch genitals, including pressing genitals together. Wild chimpanzees have also been reported to hold the genitals of their social partners during intergroup encounters (Samuni et al., 2019).

These observations indicate that affiliative genital contact contributes broadly to the management of hominid social relationships and periods of social tension (Heiman et al., 2011; Hohmann & Fruth, 2000; Sandel & Reddy, 2021). Even wild gorillas and wild orangutans have been observed to use sociosexual behaviour in homosexual pairings (Fox, 2001; Grueter & Stoinski, 2016). Like *Pan,* male homosexual interactions in wild orangutans have been associated with social tension and affiliation (Fox, 2001).

Although sex appears to play an important part in great ape life, patterns in the use of sex in these contexts has not been extensively compared in the great apes. A comparative approach can help to elucidate the evolutionary foundations for sociosexual behaviour to emerge, what functions they may serve, and the contexts they are common in. Here, focusing on context, I systematically compared the tendencies for large populations of sanctuary-living bonobos and chimpanzees to engage in genital contact behaviour during periods of social tension.

To do so, I compared the tendency for genital contact to be performed during two periods of social tension: consolation, defined as unsolicited affiliative approaches from uninvolved bystanders towards distressed conspecifics (*Part 1*) and pre-feeding affiliative interactions (*Part 2*). Sexual behaviour in bonobos has already been shown to be heightened in these contexts (Clay & de Waal, 2015), and chimpanzees appear to also engage in sexual behaviour during these contexts too (Sandel & Reddy, 2021). As sexual behaviours appear to be more significant to bonobo social life (Furuichi, 2011; Hohmann & Fruth, 2000), I tested the hypothesis that bonobos are more sexual and more likely to use genital contact behaviour during periods of social tension than chimpanzees. I predicted that bonobos would be more likely to use genital contacts during consolation and as pre-feeding affiliation than chimpanzees. In addition, as sexual behaviour is associated with social bonding and early developmental relationships in mother-infant pairings (Clay et al., 2022; Hashimoto, 1997), I predicted that kin pairs would be more likely to engage in genital contacts in these contexts than non-kin pairs. Finally, genital contacts occur in all age and sex combinations in the *Pan* apes, and thus with my analyses I also explore within-species trends by comparing likelihood for different ages and sexes to use and receive genital contact in these contexts. I predicted that, in line with previous studies (Clay & de Waal, 2015; Sandel & Reddy, 2021), older individuals would be more likely to use genital contact in these contexts, and that they would occur consistently in both sexes for both species.

7.2 Methods

7.2.1 Study sites and subjects

I directly compared data on sexual behaviour collected at two African great ape sanctuaries: Lola ya Bonobo Sanctuary in the Democratic Republic of the Congo and Chimfunshi Wildlife Orphanage Trust in the Copperbelt Province of Zambia. A collaborator, SK, observed N = 53 bonobos across N = 3 groups (N: B1 = 22; B2 = 18; B3 = 14) at Lola ya Bonobo during July-September 2019 and I observed N = 75 chimpanzees across N = 2 groups (N: C1 = 25; C2 = 50) at Chimfunshi during March-August 2019 (see *Section 3.1* for details about both field sites). For the comparison of sexual behaviour during consolation (*Part 1*), I compared two groups of bonobos (B1, B2), and one group of chimpanzees (C2). For the comparison of sexual behaviour during pre-feeding affiliation (*Part 2*), I compared all five groups. For *Part 2*, four individuals were excluded due to complete absence from observations. The age and sex composition of all groups are provided in *Table 7.1*.

Table 7.1. Social compositions of bonobo and chimpanzee groups from Lola ya Bonobo Sanctuary and Chimfunshi Wildlife Orphanage Trust respectively. Chimpanzees at Chimfunshi include mixed subspecies. *Part 1* reflects all individuals eligible for consolation analyses and *Part 2* reflects all individuals eligible for pre-feeding affiliation analyses.

Part 1: Genital contact during consolation. Table includes all individuals belonging to their respective groups from the start of observations

Species	Group	Total	Infants[a] F / M[b]	Juveniles[a] F / M[b]	Adults[a] F / M[b]
Bonobo (*Pan paniscus*)	1 (B1) 2 (B2)	22 17[c]	0 / 1 0 / 0	5 / 5 7 / 4	7 / 4 1 / 5
Chimpanzee (*Pan troglodytes*)	2 (C2)	50	4 / 2	6 / 7	23 / 8
Total	3	89	4 / 3	18 / 16	31 / 17

Part 2: Genital contact during pre-feeding affiliation. Values reflect individuals that were eligible for at least one experimental session

Species	Group	Total	Infants[a] F / M[b]	Juveniles[a] F / M[b]	Adults[a] F / M[b]
Bonobo (*Pan paniscus*)	1 (B1) 2 (B2) 3 (B3)	22 16[d] 14	0 / 1 0 / 0 0 / 0	5 / 5 7 / 4 4 / 2	7 / 4 1 / 4 4 / 4
Chimpanzee (*Pan troglodytes*)	1 (C1) 2 (C2)	25 47[d]	0 / 2 4 / 1	5 / 1 5 / 7	11/ 6 23 / 7
Total	5	124	4 / 4	26 / 19	46 / 25

[a] *Age in years: Infants = 0–2; Juveniles = 3–11; Adults = 12+ (based on Cronin et al., 2014)*

[b] *F = Number of females; M = Number of males*

[c] *Total excludes Kodoro due to lack of observations*

[d] *Total excludes Eleke (B2), Kodoro (B2), Masya (C2), Mikey (C2), and Mumba (C2) due to absence from all experimental sessions.*

7.2.2 Data collection and coding

I compared the use of genital contact behaviours during two affiliative contact interactions in two socially tense contexts: consolation towards distressed conspecifics (*Part 1*); and pre-feeding affiliation (*Part 2*). I applied the same ethogram to behavioural coding for both contexts. The full ethogram for behaviours coded during consolation and pre-feeding observations can be seen in *Table 7.2*. For both parts, contact affiliation behaviours were categorised as either "genital contact (GC)" (including genital touch, genito-genital contact, and mount) or "non-GC" (including body kiss, embrace, finger/hand in mouth, play, touch). Further details for how consolation and pre-feeding affiliation were coded can be seen in *Section 7.2.2.1* and *Section 7.2.2.2* respectively.

Table 7.2. Ethogram for contact-affiliation behaviours coded in this study as consolation and pre-feeding affiliation behaviour. Based on ethogram in *Appendix A.1,* each behaviour was further categorised as either "genital contact" if it involved genital contact in any form or "non-genital contact" if no genital contact is involved. "Genito-genital contact" and "Rump-rump touch" merged as "GG-contact" in *Figure 7.2* due to similarity in form.

"Genital contact"	**"Non-genital contact"**
GG-contact	**Body kiss
—*Genito-genital rubbing	Contact sit
—**Rump-rump touch	Embrace
Genital touch	**Finger/hand in mouth
Mount	Grasp hand
	Groom
	Hunch-over
	Mouth kiss
	Play
	Touch

** Typically, only seen in bonobos*

*** Typically, only seen in chimpanzees*

7.2.2.1 Part 1: Consolation observations

Providing consolation to distressed parties following a social conflict has been widely documented in both captive and semi-wild groups of bonobos and chimpanzees (Clay & de Waal, 2013; Palagi & Norscia, 2013; Romero et al., 2010; Webb et al., 2017). Post-conflict (PC) observations were systematically collected at both sanctuary sites to gather comparative data on the use of consolation in bonobos and chimpanzees (see *Chapter 4* for a full overview of the data collection process and reliability coding information). To do so, victims of conflicts were followed for 5-minutes. Individuals who spontaneously became distressed without conflict occurring were also followed, known as post-distress periods (PD).

Behavioural coding of PC and PD events was conducted using the video software ELAN (2019; Wittenburg et al., 2006; see *3.3 General coding methods* for full details on the coding schemes and ethograms applied throughout this research). All social interactions the victims engaged in were coded, including who initiated each behaviour and the behaviour type. Consolation was defined as an interaction spontaneously initiated by an uninvolved bystander that included one contact affiliation behaviour (de Waal & Aureli, 1996; see *Appendix A.1* for contact behaviour ethogram). Using focal all-occurrence sampling (Altmann, 1974), $N = 124$ PC/PD events were collected across both species that featured at least one instance of consolation (B1 = 37; B2 = 18; C2 = 69).

7.2.2.2 Part 2: Reassurance observations

To systematically compare pre-feeding reassurance behaviour in sanctuary-living apes, I used an established experimental measure of cofeeding tolerance—the *peanut swing*—to create a controlled arena of social tension (Cronin et al., 2014). Full details on this application of the peanut swing experiment, systematic comparison of pre-feeding affiliative tendencies in bonobos and chimpanzees, and information on reliability coding can be read in *Chapter 5* and *Chapter 6*.

A total of *N* = 60 sessions were completed across all five groups, however I only analysed data from sessions where at least 80% of the group were seen prior to the feeding. This resulted in a total session *N* of B1 = 8; B2 = 10; B3 = 10; C1 = 9; C2 = 8. Across these sessions, *N* = 124 apes (B1 = 18–22; B2 = 14–16; B3 = 12–14; C1 = 19–25; C2 = 41–47) were present for at least one session. I defined a pre-feeding interaction as at least one instance of contact affiliation between two individuals during the 5-minute pre-feeding window. All pre-feeding interactions were coded using ELAN (Wittenburg et al., 2006), including behaviour, behaviour type, and initiator. The coding scheme applied the same contact-affiliation ethogram from *Part 1* for pre-feeding interactions (see *Table 7.2*).

7.3 Part 1: Species variability in the use of consolatory genital contact in *Pan*

7.3.1 Analysis

In *Chapter 4*, I analysed full datasets of PC/PD observations to assess species and individual differences in consolatory tendencies. In order to compare species variation in the use of consolatory genital contact, I compiled reduced datasets, incorporating only events that included at least one consolatory interaction.

For these analyses, I fitted frequentist Generalised Linear Mixed Models with binomial distributions in RStudio (version 1.3.1093; Team, 2020) using the function glmer of the package lme4 (version 1.1–28; Bates et al., 2015). To compare species tendencies to use consolatory genital contacts, I analysed a consoler-level dataframe of *N* = 175 observation rows, where one row constituted an individual who offered consolation during a given PC/PD event (PC *N* = 119; PD *N* = 56). I fitted a binomial distribution GLMM (*Model 1*) to investigate whether genital contacts were more likely to occur in either species during consolation. The response variable for this model was a dichotomous 1/0 variable (1 = genital contact solicited by the consoler; 0 = no genital contact solicited by the consoler).

Alongside species, I included fixed effects for consoler age, consoler sex, victim age, victim sex, and kinship of the consoler-victim pairing. I defined each dyad as 'kin' or 'nonkin' depending on whether they shared a maternal genetic relationship or not, respectively. This therefore included all mother-infant, sibling-sibling, and grandparent-grandchild pairs as 'kin'. Some dyads at Chimfunshi represented a genetic uncle-nephew dynamic and were also included as 'kin'. Age, sex, and social relationship may influence sociosexual and consolatory behaviour in bonobos and chimpanzees (see *Chapter 4*; other examples include: Clay & de Waal, 2013, 2015; Webb et al., 2017; Sandel & Reddy, 2021; Clay et al., 2022). Thus, in *Model 1*, these variables were included as controls. However, to investigate within-species trends for these behaviours, I conducted homologous GLMMs on subsets of the main consoler-level dataframe including just bonobos (*Model 2.1*) and chimpanzees (*Model 2.2*) respectively. In all models, I included the identities of aggressor, consoler, and victim as random effects in a crossed structure. No random slope components were theoretically identifiable for any model in *Part 1*. See *Table 7.3* for the structure of *Model 1* and *Table 7.4* for the structures of *Model 2.1* and *Model 2.2*.

All covariate predictors were z-transformed. Tests of individual fixed effects across models were derived by likelihood ratio tests comparing the full model with null models lacking each fixed effect respectively using the drop1 function of the package lme4 in R (Bates et al., 2015). As in *Chapter 4* and *Chapter 6*, I assessed model stability using a function provided by Roger Mundry[3] which compares estimates obtained from the model based on all data with those obtained from models with the levels of the random effects excluded one at a time. Confidence intervals were derived using the function bootMer of the package lme4 using 1,000 parametric bootstraps and bootstrapping over the random effects too (Bates et al., 2015). As in previous chapters (see *Section 4.3.1*), model complexity was checked by calculating the number of observations per estimated term. Totals exceeding *N* = 10 were deemed sufficient for avoiding overcomplexity.

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[3] Not publicly available. For enquiries, contact Roger Mundry directly.

Table 7.3. *Model 1*—consoler-level model structure for binomial analysis of species differences in whether genital contact is used during a consolatory interaction. Full model compared to null model lacking species using the drop1 function in lme4. Abbreviation: GC = genital contact.

***Model 1:* Full model testing species differences**

Terms	Variable	Levels
Response variable	Occurrence of GC	0 = no; 1 = yes
Fixed effects	Species Consoler age Consoler sex Victim age Victim sex Kinship[a]	Bonobo[b]; Chimpanzee *Continuous* Female[b]; Male *Continuous* Female[b]; Male Kin[b]; Nonkin
Random effects	Aggressor ID Consoler ID Victim ID	*Qualitative* *Qualitative* *Qualitative*

[a] *Whether consoler-victim pair shared a maternal kin relationship*

[b] *Reference group*

Table 7.4. *Models 2.1* and *2.2*—consoler-level model structure for binomial analysis of within-species trends in whether genital contact is used during a consolatory interaction. Identical model structure performed on subsets of species-specific data: *Model 2.1* performed on bonobo-only data; *Model 2.2* performed on chimpanzee-only data. Full models compared to respective null models lacking each fixed effect respectively through the drop1 function in lme4. Abbreviation: GC = genital contact.

***Model 2.1 (bonobo-only) and 2.2 (chimpanzee-only):* Full model testing within-species trends**

Terms	Variable	Levels
Response variable	Occurrence of GC	0 = no; 1 = yes
Fixed effects	Consoler age Consoler sex Victim age Victim sex Kinship[a]	*Continuous* Female[b]; Male *Continuous* Female[b]; Male Kin[b]; Nonkin
Random effects	Aggressor ID Consoler ID Victim ID	*Qualitative* *Qualitative* *Qualitative*

[a] *Whether consoler-victim pair shared a maternal kin relationship*

[b] *Reference group*

7.3.2 Results

7.3.2.1 Species variability

Model 1 compared N = 175 consolatory interactions including N = 56 consolers, N = 50 victims, and N = 37 aggressors. Genital contacts occurred at least once in 28 of the 55 bonobo events involving consolation (50.9%) and 23 of the 69 chimpanzee events involving consolation (33.3%). Across both species, consolers offered an average of M = 1.54 contact behaviours (SD = 1.04, *range* = 1–6) during a consolatory interaction (bonobos: M = 1.74, SD = 1.27, *range* = 1–6; chimpanzees: M = 1.41, SD = 0.84, *range* = 1–6). Of these, an average of M = 0.42 (SD = 0.62, *range* = 0–3) were categorised as genital contact behaviours (bonobos: M = 0.58, SD = 0.63, *range* = 0–3; chimpanzees: M = 0.32, SD = 0.59, *range* = 0–3).

Model 1 revealed that bonobos were more likely to use genital contact during consolation than chimpanzees (estimate ± SE = 1.480 ± 0.595, $\chi2$ = 7.186, P = .007; see *Figure 7.1*). In addition, non-kin consoler-victim pairs were more likely to use genital contact during consolation than kin pairs (estimate ± SE = 2.381 ± 0.648, $\chi2$ = 20.191, $P < .001$; see *Figure 7.1*). There were no significant effects for consoler age, consoler sex, victim age, or victim sex (see *Table 7.5* for estimates and results for respective full-null LRTs). Model stability checks revealed these effects were robust (see *Table 7.5*). Checks of variance inflation factors revealed maximum collinearity between the fixed effects of 1.79, indicating no problem with collinearity. *Model 1* featured N = 17.5 observations per estimated term, indicating, alongside stability checks (see *Table 7.5*), that model overcomplexity was not a significant issue. Statistical output for *Model 1* can be seen in *Table 7.5*.

Table 7.5. Results for *Model 1*—did a consoler initiate genital contact during a consolatory interaction? Estimates and standard errors, together with confidence intervals, results of likelihood ratio tests, and the range of estimates obtained when dropping levels of random effects one at a time. Significant effects at the $P < .05$ level are in ***italicised bold***. Abbreviations: C = Consoler; V = Victim.

***Model 1*: Full model testing species differences**

Term	Estimate	SE	CI_{95}	$\chi2$	z	*P*-value	Min	Max
Fixed effects								
(Intercept)	***-1.518***	***0.661***	***-3.662 to -0.321***		***-2.295***	***.022***	***-2.493***	***-1.130***
Species^a	***-1.480***	***0.595***	***-2.776 to -0.462***	***7.186***	***-2.487***	***.007***	***-1.878***	***-1.058***
Consoler Age^b	0.137	0.216	-0.320 to 0.608	0.398	0.635	.528	0.005	0.245
Consoler Sex^c	0.090	0.438	-0.908 to 0.985	0.043	0.206	.836	-0.332	0.864
Victim Age^b	-0.036	0.253	-0.608 to 0.501	0.020	-0.141	.888	-0.225	0.111
Victim Sex^c	-0.742	0.483	-1.788 to 0.217	2.533	-1.535	.111	-1.507	-0.274
C-V Kinship^d	***2.381***	***0.648***	***1.374 to 4.496***	***20.191***	***3.673***	***< .001***	***1.990***	***3.164***
Random effects								
Aggressor ID	0.000						0.000	0.206
Consoler ID	0.553						0.280	0.731
Victim ID	0.000						0.000	0.406

^{a} *Reference category = Bonobo*

^{b} *Z-transformed to a mean of 0 and a standard deviation of 1*

^{c} *Reference category = Female*

^{d} *Reference category = Kin*

7.3.2.2 Within-species trends

In bonobos, *Model 2.1* compared $N = 69$ consolatory interactions including $N = 25$ consolers, $N = 24$ victims, and $N = 16$ aggressors. This revealed that only kinship was a significant predictor, where non-kin consoler-victim pairs were more likely to use genital contact during consolation than kin pairs (estimate ± SE = 2.928 ± 1.007, $\chi2 = 12.542$, $P < .001$; see *Figure 7.1*). Model stability checks revealed this effect was not robust (min = 2.518, max = 23.877), which upon inspection was caused when the stability function dropped "no aggressor" under the aggressor identity random effect, which created a reduced dataframe with only $N = 22$ observations. In addition, this model featured $N = 7.67$ observations per estimated term. These checks indicate model overcomplexity, and thus results should be interpreted with caution. Consoler age, consoler sex, victim age, and victim sex did not significantly predict the occurrence of genital contact during bonobo consolatory interactions (see *Table 7.6* for estimates and results of respective full-null LRTs). Checks of variance inflation factors revealed maximum collinearity between the fixed effects of 1.31, indicating no problem with collinearity. Statistical output can be seen in *Table 7.6*.

In chimpanzees, *Model 2.2* compared *N* = 106 consolatory interactions including *N* = 31 consolers, *N* = 26 victims, and *N* = 22 aggressors. This revealed that kinship too was a significant predictor, where non-kin consoler-victim pairs were more likely to use genital contact during consolation than kin pairs (estimate ± SE = 2.149 ± 0.811, $\chi 2$ = 9.955, *P* = .002; see *Figure 7.1*). There was also a significant effect of victim sex, where consolation towards female chimpanzees was more likely to feature genital contact than consolation towards male chimpanzees (estimate ± SE = -2.102 ± 1.157, $\chi 2$ = 4.666, *P* = .031; see *Figure 7.2*), regardless of victim sex. Model stability checks revealed that these effects were not robust (victim sex: min = -20.078, max = -1.019; kinship: min = 1.625, max = 20.130), which upon inspection was caused when the stability function dropped individuals with the most observations in each random effect. Whilst this model featured *N* = 11.78 observations per estimated term, the stability checks indicate model overcomplexity, and thus results should be interpreted with caution. Consoler age, consoler sex, and victim age did not significantly predict the occurrence of genital contact during consolatory interactions in chimpanzees (see *Table 7.6* for estimates and results of respective full-null LRTs). Checks of variance inflation factors revealed maximum collinearity between the fixed effects of 1.24, indicating no problem with collinearity. Statistical output for *Model 2.2* can be seen in *Table 7.6*.

Table 7.6. Results for *Model 2.1* and *2.2*—within-species trends for whether consoler initiated genital contact during a consolatory interaction. Estimates and standard errors, together with confidence intervals, results of likelihood ratio tests, and the range of estimates obtained when dropping levels of random effects one at a time. Significant effects at the $P < .05$ level are in ***italicised bold***. Abbreviations C = Consoler; V = Victim.

***Model 2.1*: Full model testing within-species trends in bonobos**

Term	Estimate	SE	CI_{95}	$\chi2$	z	*P*-value	Min	Max
Fixed effects								
(Intercept)	***-2.360***	***0.981***	***-20.094 to -0.880***		***-2.407***	***.016***	***-22.837***	***-1.860***
Consoler Age^{a}	0.456	0.359	-0.218 to 1.970	1.620	1.269	.203	0.137	1.841
Consoler Sex^{b}	-0.235	0.615	-1.899 to 1.396	0.145	-0.382	.703	-0.782	0.659
Victim Age^{a}	-0.541	0.347	-2.496 to 0.051	2.878	-1.560	.090	-1.087	-0.372
Victim Sex^{b}	0.159	0.568	-1.196 to 1.955	0.078	0.280	.781	-0.745	0.558
C-V Kinship^{c}	***2.928***	***1.007***	***1.562 to 20.879***	***12.542***	***2.909***	***< .001***	***2.518***	***23.877***
Random effects								
Aggressor ID	0.000						0.000	0.000
Consoler ID	0.000						0.000	0.649
Victim ID	0.000						0.000	0.451

***Model 2.2*: Full model testing within-species trends in chimpanzees**

Term	Estimate	SE	CI_{95}	$\chi2$	z	*P*-value	Min	Max
Fixed effects								
(Intercept)	***-2.878***	***0.865***	***-18.852 to -1.681***		***-3.328***	***.001***	***-20.928***	***-2.261***
Consoler Age^{a}	0.040	0.278	-0.667 to 0.654	0.021	0.145	.885	-0.274	0.223
Consoler Sex^{b}	0.426	0.538	-0.716 to 1.754	0.634	0.790	.426	-0.276	0.898
Victim Age^{a}	0.132	0.276	-0.406 to 0.813	0.229	0.477	.632	0.004	0.433
Victim Sex^{b}	***-2.102***	***1.157***	***-18.268 to -0.328***	***4.666***	***-1.817***	***.031***	***-20.078***	***-1.019***
C-V Kinship^{c}	***2.149***	***0.811***	***0.942 to 18.131***	***9.955***	***2.651***	***.002***	***1.625***	***20.130***
Random effects								
Aggressor ID	0.000						0.000	0.268
Consoler ID	0.000						0.000	0.501
Victim ID	0.594						0.000	1.037

[a] *Z-transformed to a mean of 0 and a standard deviation of 1*

[b] *Reference category = Female*

[c] *Reference category = Kin*

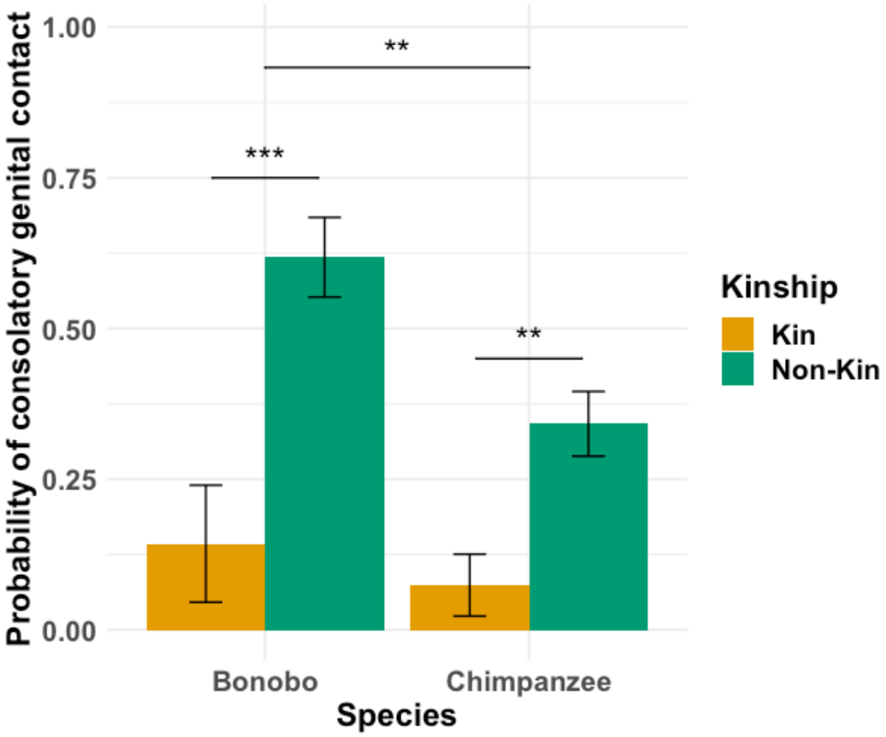

Figure 7.1. Barplot showing significant effects of kinship and species regarding use of genital contact during consolatory interactions. Results obtained from *Model 1*, *Model 2.1*, and *Model 2.2*. Whiskers show one standard error above and below mean. Asterisks show significant effects at: ** = *P* < .01; *** = *P* < .001.

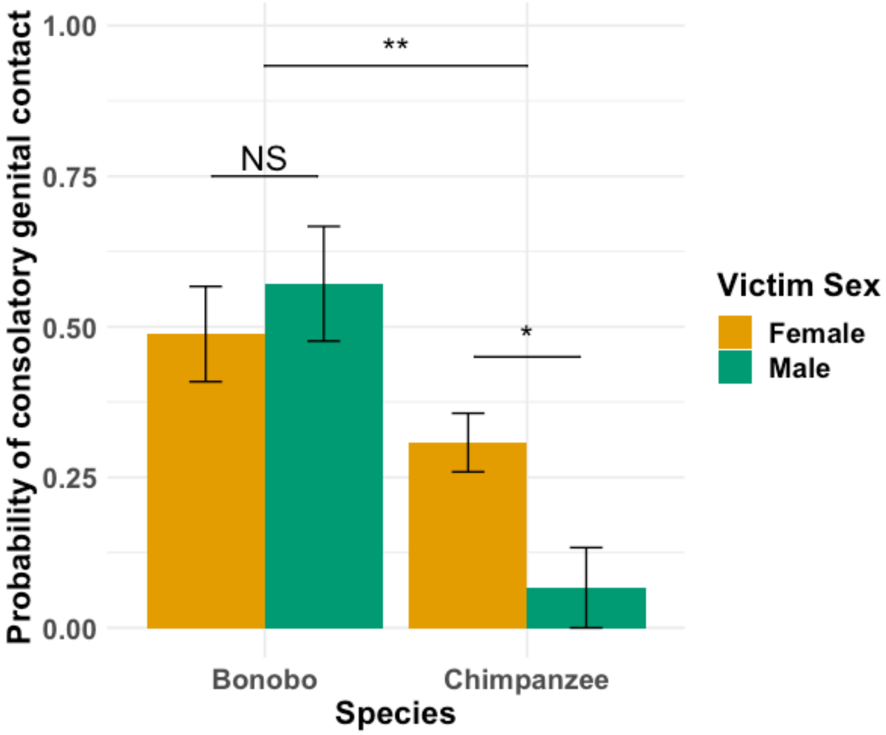

Figure 7.2. Barplot showing effects of victim sex and species regarding use of genital contact during consolatory interactions. Results obtained from *Model 1*, *Model 2.1*, and *Model 2.2*. Whiskers show one standard error above and below mean. Asterisks show significant effects at: * = *P* < .05; ** = *P* < .01; NS = not significant.

7.4 Part 2: Species variability in use of genital contact as a form of pre-feeding affiliation in *Pan*

7.4.1 Analysis

In *Chapter 5*, I analysed full datasets of pre-feeding affiliative interactions to assess species and group differences in general contact affiliation tendencies during a period of social tension. In order to compare species and within-species variability in the use of genital contacts during pre-feeding affiliation, I compiled reduced datasets from these, incorporating only dyads within events that engaged in at least one contact affiliative behaviour. I defined a pre-feeding interaction as the onset of a dyadic affiliative interaction involving at least one form of contact affiliation during the 5-minute pre-feeding window.

For these analyses, I used the same approach as *Part 1*, fitting frequentist GLMMs with binomial distributions in RStudio (version 1.3.1093; RStudio Team, 2020) using the function glmer of the package lme4 (version 1.1–28; Bates et al., 2015). To compare bonobos and chimpanzees in their tendencies to engage in genital contacts during a pre-feeding period, I analysed an interaction-level dataframe of $N = 864$ observation rows, where one row constituted a unique initiator-recipient dyad who engaged in at least one form of contact affiliation prior to a given feeding ($N = 233$ bonobo dyads and $N = 631$ chimpanzee dyads; B1 = 99; B2 = 87; B3 = 47; C1 = 168; C2 = 463).

Firstly, I fitted a binomial distribution GLMM (*Model 3*) to investigate whether genital contacts occur more in either species during pre-feeding interactions. The response variable for this model was a dichotomous 1/0 variable (1 = genital contact was solicited by the initiator; 0 = genital contact was not solicited by the initiator). Similar to *Part 1*, I included control fixed effects of initiator age, initiator sex, recipient age, recipient sex, and kinship, as these variables can influence sociosexual and pre-feeding affiliation behaviour in bonobos and chimpanzees (see *Chapter 5*; other examples include: Clay & de Waal, 2013, 2015; Sandel & Reddy, 2021; Clay et al., 2022). I included random effects of group, initiator identity, recipient identity, and session number, as well as all theoretically identifiable random slope components (initiator sex within group, recipient age within initiator, and initiator sex, kinship, recipient age, and recipient sex within session number). See *Table 7.7* for full structure of *Model 3*. As in previous chapters, I proceeded with a crossed random effects structure for these models due to managed migrations between communities leading to individual identities not being fixed to group identities.

To investigate within-species trends for these behaviours, I conducted homologous GLMMs on subsets of the main interaction-level dataframe including just bonobos (*Model 4.1*) and chimpanzees (*Model 4.2*) respectively. In these species-specific models, I included the identities of the initiator, recipient, and session number as random effects. Group was moved from the random effects structure to the fixed effects structure and species was dropped as a variable entirely. All theoretically identifiable random slope components were included in these models (*Model 4.1*: initiator sex, kinship, and recipient sex within session number; *Model 4.2*: recipient age within initiator, initiator sex within recipient, and kinship and recipient age within session number). All factor variables were dummy coded and centred prior to their inclusion as random slopes. See *Table 7.8* for full structures of *Model 4.1* and *Model 4.2*. For *Part 2*, I applied the same frequentist framework as *Part 1*, using LRTs to derive full-null comparisons for each fixed effect, as well as the same process for assessing model stabilities and confidence intervals.

Table 7.7. *Model 3.1*—interaction-level model structure for binomial analysis of species differences in whether genital contact is used during a pre-feeding affiliative contact interaction. Full model compared to null model lacking species using the drop1 function in lme4. Abbreviation: GC = genital contact.

***Model 3.1:* Full model testing species differences**

Terms	Variable	Levels
Response variable	Occurrence of GC	0 = no; 1 = yes
Fixed effects	Species Initiator age Initiator sex Recipient age Recipient sex Kinship[a]	Bonobo[b]; Chimpanzee *Continuous* Female[b]; Male *Continuous* Female[b]; Male Kin[b]; Nonkin
Random effects	Group[c] Initiator ID[d] Recipient ID Session[e]	*Qualitative* *Qualitative* *Qualitative* 1-13

[a] *Whether initiator-recipient pair shared a maternal kin relationship*

[b] *Reference group*

[c] *Includes random slope of initiator sex*

[d] *Includes random slope of recipient age*

[e] *Includes random slopes of initiator sex, kinship, recipient age, and recipient sex*

Table 7.8. *Model 4.1 and 4.2*—interaction-level model structure for binomial analysis of within-species trends in whether genital contact is used during a pre-feeding affiliative contact interaction. Identical model structure performed on subsets of species-specific data: *Model 4.1* performed on bonobo-only data; *Model 4.2* performed on chimpanzee-only data. Full models compared to respective null models lacking each fixed effect respectively through the drop1 function in lme4. Abbreviation: GC = genital contact.

***Model 4.1 and 4.2:* Full model testing within-species differences**

Terms	Variable	Levels
Response variable	Occurrence of GC	0 = no; 1 = yes
Fixed effects	Group	*Model 4.1*: B1^b; B2; B3 *Model 4.2*: C1^b; C2
	Initiator age	*Continuous*
	Initiator sex	Female^b; Male
	Victim age	*Continuous*
	Victim sex	Female^b; Male
	Kinship^a	Kin^b; Nonkin
Random effects	Initiator ID^c	*Qualitative*
	Recipient ID^d	*Qualitative*
	Session^c	1-13

[a] *Whether initiator-recipient pair shared a maternal kin relationship*

[b] *Reference group*

[c] *Model 4.2 includes random slope of recipient age*

[d] *Model 4.2 includes random slope of initiator sex*

[e] *Model 4.1 includes random slope of initiator sex, kinship, and recipient sex; Model 4.2 includes random slope of kinship and recipient age*

7.4.2 Results

7.4.2.1 Species variability

Model 3 compared N = 864 pre-feeding affiliative interactions with at least one contact behaviour, across N = 5 groups including N = 106 initiators, N = 109 recipients, and up to N = 13 sessions. Genital contacts occurred in 73 of the 233 bonobo pre-feeding interactions involving contact (31.3%) and 168 of the 631 chimpanzee pre-feeding interactions involving contact (26.6%). Across both species, initiators offered an average of M = 1.85 contact behaviours (SD = 1.56, *range* = 1–13) during a pre-feeding interaction (bonobos: M = 2.09, SD = 1.91, *range* = 1–12; chimpanzees: M = 1.77, SD = 1.40, *range* = 1–13). Of these, an average of M = 0.34 (SD = 0.66, *range* = 0–5) were categorised as genital contact behaviours (bonobos: M = 0.46, SD = 0.90, *range* = 0–5; chimpanzees: M = 0.30, SD = 0.54, *range* = 0–4).

Model 3 revealed that species did not significantly predict genital contact occurring at least once during a pre-feeding affiliative interaction (estimate ± SE = -0.501 ± 0.372, χ2 = 1.797, *P* = .180; see *Figure 7.3*). See *Table 7.9* for full statistical output from *Model 3*. *Model 3*, and both species-specific models, revealed that recipient sex was significant whereby females were more likely than males in each species to receive a genital contact during a pre-feeding interaction (estimate ± SE = -1.520 ± 0.331, χ2 = 16.170, *P* < .001; see *Figure 7.3* and *Table 7.10* for estimates for each species). In all models, thus for both species, initiator sex was not a significant predictor (estimate ± SE = -0.369 ± 0.585, χ2 = 0.393, *P* = .531; see *Table 7.10* for species-specific estimates). In addition, there was a significant effect of kinship where non-kin initiator-recipient pairs were more likely to use genital contact during pre-feeding interactions than kin pairs (estimate ± SE = 1.632 ± 0.542, χ2 = 8.880, *P* = .003; see *Figure 7.4*). These effects were seen in each species-specific model (see *Table 7.10*).

7.4.2.2 Within-species trends

Model 4.1 compared *N* = 233 pre-feeding affiliative interactions in bonobos with at least one contact behaviour with *N* = 44 initiators, *N* = 41 recipients, and up to *N* = 13 sessions. *Model 4.2* compared *N* = 631 pre-feeding affiliative interactions in chimpanzees with at least one contact behaviour with *N* = 65 initiators, *N* = 65 recipients, and up to *N* = 11 sessions.

In both *Model 4.1* and *Model 4.2*, group was not a significant predictor of genital contact (bonobos: χ2 = 0.579, *P* = .749; chimpanzees: χ2 = 0.181, *P* = .670; estimates are presented in *Table 7.10*). Across both species in *Model 3*, older individuals were more likely to use at least one genital contact (estimate ± SE = 0.442 ± 0.148, χ2 = 9.207, *P* = .002). However, *Models 4.1* and *4.2* revealed that the effect for initiator age was only significant for chimpanzees (bonobos: estimate ± SE = 0.461 ± 0.329, χ2 = 1.790, *P* = .181; chimpanzees: estimate ± SE = -0.404 ± 0.156, χ2 = 7.115, *P* = .008; see *Figure 7.5*).

Model stability checks revealed that estimates for all fixed and random effects for *Model 3*, *Model 4.1* and *Model 4.2* were robust (see *Table 7.9–7.10*). Checks of variance inflation factors indicated no problem with collinearity (*Model 3* = 1.30; *Model 4.1* = 1.35; *Model 4.2* = 1.34). Checks of the number of observations per estimated term revealed *N* = 50.82 for *Model 3*, *N* = 16.64 for *Model 4.1*, and *N* = 45.07 for *Model 4.2*. These checks indicate, alongside stability checks, that there was no issue with model overcomplexity. Full statistical output for *Model 3* can be seen in *Table 7.9* and *Model 4.1* and *4.2* in *Table 7.10*.

Table 7.9. Results for *Model 3*—species variability in use of genital contact as a form of pre-feeding affiliation in *Pan*. Estimates and standard errors, together with confidence intervals, results of likelihood ratio tests, and the range of estimates obtained when dropping levels of random effects one at a time. Significant effects at the $P < .05$ level are in ***italicised bold***. Abbreviations I = Initiator; R = Recipient.

***Model* 3: Full model testing species differences**

Term	Estimate	SE	CI$_{95}$	$\chi 2$	z	*P*-value	Min	Max
Fixed effects								
(Intercept)	***-1.590***	***0.610***	***-3.026 to -0.541***		***-2.608***	***.009***	***-1.929***	***-1.026***
Species^{a}	-0.501	0.372	-1.253 to 0.195	1.797	-1.345	.180	-0.769	-0.348
Initiator Age^{b}	***0.442***	***0.148***	***0.125 to 0.771***	***9.207***	***2.987***	***.002***	***0.385***	***0.525***
Initiator Sex^{c}	-0.369	0.585	-1.417 to 0.823	0.393	-0.630	.531	-0.682	0.246
Recipient Age^{b}	0.250	0.177	-0.114 to 0.617	1.894	1.418	.169	0.007	0.333
Recipient Sex^{c}	***-1.520***	***0.331***	***-2.193 to -0.899***	***16.170***	***-4.597***	***< .001***	***-1.742***	***-1.319***
I-R Kinship^{d}	***1.632***	***0.542***	***0.675 to 3.046***	***8.880***	***3.011***	***.003***	***1.378***	***1.915***
Random effects								
Group	0.000						0.000	0.000
Initiator ID	0.615						0.491	0.751
Recipient ID	0.826						0.683	0.941
Session	0.000						0.000	0.000

[a] *Reference category = Bonobo*

[b] *Z-transformed to a mean of 0 and a standard deviation of 1*

[c] *Reference category = Female*

[d] *Reference category = Kin*

Table 7.10. Results for *Model 4.1* and *4.2*—within-species trends in the likelihood for genital contact to occur in bonobo (*4.1*) and chimpanzee (*4.2*) pre-feeding affiliative contact interactions respectively? Estimates and standard errors, together with confidence intervals, results of likelihood ratio tests, and the range of estimates obtained when dropping levels of random effects one at a time. Significant effects at the $P < .05$ level are in ***italicised bold***. Abbreviations I = Initiator; R = Recipient.

***Model 4.1*: Full model testing within-species trends in bonobos**

Term	Estimate	SE	CI_{95}	$\chi 2$	z	*P*-value	Min	Max
Fixed effects								
(Intercept)	-2.222	1.488	-12.439 to -0.131		-1.493	.135	-3.992	-1.170
Group[a]				0.579		.749		
B2	-0.685	0.976	-2.731 to 1.216		-0.702		-1.205	-0.304
B3	-0.027	1.073	-2.284 to 2.271		-0.025		-0.848	0.850
Initiator Age[b]	0.461	0.329	-0.161 to 1.239	1.790	1.404	.181	0.290	0.719
Initiator Sex[c]	-1.065	0.917	-3.427 to 0.776	1.290	-1.161	.256	-1.583	-0.635
Recipient Age[b]	-0.172	0.353	-0.946 to 0.421	0.246	-0.486	.620	-0.387	0.100
Recipient Sex[c]	***-1.975***	***0.899***	***-4.241 to -0.511***	***5.216***	***-2.197***	***.022***	***-2.744***	***-1.139***
I-R Kinship[d]	***2.227***	***1.386***	***0.452 to 11.818***	***5.274***	***1.607***	***.022***	***1.293***	***3.837***
Random effects								
Initiator ID	0.761						0.900	1.842
Recipient ID	1.388						0.843	1.872
Session	1.960						0.000	0.726

***Model 4.2*: Full model testing within-species trends in chimpanzees**

Term	Estimate	SE	CI_{95}	$\chi 2$	z	*P*-value	Min	Max
Fixed effects								
(Intercept)	***-2.202***	***0.605***	***-3.596 to -1.253***		***-3.636***	***< .001***	***-2.537***	***-1.901***
Group[e]				0.181		.670		
C2	0.173	0.408	-0.629 to 1.063		0.423		-0.127	0.425
Initiator Age[b]	***0.404***	***0.156***	***0.090 to 0.728***	***7.115***	***2.587***	***.008***	***0.289***	***0.538***
Initiator Sex[c]	0.259	0.315	-0.408 to 0.862	0.673	0.821	.412	0.035	0.436
Recipient Age[b]	0.373	0.198	0.010 to 0.770	3.370	1.878	.066	0.264	0.475
Recipient Sex[c]	***-1.436***	***0.375***	***-2.249 to -0.774***	***12.610***	***-3.830***	***< .001***	***-1.606***	***-1.245***
I-R Kinship[d]	***1.486***	***0.556***	***0.552 to 2.778***	***7.190***	***2.672***	***.007***	***1.204***	***1.796***
Random effects								
Initiator ID	0.477						0.306	0.585
Recipient ID	0.752						0.557	0.841
Session	0.000						0.000	0.000

[a] *Reference category = B1*

[b] *Z-transformed to a mean of 0 and a standard deviation of 1*

[c] *Reference category = Female*

[d] *Reference category = Kin*

[e] *Reference category = C1*

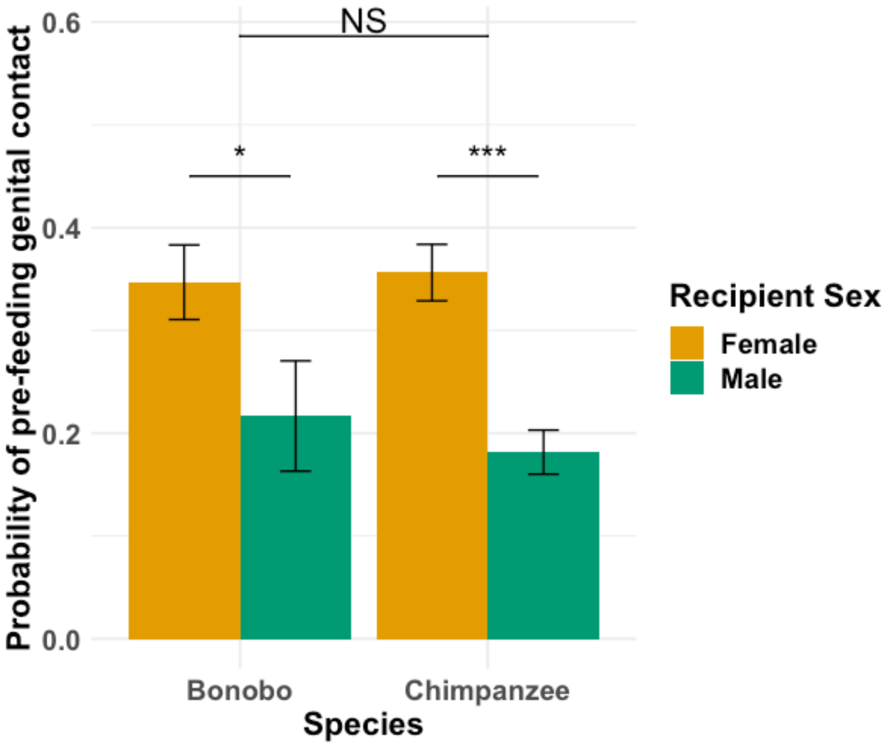

Figure 7.3. Barplot showing significant effects of recipient sex for each species in use of genital contact during pre-feeding interactions. Results from *Models 3*, *Model 4.1*, and *Model 4.2*. Whiskers show one standard error above and below mean. Asterisks show significant effects at: * = *P* < .05; *** = *P* < .001; NS = not significant.

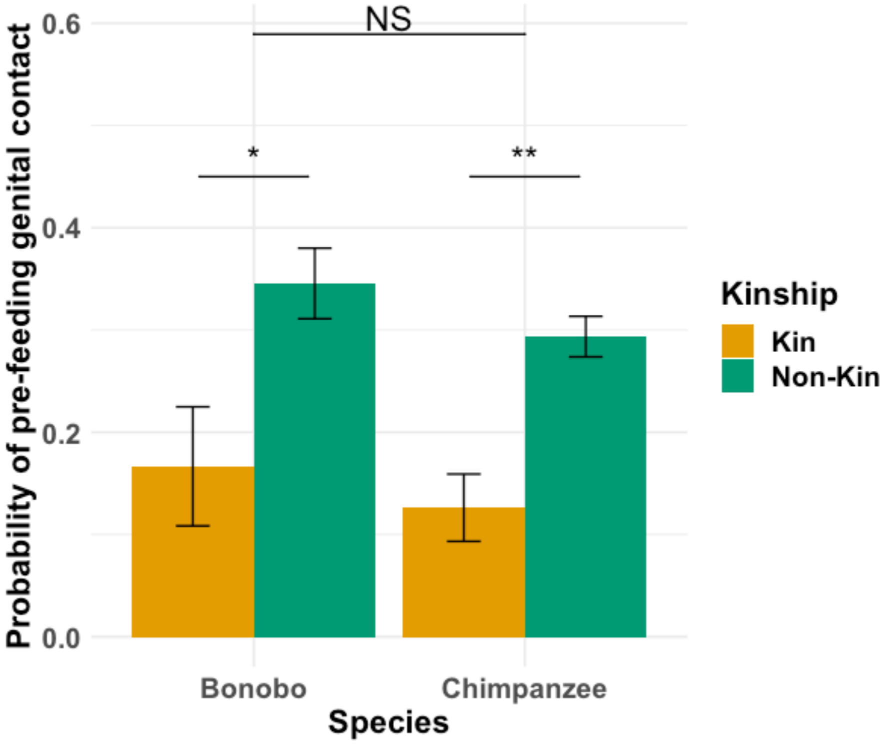

Figure 7.4. Barplot showing significant effects of kinship for each species in use of genital contact during pre-feeding interactions. Results from *Models 3*, *Model 4.1*, and *Model 4.2*. Whiskers show one standard error above and below mean. Asterisks show significant effects at: * = *P* < .05; ** = *P* < .01; NS = not significant.

7.5 Discussion

The *Pan* apes perform a wide repertoire of affiliative contact behaviours that are purported to have reassuring functions when used in specific contexts, such as post-conflict consolation (Clay & de Waal, 2013; Fraser et al., 2008). This repertoire includes a rich subset of sociosexual contacts including genital touching, genito-genital contact, and mounting (with and without intromission) that occur in various contexts, notably periods of social tension (Clay & de Waal, 2015; Goodall et al., 1979; Hohmann & Fruth, 2000; Sandel & Reddy, 2021). Sociosexual behaviour is thought to be particularly pronounced in bonobos compared to other primates, including chimpanzees (Gruber & Clay, 2016; Woods & Hare, 2011) and is linked with cooperation, closeness during feeding, and even food sharing (Moscovice et al., 2017; Moscovice et al., 2019). However, genital contacts between individuals of all age and sex combinations can be common in both *Pan* apes (de Waal, 1990; Sandel & Reddy, 2021).

Here, I demonstrate that sanctuary-living populations of the two species use genital contacts during two socially tense contexts: 1) naturalistically through observations of post-conflict consolation; and 2) prior to competition during a controlled feeding experiment. A direct comparison of bonobo and chimpanzee genital contact behaviour during these social tension contexts revealed both between- and within-species differences and overlaps. As predicted, bonobos were more likely to perform genital contacts during consolatory interactions than chimpanzees. However, during a competitive period prior to feeding, the rate of genital contacts during affiliative interactions were comparable between bonobos and chimpanzees. Bonobos have been purported as the most sexual ape (de Waal & Lanting, 1997; Stanford, 2000), however these findings indicate a considerable overlap between the two species in the importance of genital contact behaviour during periods of social tension (de Waal, 1990; Sandel & Reddy, 2021).

Even in the case of consolation, whilst bonobos used genital contacts at a higher tendency, rates were still high in chimpanzees, indicating a shared role in the use of sexual behaviour and empathy in *Pan* (Clay & de Waal., 2015). This parallels previous studies of chimpanzee consolation and other post-conflict interactions, where genital touching and mounting is typically included in behavioural ethograms and recorded in these contexts (e.g., de Waal & van Roosemalen, 1979; Romero et al., 2010; Wittig & Boesch, 2003). Sexual behaviour is purported to function to alleviate social tension and reduce stress in bonobos (Clay & de Waal, 2015; Hohmann & Fruth, 2000). My results support this view and also indicate that genital contacts may share a similar function in chimpanzees (Sandel & Reddy, 2021). Chimpanzees appear to have a wider overall repertoire of reassurance behaviours than bonobos, as they are known to engage in several vulnerable mouth-to-body behaviours—including body kissing and finger/hand in mouth (de Waal & van

Roosemalen, 1979; de Waal, 1989b; Nishida et al., 1999; Wittig & Boesch, 2003; see *Chapter 5*)—that have not been reported in bonobos.

Regardless of the frequency of mouth-to-body behaviours during these contexts, genital contacts still constituted a sizeable portion of chimpanzee consolatory and pre-feeding affiliative behaviour. Engaging in vulnerable behaviour in risky contexts is purported to promote trust between possible competitors and test social bonds (East et al., 1993; Palmer & Pomianek, 2007; Perry, 2011). The methods employed in this study mean it would be difficult to ascertain stress-reducing or social bond testing functions in these cases, particularly in the pre-feeding context as we recorded affiliative contacts for every dyadic interaction in large populations. However, both mouth-to-body and genital contact behaviour place one at homologous risk when engaging during a period where risk of aggression is elevated, especially for chimpanzees (de Waal, 1986; Wilson et al., 2004; Wilson et al., 2014).

Thus, genital contacts may constitute the dominant form of reassurance in bonobos (Furuichi, 2011; Hohmann & Fruth, 2000), whereas in chimpanzees they may represent one of several possible forms of reassurance (Arnold & Whiten, 2001; Goodall et al., 1979; Herbinger et al., 2009; Romero et al., 2011; Sandel & Reddy, 2021). My findings indicate that tendency to use genital contacts during social tension may instead depend on context in chimpanzees. For example, conflict appears to be riskier in chimpanzees than bonobos (de Waal, 1986; Wilson et al., 2004; Wilson et al., 2014) and during post-conflict periods, redirected or renewed aggression can be common (Wittig & Boesch, 2003; Romero & de Waal, 2010). Other affiliative contacts—such as touching, embracing, or mouth-to-body behaviours—may be preferred during post-conflict contexts in chimpanzees to more clearly communicate benign intentions. In contrast, during a pre-feeding competitive context, whilst tension may be high, individuals may have more trust to initiate genital contacts if conflict has not yet occurred. Deciphering communicative intentions in great apes is difficult, yet a direct investigation into comparing forms and outcomes of consolation behaviours could reveal whether use of a specific contact is dependent on variables beyond the demography of the parties.

Prevalent already in infancy, sociosexual behaviour is significant to the social ontogeny of both sexes in bonobos and chimpanzees (Clay & de Waal, 2015; de Waal, 1990; Furuichi et al., 2014; Sandel & Reddy, 2021; Savage-Rumbaugh & Malick, 1977). Both *Pan* apes engage in genital contacts across a variety of contexts with their peers, including play (Enomoto, 1990; Savage & Malick, 1977), but predominantly during social tension and feeding (Clay et al., 2022; Clay & de Waal, 2015; de Waal, 1990; Hohmann & Fruth, 2000; Moscovice et al., 2019). Bonobo sexuality typically emerges in infants during interactions with their mothers when either party are distressed or anxious (Clay et al., 2022; Hashimoto, 1997). In line with previous findings, genital contacts were offered by and received by individuals of all ages and sexes in both species. Neither the age of consolers nor of victims predicted the use of genital contact during consolatory interactions in bonobos or in chimpanzees. During the pre-feeding period, there were indications that older apes are more likely to initiate genital contacts than younger apes, however, due to limited data, this trend was only clear in chimpanzees. In addition, whilst genital contacts did occur between kin pairs, they were more likely during interactions between non-kin.

As previously suggested (Moscovice et al, 2017), the use of sociosexual behaviour during pre-feeding periods may function to foster greater social closeness during feeding for both species. Due to limited data and overcomplexity, it was not possible to also assess how dyadic social relationships affect tendency to use genital contacts in these tense contexts. However, in my study, genital contacts were performed across all groups of sanctuary-living bonobos and chimpanzees, occurring across groups, ages, and sexes at comparable rates (de Waal, 1990; Sandel & Reddy, 2021). It was also notable that genital contacts were more likely to occur between non-kin pairs than kin pairs, suggesting different behavioural strategies for these periods contingent on social relationship. It may be the case that genital contacts are particularly common between non-kin close social partners to reinforce social bonds and foster closeness during feeding, akin to Moscovice et al. (2017) for bonobos. Demuru et al. (2022) found that females that were less socially bonded were more likely to synchronise regarding their maximum sexual swelling. As synchronisation is also associated with increased genito-genital rubbing in bonobos (Demuru et al., 2022), my findings support the notion that sexual contacts may be used to strengthen social bonds in certain contexts.

Given the overlap between the two species in their uses of consolation (see *Chapter 4*), pre-feeding affiliation (see *Chapter 5*), and sexual behaviour, chimpanzees may also share a similar function of sex in these contexts. Future research could directly target assessing this function. Collecting more observations and directly assessing grooming and play relationship association networks could reveal the importance of sex for fortifying alliances beyond kin relationships during competitive or tense periods that may threaten group cohesiveness and stability (de Waal, 1986). In addition, studying the directionality and form of sexual encounters may reveal group-specific trends that parallel with their respective social climates.

Overall, these findings support the notion that beyond a pure reproductive function, our closest living relatives possess rich socio-sexual lives, whereby affiliative genital contacts appear to contribute to the management of social relationships and periods of social tension (Heiman et al., 2011; Hohmann & Fruth, 2000; Sandel & Reddy, 2021). The reputation that bonobos have for being the species more focused on sociosexual interactions is only partly supported by these findings given the occurrence of genital contacts in both species in comparable contexts. In fact, the importance of sociosexuality in chimpanzee social life generally should not be understated, particularly in relation to social tension management. Further comparative research into within-species trends across ages and sexes will shed more light on the overall significance of sexual behaviour in the evolutionary history of our closest living relatives.

Chapter 8: Fellatio among male sanctuary-living chimpanzees during a period of social tension

The following chapter was published online as an anecdotal report in a Special Issue of Behavior in December 2020.

Brooker, J. S., Webb, C. E., & Clay, Z. (2021). Fellatio among male sanctuary-living chimpanzees during a period of social tension, Behaviour, 158(1), 77-87. doi: 10.1163/1568539X-bja10053

Abstract

Same-sex sexual behaviour has been documented across the animal kingdom, and is thought to reflect and enhance dyadic cooperation and tolerance. For instance, same-sex fellatio—the reception of a partner's penis into another's mouth—has been reported in several mammalian species other than humans. Although same-sex sexual behaviour is observed in our close relatives, the chimpanzees, fellatio appears to be very rare—as yet there are no published reports clearly documenting its occurrence. At Chimfunshi Wildlife Orphanage in Zambia, we observed an instance of fellatio occurring during a post-conflict period between two adult male chimpanzees (born and mother-reared at the sanctuary) where one of the males was a conflict victim. We discuss this event with respect to the putative functions of homosexual behaviour in great apes. Given its rarity in chimpanzees, this fellatio between adult males also highlights the apparent behavioural flexibility present in our close relatives.

8.1 Introduction

Same-sex sexual interactions, i.e., genital contacts, mounting or other sexual solicitations between same-sex partners have been documented in many animal taxa including mammals, birds, marine life, and insects (Bailey & Zuk, 2009; Sommer & Vasey, 2006). A varied and widespread behaviour in the natural world, homosexual or same-sex sexual behaviour may have diverse as well as species-specific functions (Hanby, 1976; Moscovice et al., 2019), and, in some cases, represent idiosyncratic innovations for behaviourally flexible animals. Among our close relatives, the nonhuman primates, proposed functions include promoting cooperation and coalitionary support as well as preventing and reducing social tension, such as through post-conflict reconciliation (Clay & de Waal, 2013; Moscovice et al., 2019; Paoli et al., 2007; Vasey, 1996). Nevertheless, as has been suggested for same-sex mounting among female Japanese macaques (*Macaca fuscata*; Vasey, 2006), same-sex sexual behaviours do not always appear to convey an adaptive benefit.

Although same-sex sexual behaviour is habitual and particularly pronounced among bonobos (*Pan paniscus*; de Waal, 1990), chimpanzees (*Pan troglodytes*) are also known to engage in same-sex sexual behaviour across multiple contexts (Sandel & Reddy, 2021; Savage-Rumbaugh & Wilkerson, 1978). *Pan* same-sex sexual behaviours include mounting, genital touching, and rump-rump touching (de Waal, 1988; Goodall, 1989). Although same-sex sexual behaviours can occur in a range of contexts in animal taxa, in both chimpanzees and bonobos, these behaviours are especially common during socially tense periods including pre-feeding, post-conflict periods, inter-group encounters, and, for chimpanzees, before boundary patrols (Clay & de Waal, 2015; Herbinger et al., 2009; Paoli et al., 2007; Samuni et al., 2019; Wilson et al., 2007; Wittig et al., 2016). Compared to bonobos, same-sex sexual behaviour is rare in chimpanzees, although males in the wild regularly share body contacts, including genital touches and mounting, prior to events that benefit from cooperation and group cohesiveness, such as intergroup encounters (Samuni et al., 2019; Wittig et al., 2016). Genital contacts also occur in chimpanzee conflict contexts although they are no more common than kissing, embracing, and submissive gestures (de Waal & van Roosmalen, 1979).

Despite the prevalence of sexual behaviours in primates, fellatio—whereby a partner's penis is taken into another's mouth—appears to be rare. Thus far, it has been reported between male-male dyads of laboratory-housed stump-tailed macaques (*Macaca arctoides*; Chevalier-Skolnikoff, 1974) and during periods of crowding among male Tibetan macaques (*Macaca thibetana*), with the author suggesting it to play a role in greeting and tension reduction (Ogawa, 2006). Furthermore, two published reports in chimpanzees also documented oral-genital contact between juveniles in the context of play, however they do not specify whether fellatio was observed (Savage & Malick, 1977; Savage-Rumbaugh & Wilkerson, 1978). In this report, we contribute a novel observation of same-sex fellatio occurring among two sanctuary-living adult male chimpanzees during a period of social tension. Arising among adults during a post-conflict period, this observation differs notably from previous unpublished observations in great apes describing the very rare occurrence of fellatio during play among captive immature chimpanzees at La Vallée des Singes, France (Heesen, personal communication) and among immature bonobos at Lola ya Bonobo Sanctuary (Clay, personal observation). By reporting on the occurrence of fellatio among adult male chimpanzees during a socially tense period, we believe our observation can contribute to a richer understanding of the form and function of same-sex sexual behaviours in primates.

8.2 Study site and methods

A group of sanctuary-living chimpanzees was observed between March and August 2019 at Chimfunshi Wildlife Orphanage (hereafter "Chimfunshi") in the Copperbelt Province of Zambia as part of a larger research project examining post-conflict behaviours and empathic tendencies. A member of the Pan African Sanctuary Alliance (PASA), Chimfunshi houses wild-born chimpanzees rescued from the pet and bushmeat trades as well as mother-reared individuals born at the sanctuary, across four stable social groups. These groups are accessible to approved observational and non-invasive research projects. Our study population (Group 2) consisted of 52 chimpanzees comprising all age- and sex-classes (see *Table 8.1* for selected relevant IDs). The chimpanzees live in an expansive outdoor enclosure of 0.65 km2 incorporating densely vegetated miombo forest and grassland. Individuals nest independently and are fed several times per day by carers.

Table 8.1. Select IDs from Group 2 at Chimfunshi Wildlife Orphanage, Zambia. Includes all individuals referred to in *Section 8.3*. Age presented in years and rank presented as a linear ELO scored hierarchy (lower number corresponds to higher rank).

ID	Sex	Age (Years)[a]	Rank (ELO)[b]	Origin[c]
Daisey	F	14	31	c
David	M	17	5	c
Doug	M	16	1	c
Little Jacky	M	7	22	c
Misha	F	31	25	w
—Max[d]	M	12	8	c
—Maxine[d]	F	18	32	c
Moyo	M	11	6	c
Nina	F	16	14	c
Tina	F	4	N/A	c
Violet	F	28	7	w
Zsabu	M	29	3	w

[a] *On July 11th, 2019*

[b] *Based on dyadic agonistic interactions including high- and low-contact aggression and chases from April 16th—August 3rd, 2019*

[c] *c = captive-born; w = wild-born*

[d] *Em-dash (“—“) indicates individual is infant of the above mother.*

To assess the group-level hierarchy, we used the R package ‘EloRating’ to create dominance scores for 34 individuals based on dyadic agonistic interactions involving high-contact aggression, low-contact aggression, and chases (v.0.46.11; Neumann & Kulik, 2020). Each agonism type was assigned a different optimised K-value based on intensity and likelihood of winning probabilities. Only individuals aged four years and older with at least six observed dyadic agonistic interactions were included in our ELO analysis. Dominant individuals were considered those clustered in the top 25% of the group.

8.3 Observation

Our observation took place on July 11, 2019 at approximately 14:16 PM during a routine afternoon feeding session. It was recorded within a systematic five-minute post-conflict focal follow of Max (12-year-old male) born in Chimfunshi to Misha, a wild-born adult female. ELO dominance analyses reveal Max as the second lowest-ranked adult male (10 years and older) out of eight males in the group.

Following a chase and threat by Violet, a dominant adult female, Max expressed victim behaviour, including a bared-teeth display and screaming, and thereafter interacted with various bystanders. At 2 s after the conflict, Moyo, another adult male, made a bluff display towards Max, who subsequently approached Moyo submissively, who responded with a body kiss on Max's back. Approximately one minute after the original conflict with Violet, Max received a body kiss from Nina, an adult female, and was touched by Little Jack, a juvenile male. Max then mounted Tina, an infant female with thrusts (intromission was indiscernible).

Following these contacts, Max directed submissive gestures, including bared-teeth displays and crouching, towards several dominant adult male individuals including Doug and Zsabu. At 1 min 32 s, Max approached David (a 17-year-old male) while presenting his penis. Max thrusted it towards David's arm (*Figure 8.1*), who appeared to touch it briefly (*Figure 8.2*) before Max bared his teeth at Zsabu, whimpered, and walked several metres away. At 2 min 7 s, David approached Max with his mouth open and gaze directed at Max's groin (*Figure 8.3*). Max placed his right knuckles on the ground, his left hand on the right side of David's face and used his hips to manoeuvre his erect penis into David's mouth (*Figure 8.4*). Max then made slight thrusts and moved his left hand to David's chin, who placed his lips around Max's penis tip (*Figure 8.5*). During the fellatio, Max bared his teeth and appeared to whimper. The fellatio lasted for approximately 3.5 s before Zsabu stepped towards the pair and Max withdrew. Following this encounter, Max initiated copulation with Daisey, an adult female.

Figure 8.1. [01:58] Max approaching David with a bared-teeth display and subsequently thrusting his erect penis towards David's lower right arm.

Figure 8.2. [01:59] David responding to Max's advance with a slight movement of his hand towards Max's penis, appearing to touch it as Max starts to walk away.

Figure 8.3. [02:07] Max with a bared-teeth display looking towards David who is approaching with his mouth open and teeth on display, whilst appearing to gaze towards Max's groin.

Figure 8.4. [02:09] Max still baring his teeth with his penis placed inside David's mouth, whilst touching the right side of David's face.

Figure 8.5. [02:10] Max has moved his hand to David's chin and makes gentle thrusts with his hips, moving his penis slightly in and out of David's mouth.

During several months prior to this interaction, Max made other unaccepted sexual invitations following dyadic conflicts where he expressed victim behaviour. On two occasions Max presented his penis towards uninvolved bystanders—on April 27 towards his adult sister, Maxine, and on May 7 towards Zsabu. On these occasions, Max made a concave back and thrusted his erect penis towards the recipient with one or both hands placed on the ground behind his feet. On July 6, the only observed dyadic agonistic interaction between Max and David occurred. David chased Max who fled and responded with a bared-teeth display and presented his rump towards David who did not appear to engage. On two occasions during high-tension feeding periods following the observed fellatio (July 13 and July 19), Max ventro-dorsally embraced David with pelvic thrusts. We did not observe ejaculation during any of these events. All of these interactions are video-recorded and can be seen at doi: 10.6084/m9.figshare.13325171. Social affiliation scan data from the full observation period revealed no recording of Max and David gathering in close proximity (<1 metre) or engaging in affiliative behaviours, including grooming or play.

8.4 Discussion

In this report, we described an instance of same-sex fellatio occurring between two sanctuary-living adult male chimpanzees. Although fellatio has been observed in other mammals (Ogawa, 2006; Sergiel et al., 2014; Sugita, 2016; Tan et al., 2009), including captive/semi-captive bonobos (de Waal, 1988; Clay, personal observation) and chimpanzees (Heesen, personal communication) it has not yet been reported among adult chimpanzees during social tension, with two previous reports noting the occurrence of oral-genital contact among play in immature chimpanzees (Savage & Malick, 1977; Savage-Rumbaugh & Wilkerson, 1978). Moreover, while bonobos habitually engage in diverse same-sex sexual behaviour, fellatio appears to be rare and constrained to play contexts involving immatures (de Waal, 1988; Clay, personal observation). To our knowledge, fellatio has not been reported to occur in post-conflict affiliative interactions among either chimpanzees or bonobos. This observation thus provides relevant insights into the potential diversity of its functions in our closest living relatives.

Homosexual interactions, such as those reported here between Max and David, have been hypothesised to reinforce same-sex alliances and increase the propensity to support and cooperate (Kirkpatrick, 2000; Moscovice et al., 2019). Creating such connections may facilitate alliance formation and provide greater opportunities for future cooperation and support during agonism between non-kin. As a low-ranking chimpanzee, it is possible that Max's request for fellatio in this case may have been driven by a motivation to associate with potential coalition partners, with genital contacts having been shown to facilitate coalitionary support in bonobos, the close relative of chimpanzees (Moscovice et al., 2019). As our closest phylogenetic relatives, studying genital contacts in chimpanzees, including fellatio, in specific contexts may provide clarity on the evolutionary origins of same-sex sexual behaviour within and between the sexes.

Our observation may also reflect fellatio serving a reassurance and alliance testing function by a subordinate male, akin to genital touches and mounting commonly observed between wild male chimpanzees during socially tense periods such as before boundary patrols and intergroup encounters (Samuni et al., 2019; Wittig et al., 2016). It has been proposed that engaging in intimate, risky behaviour such as fellatio can be used to test social relationships and tolerance (Kirkpatrick, 2000).

Chimpanzees are behaviourally innovative and spontaneously develop unique behaviour that may culturally transmit, even if such actions appear to lack adaptive benefits (van Leeuwen et al., 2014). As chimpanzees are not known to habitually engage in same-sex sexual interactions, Max's repeated attempts to initiate genital contact for reassurance may also represent a behavioural innovation. Observing Max's group in varying contexts would be necessary to detect whether he possesses a more general tendency for same-sex sexual interactions. Further, longitudinal investigations may show that idiosyncratic sexual behaviour, such as fellatio, is culturally transmitted over time.

Although the functions of fellatio remain to be explored in great apes, its initiation by a lower ranking male towards a dominant male in a socially tense context makes a novel contribution to the literature. Given the apparent overlaps between this behaviour and genital contacts occurring among the close sister species, the bonobos, systematically comparing sexual behaviours during periods of social tension between *Pan* would provide greater clarity on how sexual behaviours may be adapted and deployed to fortify and repair social relationships.

"Every creature alive today shares a common genesis in the ancient seas of earth, and so alike are we in various ways that there is possibly a single ancestor for us all—the last universal common ancestor (LUCA). Lions, trees, birds, flowers, elephants, snails, and all other living things are therefore the result of the same number of years of evolution as human beings, none more and none less. ***All of us alive today have journeyed this far together****."*

— Les Mitchell in 'The Palgrave Handbook of Practical Animal Ethics'

Chapter 9: General discussion

In this chapter, I reflect upon the implications of my empirical findings described in *Chapters 4–8*. I discuss how these studies address my research questions and how they contribute towards the wider literature on *Pan* empathy (see *Chapter 2*) and comparative psychology as a whole. I also outline the shortcomings of my research and how they could be addressed in future studies.

9.1 Overview

Comparative research often seeks to identify species-level variation in socio-emotional and cognitive behaviours. This thesis focuses on understanding intra- and inter-specific variation in the role of affiliative contact during periods of social tension for our closest living relatives, bonobos and chimpanzees. Despite greater focus on bonobos over recent decades (Gruber & Clay, 2016; Hare & Yamamoto, 2017), they remain an understudied species in comparison to chimpanzees. Systematic comparisons of the two *Pan* apes are more common in recent years, however they are often based on single groups of often small captive populations (Kaufhold & van Leeuwen, 2019).

More recent captive observations have indicated that the two species may overlap more than previously thought. For example, both species appear capable of recognising and attending to the emotions of conspecifics (e.g., Clay & de Waal, 2013; Heesen et al., 2022; Izumi & Kojima, 2004; Kano et al., 2008; Kret et al., 2014; Kret et al., 2016; Parr, 2003; Romero et al., 2010), as well as humans (Buttelmann et al., 2009). Recent studies have indicated that cognitive and emotional behaviours in bonobos and chimpanzees can vary considerably at the individual- (Hermann et al., 2010; Pika et al., 2005; Webb et al., 2014; Webb et al., 2017) and group-level (Cronin et al., 2014; van Leeuwen et al., under review). Thus, previous comparisons of small populations or single groups may have led to inaccurate estimations of the extent of inter-individual and intergroup variation (Kaufhold & van Leeuwen, 2019).

With this thesis, I conducted a comprehensive between-species comparison on multiple groups of bonobos and chimpanzees, varying in group size, temperaments, and social composition. The *Pan* apes are well documented in their proclivity to use affiliative contact behaviours in a variety of socially tense contexts (see *Chapter 1*). Here, I systematically compared sanctuary-living bonobos and chimpanzees regarding their tendencies to offer affiliative contact as post-conflict consolation and as pre-feeding affiliation. I have used these contexts to examine between- and within-species trends in the use of affiliative contact as an empathic behaviour as well as a possible reassurance strategy to manage social tension. I refer to social tolerance levels assessed by van Leeuwen et al.

(under review) on data collected during the field seasons for my research for context behind associations during these periods.

9.2 Empathy

Observational and experimental research methods indicate that bonobos and chimpanzees can perceive and respond to the states of others in sophisticated ways. Studies, primarily in captivity, have indicated that mimicry, behavioural contagion, perspective-taking, consolation, and targeted helping feature in the social lives for both species (see *Chapter 2* for a comprehensive review). These behaviours are associated with empathy (de Waal, 2007; de Waal & Preston, 2017), although expression of one is not necessarily a reflection of one's own empathic capacity (Adriaense et al., 2020). To build an inclusive picture of *Pan* empathy, we need a systematic programme of comparative investigations across many groups. A suite of within- and between-species studies would reveal how group and species differences facilitate tendencies to engage in socio-emotional behaviours.

Past comparative research has indicated differences between the *Pan* apes. Behaviourally, bonobos are purported to be more socially attentive (Kano et al., 2015), less aggressive (Hare et al., 2012; Parish et al., 2000; Wilson et al., 2014), and potentially more socially tolerant than chimpanzees (Furuichi, 2011; Hare et al., 2007; Idani, 1990). These apparent species differences are thought to be supported by biological and neurological mechanisms (Rilling et al., 2012; Staes et al., 2014; Stimpson et al., 2016). These findings support experimental research indicating that bonobos rapidly respond to the emotional expressions of others (Kret et al., 2016).

Therefore, it is reasonable to expect bonobos to be more emotionally responsive and empathic than chimpanzees (de Waal & Lanting, 1997). Thus far, comparative investigations have indicated that bonobos may excel over chimpanzees in perspective-taking capacities (Hermann et al., 2010), whilst other findings have indicated similar capacities in the two species (Kano et al., 2019; Krupenye et al., 2016). Other direct comparative insights are lacking, primarily due to the difficulty to collect systematic data on these behaviours across *Pan* groups living in comparable conditions. However, both species appear capable of comprehending other's beliefs (see *Section 2.3.3*) and responding to fellow group members in distress (see *Section 2.3.4*) or those requiring specific assistance or support (see *Section 2.3.5*). Thus, whilst proclivities to engage in these behaviours may vary at the species level, it is at least apparent that empathic behaviour, related to comprehending and responding to the states and emotions of others, is observable in both *Pan* apes.

In *Chapter 4*, I provide the first direct comparison of bonobos and chimpanzees in consolation, a behaviour purported to be motivated by sympathetic other-oriented concern (de Waal & Preston, 2017). I tested the hypothesis that bonobos are more empathic than chimpanzees due to an apparent increased sensitivity to the emotional and social states of others. Thus, I predicted that consolatory tendencies would be higher in bonobos than chimpanzees. However, I found no clear cross-species differences in general tendencies for the *Pan* apes to console. However, I did uncover some within-species trends that may drive increased individual consolation tendencies.

Firstly, in support of the movement towards comparing multiple groups to assess whether species-level differences exist (Kaufhold & van Leeuwen, 2019), I found that two bonobo groups differed significantly in their tendencies to console. According to the *Social Constraints Hypothesis* (de Waal & Aureli, 1996; Palagi et al., 2014), social tolerance, which can vary within species (see *Chapter 6*), is purported to facilitate empathic behaviours such as consolation. My findings challenge the *Social Constraints Hypothesis*. Parallel with my research for this thesis, I collaborated on a large-scale cross-group comparison of social tolerance on zoo- and sanctuary-living bonobos and chimpanzees (van Leeuwen et al., under review). In relation to these findings, I found that a despotic bonobo group (B1) had higher tendencies to console compared to a relatively tolerant bonobo group (B2). Aggression is lower in bonobos than chimpanzees (Hare et al., 2012; Wilson et al., 2014), and thus consoling distressed individuals may be less important in a tolerant bonobo group, if there is lower risk of spontaneous or redirected aggression. The next step is to systematically investigate the motivations to console in more detail with intraspecies variation and the interplay between aggression and social tolerance taken into account.

By comparison, I was unable to collect consolation observations of multiple groups of chimpanzees due to time constraints. However, expressions of empathy-related behaviour have been shown to vary in wild chimpanzee communities of the same subspecies (Arnold & Whiten, 2001; Kutsukake & Castles, 2004; see *Section 2.3.4*). Thus, certain socio-ecological conditions may influence the relative tendencies for individuals in one community to use consolation compared to others. Some chimpanzee intergroup variation is thought to be driven by social learning, for example in foraging (Luncz et al., 2012) and hunting behaviours (Pruetz & Bertolani, 2007), as well as a socio-cultural grooming practice, handclasping (van Leeuwen et al., 2012). My finding of intraspecies group variation in bonobo consolation complements this literature. Empathic tendencies may too be influenced by broader socioenvironmental circumstances. If other social behaviours can be influenced at the individual- and group-level in chimpanzees, behaviours like consolation may too vary according to individual and collective influences (Webb et al., 2017). This within-species variation in consolatory tendencies mirrors some empathy research in humans, where empathy appears to vary across diverse cultures (Chopik et al., 2017; Vreden et al., in prep).

Some socio-ecological pressures appear to be associated with the development of empathy, such as social living and maternal care (de Waal & Preston, 2017). In humans, empathy has been suggested to represent part of a broader prosocial personality domain (Allemand et al., 2015), as stable individual differences have been identified in longitudinal studies (Eisenberg et al., 1995; Eisenberg et al., 1999; Knafo et al., 2008; Zahn-Waxler, Radke-Yarrow et al., 1992; Zahn-Waxler, Robinson & Emde, 1992). Similar trends have been described in captive chimpanzees over a period of eight years (Webb et al., 2017). In this study, chimpanzees differed consistently in their tendencies to console others, and these differences remained relatively stable over this timeframe. Like humans, there is individual variation in animals regarding levels of personality traits (Dall & Griffith, 2014; Nettle, 2006), which may be influenced by collective factors (Bengston & Jandt, 2014).

Consolation is considered a prosocial behaviour (de Waal, 2007; Yamamoto, 2017) in that it has a tension-relieving function in the recipient (Clay & de Waal, 2013; Fraser et al., 2008), and is thought to be motivated by other-oriented concern (de Waal & Preston, 2017). However, engagement in prosocial behaviours can also be influenced by various factors, including egoistic, self-motivated concerns (Eisenberg, 2006). For example, consolers may gain social rewards and receive reciprocal support in the future or avoid punishment (Batson, 2010; Watts, 2002). Regardless of the motivation however, spontaneous consolation still appears to reduce conspecific distress (Clay & de Waal, 2013; Fraser et al., 2008). Furthermore, there are also indications that consolation can serve to protect victims from further aggression in bonobos (Palagi & Norscia, 2013), indicating additional prosocial outcomes. Nonetheless, testing and comparing the inner motivations and mechanisms that drive consolation in *Pan* is difficult. To assess physiological influences of arousal and cognitive perspective-taking, one needs to combine these naturalistic observations with explicit experimental tasks (see Lewis & Krupenye, 2021) and measures of underlying affective states (e.g., Dezecache et al., 2017).

Increased sensitivity to the states of others (Kano et al., 2015; Kret et al., 2016; Rilling et al., 2012 Stimpson et al., 2016) has been suggested to facilitate an increased capacity for empathy in bonobos, which may lead to greater other-oriented concern. In the population of bonobos that I studied, I found that younger victims were more likely to be consoled than older individuals, and that younger bystanders were more likely to offer consolation than older individuals, complementing previous work (Clay & de Waal, 2013). Furthermore, whilst kin victims were more likely to be consoled than non-kin, bonobo consolation was not biased towards non-kin close social partners. There is evidence from a previous cohort in the same bonobo population that victims producing paedomorphic signals have increased likelihood of being consoled than other signal types (Heesen et al., 2022). Whilst I did not compare victim signalling explicitly, younger victims were generally more likely to be consoled in my sample, supporting these recent findings. Collectively, these species trends may indicate a broader social attentiveness in bonobos (Kano et al., 2015), where they are more motivated by the emotional expressions of others. Future research should seek to assess sensitivity to the distress of close and non-close social partners, and whether this predicts consolatory tendencies in both bonobos and chimpanzees. A victim signalling study in chimpanzees (akin to Heesen et al., 2022 in bonobos) could determine which signals are more likely to result in a victim receiving consolation.

Although, given their close phylogenetic relationships, both ape species can be expected to share similar empathic behaviours and functions, there may nevertheless be certain species differences based on variation in social tendencies and dominance dynamics. Whilst my data also showed that younger individuals are also more likely to console others (see *Chapter 4* and Webb et al., 2017), chimpanzees may be broadly more selective in their responses. Wild and captive chimpanzee societies are centred around strong adult male-male alliances whereas in bonobos, they are centred around alliances between female-female pairs and mothers and sons (Gruber & Clay, 2016). Dominance relationships and displays of subordinacy appear to be more pronounced in chimpanzees, which may be a result of this strong male dominance and related risk of physical aggression (see *Section 1.2.1.2*).

In both species, consolation may provide benefits to maintain group cohesion and protect personal status and kin (Batson, 2010; Watts, 2002). However, in chimpanzees this may be especially important as the prevalence and risks of aggression are generally more severe (Hare et al., 2012; Wilson et al., 2014). Furthermore, my investigation in *Chapter 4* revealed that young chimpanzee males were more likely to console others than young females. Young male chimpanzees begin to form strong social bonds with other males before they reach adulthood, which appears to facilitate the formation of alliances for later life (Sandel et al., 2020). The apparent increased motivation for young males to console more often than females of a similar age may represent this drive to form and reinforce social bonds with close peers and other individuals they will spend their lives with. In addition, young males are more likely to be aggressed in the wild by dominant males (Sabbi et al., 2021). An enhanced urge to console others may be facilitated by repeatedly observing their peers being aggressed during a period when they are building foundational relationships for later life. Future research could dig deeper into the social connectedness of female and male chimpanzees to elucidate whether this interaction effect is driven by young males responding to other young males, or if they offer consolation more broadly.

The *Pan* apes, like many species (Bolnick et al., 2011; Lott, 1984), are behaviourally flexible and diverse (Boesch et al., 2002). These intraspecies variations can manifest in group-specific signatures of social behaviours (Kaufhold & van Leeuwen, 2019), and empathy may vary on a group or cultural level too, akin to humans (Chopik et al., 2017). Ultimately, comparing more groups of the same species and investigating within-group drivers of various empathy-related behaviours is vital to reveal the deep evolutionary history of empathy (Decety, 2015). It is now key for further research to dig deeper into the dyadic or group dynamics that influence consolation tendencies in bonobos and chimpanzees, and how these species compare regarding motivations to console. Continued between-group and between-species comparisons will continue to reveal the flexibility of emotional responsiveness, and how individual and collective features promote or hinder the expression of empathy.

9.3 Reassurance

Bonobos and chimpanzees are known to use affiliative contact to reassure themselves and others during periods of social tension (de Waal, 1992). These *reassurance* interactions are purported to serve tension-reducing and conflict-prevention functions (de Waal, 1992; van Hooff, 1967). In this thesis, I provide the first direct comparison of bonobos and chimpanzees in their tendencies to engage in affiliative contact during two periods of social tension: as post-conflict consolation (*Chapter 4* and *Chapter 7*) and as pre-feeding affiliation (*Chapter 5, Chapter 6*, and *Chapter 7*). I tested the hypothesis that reassurance would be more common in chimpanzees than bonobos due to a general increased risk of conflict at the species level (Hare et al., 2012; Wilson et al., 2014). I found that pre-feeding contact affiliation tendencies did not vary at the species- or group-level. Instead, my findings revealed species-specific trends regarding affiliation among dyadic sex-pairings. Below I discuss these findings in more detail.

Mixed sex relationships are important in both bonobo and chimpanzee social dynamics, particularly between mother-son pairs in bonobos (Furuichi, 1989; Reddy & Sandel, 2020; Schubert et al., 2013). However, female-female relationships in bonobos and male-male relationships in chimpanzees have typically been described as those with the strongest bonds and alliances, which have the most influence over the social hierarchies (Boesch, 2009; Furuichi, 2011; Mitani, 2009; Nishida, 2011; Parish, 1996; White & Wood, 2007). In bonobos, female-female social bonds support coalitionary relationships and greater female social power in competitive contexts, allowing clusters of adult females to dominate over other group members (Furuichi, 2011; Parish, 1996; Surbeck et al., 2012; Vervaecke et al., 2000; White & Wood, 2007). In chimpanzees, an alpha male and his closest adult male allies dominate the group (Boesch, 2009; Nishida, 2011) and stronger social bonds facilitate cooperation, resource-sharing, and tolerance for inequity (Brosnan et al., 2005; Samuni et al., 2018). Although I did not collect sufficient data to compare the relative bonding between the sexes across all groups, my findings do indicate that increased affiliation between the most socially central sex (chimpanzee males, bonobo females) prior to competition facilitated more crowded, peaceful feedings in *Pan*.

Consolation has been shown to reduce victim distress in bonobos and chimpanzees (Clay & de Waal, 2013; Fraser et al., 2008). However, the tension-relieving function of pre-feeding affiliation was not tested in my thesis. Thus, the next step in the study of pre-feeding reassurance would be to directly assess function. Firstly, one could test if reassurance reduces arousal by testing if dyadic pre-feeding associations between sex pairings are associated with a marked reduction in anxiety levels in either party, measured through self-directed behaviours or physiological measures of cortisol. Furthermore, one could directly test a conflict prevention function of reassurance by investigating whether reassurance prevents conflict by comparing contact associations and likelihood of dyadic aggression during competitive contexts.

Social bonding and cohesion are promoted by affective touch in primates (Jablonski, 2021). This notion has some support through my findings in *Chapter 6*, where individuals who engaged in more tactile pre-feeding affiliation appeared to have greater access to the cofeeding zone across both species. However, my findings indicate that pre-feeding affiliative contact may not have a simple positive linear influence on cofeeding tolerance. Whilst there were general trends for both bonobos and chimpanzees, there were indications that pre-feeding contacts do not facilitate tolerance in some bonobo groups. Consideration of the contribution of strong dyadic relationships between socially central individuals appears to be vital in future studies of the connection between reassurance and tolerance (Lee & Yamamoto, 2023; see *Chapter 5*). Prestige and social status have been shown to influence socio-cultural behaviours in chimpanzees (Horner et al., 2010; Kendal et al., 2015), and thus may influence social behaviours such as reassurance.

The potential link between strong social bonding in chimpanzees and increased social tolerance has further support through my findings regarding the use of vulnerable behaviour during this competitive pre-feeding period. Body kiss and finger/hand in mouth are species-specific to chimpanzees and have been observed during consolatory and reconciliatory encounters (de Waal & van Roosemalen, 1979; de Waal, 1989b; Nishida et al., 1999; Wittig & Boesch, 2003). The use of vulnerable behaviours during tension may appear paradoxical—especially when considering the aggressivity of chimpanzees (de Waal, 1986; Wilson et al., 2004; Wilson et al., 2014). However, as demonstrated in capuchins (*Cebus*; Perry, 2011) and hyenas (*Crocuta crocuta*; East et al., 1993), use of vulnerable behaviours in tense contexts may reflect 'rituals of trust' where individuals communicate benign intent to test social bonds and foster trust (Palmer & Pomianek, 2007). In support of the association between strong social bonds, social tolerance, and trust, vulnerable behaviours in my sample for chimpanzees were offered and received more by males but were considerably more likely to occur in the tolerant chimpanzee group, compared to the despotic group. Comparably, whilst mouth-to-body behaviours are atypical in bonobos, the use of sexual behaviour in these contexts (Clay & de Waal, 2015; see *Chapter 7*) may serve homologous functions.

In my studies of pre-feeding affiliation, I show substantial species and group differences in the forms of tactile affiliation that are common in these contexts, and who they are directed towards. These findings provide further support that intergroup variation is vital for understanding the extent of *Pan* behavioural diversity (Boesch et al., 2002; Kaufhold & van Leeuwen, 2019). I show that these previously documented 'celebration' behaviours (de Waal, 1992) are associated with reduced levels of conflict around a competitive feeding context in both species. The nature of my methods prevented me from directly assessing whether any individual pre-feeding affiliative interaction directly reduced individual or collective tension or the likelihood of conflict occurring. However, I demonstrate that affiliation is high during the pre-feeding period whilst conflict remains low in both species. When feeding occurred, conflict generally peaked slightly, and affiliation quickly rose as conflict reduced.

Bonobos and chimpanzees therefore appear to use rich forms of affiliative contact, including consolation and reassurance, as conflict management behaviours (Palagi et al., 2006; von Rohr et al., 2012). Therefore, to determine whether pre-feeding affiliation does serve reassurance functions, more direct systematic comparisons of social interactions in various tense contexts across groups are needed. Assessments of individual and collective anxiety prior to and following affiliative contact (Clay & de Waal, 2013; Fraser et al., 2008) could reveal if reassurance directly reduces tension. In addition, exploring the association between affiliation and conflict in more depth with a dyadic perspective could reveal whether reassurance can be used as a conflict prevention strategy (Palagi et al., 2006). Further research could also help to elucidate how ubiquitous reassurance is among *Pan*, and what group-signatures of reassurance exist across different communities (Boesch et al., 2002; Kaufhold & van Leeuwen, 2019). Furthermore, crucially, consolation represents a specific form of reassurance. My findings indicate that both consolation and pre-feeding reassurance are offered by bonobos and chimpanzees across ages and sexes and biased towards close social partners. I also observed species-specific trends regarding the direction of these behaviours. Thus, a broad investigation of individual tendencies to reassure others in various contexts—including post-distress, pre-competition, and intergroup encounters—would provide a substantial insight into whether the mechanisms and functions that underlie reassurance as a whole are linked in *Pan*.

9.4 Sexuality

Sociosexuality—non-conceptive genital contact occurring within and between the sexes—is a common part of human and animal social behaviour (Shackelford, 2022). Across animals, sociosexual behaviour occurs between different-sex and same-sex pairings (Orille, 2020; Shackelford, 2022; Sommer & Vasey, 2006) suggesting functions beyond reproduction, the most important of which appears to be for managing and enhancing social relationships on different time-scales (Cocks, 2010). The proclivity of nonconceptive sexual behaviour across the natural world indicates a deep evolutionary origin of sociosexuality (Roughgarden, 2013).

In primates, sociosexuality is widespread, having been observed in macaques (*Macaca fuscata*; Hanby & Brown, 1974), baboons (*Papio anubis;* Owens, 1976), Sichuan golden monkeys (*Rhinopithecus roxellana*; Clarke, 1991), marmosets (*Callithrix jacchus*; Cavanaugh et al., 2014), cotton-top tamarins (*Saguinus oedipus oedipus*; Savage et al., 1988), the great apes (see *Chapter 7*), and many more (Dixson, 2012). Bonobos and chimpanzees are well documented in their use of sociosexual behaviour in various contexts, including play but primarily during periods of social tension (Clay & de Waal, 2015; Enomoto, 1990; Sandel & Reddy, 2021; Savage & Malick, 1977). The *Pan* apes perform many affiliative contact behaviours for reassurance (de Waal, 1988; Goodall, 1986; Kano, 1992; Nishida et al., 2010), which includes genital contacts such as genital touching, mounting, genito-genital contact in bonobos, and rump-rump touching in chimpanzees (Clay & de Waal, 2015; Goodall et al., 1979; Hohmann & Fruth, 2000; Sandel & Reddy, 2021).

The role of sexual contacts in the social lives of bonobos has received more attention than those in any other primates, including chimpanzees (Gruber & Clay, 2016; Woods & Hare, 2011; Clay et al., 2022). Sexual interactions emerge during the first year of life for both female and male bonobos (Furuichi et al., 2014), typically between mother-infant pairings when either party are distressed or anxious (Clay et al., 2022; Hashimoto, 1997). Bonobo sociosexual behaviour is linked with cooperation, proximity during feeding, and even food sharing (Moscovice et al., 2017; Moscovice et al., 2019). However, genital contacts between individuals of all age and sex combinations can be common in both *Pan* apes (de Waal, 1990; Sandel & Reddy, 2021). In chimpanzees, genital touches and mounting between wild male chimpanzees may serve reassurance and alliance testing functions during socially tense periods such as before boundary patrols and intergroup encounters (Samuni et al., 2019; Wittig et al., 2016). Broadly, genital contacts appear to occur in both species during social tension and may function to reinforce social bonds and mediate arousal (Clay & de Waal, 2015; Sandel & Reddy, 2021).

Sexual behaviour is purported to function to alleviate social tension and reduce stress in bonobos (Clay & de Waal, 2015; Hohmann & Fruth, 2000) and chimpanzees (Sandel & Reddy, 2021). Whilst I was unable to explicitly test this function, my results in *Chapter 7* support this view as genital contacts were common in both social tension contexts. Neither species were more likely than the other to use genital contacts during the pre-feeding affiliation context. Furthermore, whilst bonobos were more likely to use genital contacts during consolation, genital touching and mounting still occurred in a considerable proportion of chimpanzee victim focal follows. During and outside of formal study observations, I noticed a variety of vulnerable sexual behaviours occurring between chimpanzees (Brooker, personal observation). Akin to observations of wild chimpanzees (e.g., Samuni et al., 2019; Wittig et al., 2016), this included testicle touching and mounting with thrusts (Brooker, personal observations). I even observed one case of fellatio between two adult males during a victim focal follow (*Chapter 8*, Brooker et al., 2020). This anecdotal observation highlights scope for behavioural flexibility and innovation of chimpanzees to spontaneously develop idiosyncratic behaviours (Boesch et al., 2002), some of which may even culturally transmit (van Leeuwen et al., 2014). No such cultural emergence or transmission of sexual behaviours have been documented in the *Pan* apes to my knowledge, however this would be a fascinating avenue for inspection for behavioural primatologists.

Behaviourally, I did observe some inter-species differences regarding repertoire. Chimpanzees use other forms of affiliative contact during tense periods that are not seen in bonobos (as described in *Section 9.3*). Likewise, whilst chimpanzees may rarely engage in rump-rump touching for reassurance (Goodall, 1986; Nishida et al., 2010; Sandel & Reddy, 2021; see *Chapter 5*), genito-genital contact is a common behaviour in bonobos of all ages and sexes (de Waal, 1990; Hohmann & Fruth, 2000; see *Chapter 5*). The use of mouth-to-body behaviours such as body kissing and finger/hand in mouth for chimpanzees in these contexts (de Waal & van Roosemalen, 1979; de Waal, 1989b; see *Chapter 5*) may serve similar functions to genito-genital rubbing in bonobos.

Both mouth-to-body and sexual behaviours increase vulnerability of both parties, especially when they are used in a context where conflict is likely (de Waal, 1986; Wilson et al., 2004). The apparent reduced aggressivity of bonobos compared to chimpanzees (Hare et al., 2012; Wilson et al., 2014) may have facilitated an increase in the use of sexual behaviour for social closeness and reassurance functions. Comparing the two species broadly in the role of all forms of vulnerable affiliative behaviour could elucidate whether these species overlap in the functions that these intimate, risky contacts serve (Kirkpatrick, 2000; Palmer & Pomianek, 2007). A future direction for this research would be to specifically test if genital contacts and mouth-to-body behaviours during pre-feeding and victim follow contexts in chimpanzees both serve social bonding and reassurance functions, akin to genital contacts for bonobos (Clay & de Waal, 2015; Moscovice et al., 2017). This could be tested by assessing whether these behaviours are associated with marked reductions in arousal for the initiator and or recipient, and if they are strongly predicted by non-kin alliance relationships.

Broadly, my findings support the notion that sexual behaviour in our close relatives has functions beyond reproduction (Cocks, 2010; Roughgarden, 2003). Our closest living relatives possess rich socio-sexual lives, where affiliative genital contacts contribute to managing relationships and socially tense contexts (Heiman et al., 2011; Hohmann & Fruth, 2000; Sandel & Reddy, 2021). Sexuality is central to bonobo social life, however the same appears to be true for chimpanzees. Further comparative investigation into the functions of sexual behaviour in both species can shed more light on how *Pan* sexuality overlaps and what makes either ape distinct in their sexual engagements. Finally, documenting rare occurrences of sexual behaviour provides extra nuance to this discussion and should be encouraged.

9.5 Sanctuary research

As mentioned, bonobos and chimpanzees are both critically endangered due to threats from habitat loss and poaching (Fruth et al., 2016; Humle et al., 2016). Whilst much research on nonhuman primates over the past century has been concentrated on laboratory and zoo facilities (Hopper, 2017; Lankau et al., 2014), the persistent abduction of great apes from the wild has caused sanctuaries, primarily located in range countries, to grow quickly in recent decades (PASA, 2022). Sanctuary staff focus their efforts on rescue, rehabilitation, and husbandry for their residents. However, over time, these sites have become increasingly important as locations to conduct non-invasive behavioural studies of sociality and cognition (Ross & Leinwand, 2020). Beyond the empirical contributions of my research, these studies reveal the benefits that sanctuaries can provide towards the study of socio-emotional and socio-cognitive behaviours in non-human apes (Ross & Leinwand, 2020). Systematic comparative research across field sites is possible and capable of revealing group- and species-specific trends in socio-emotional behaviours.

Studying behaviour in sanctuary environments provides some ecological and logistical benefits. Residents can engage in naturally occurring social and ecological behaviour such as alliance formation, boundary patrols, foraging, independent nesting, and even vigilance from natural threats such as snakes. Conducting this research at Chimfunshi Wildlife Orphanage and Lola ya Bonobo Sanctuary enabled me to compare multiple diverse groups of chimpanzees and bonobos respectively, all living in comparable naturalistic environments. Groups are usually supported by caregiving and veterinary staff, yet they are generally able to roam and navigate their habitats in large populations where they can form and manage broad social networks beyond kin. Therefore, sanctuaries allow researchers to observe naturally occurring social dynamics without tracking. In addition, the scale of sanctuary enclosures allows individuals to avoid being followed and observed if they choose.

However, sanctuaries provide their own unique challenges to the study of animal behaviour. For example, escapes were unavoidable at both field sites, which led to disruption of data collection on multiple occasions. A key issue with studying sanctuary-living populations, however, is extrapolation to natural behaviour. Individuals who arrive at sanctuaries are often young, traumatised infants, having experienced hardship at the hands of poachers or captors (PASA, 2022). Such upbringings are known to affect the early development of great ape socio-emotional behaviour (Clay & de Waal, 2013). Most of the residents at Lola ya Bonobo and Chimfunshi have been successfully rehabilitated and integrated into social groups, yet the scars of their early life may still influence their later behaviour. Rescued great apes can exhibit stereotypic behaviour for the rest of the lives following rescue from adverse circumstances (Lopresti-Goodman et al., 2013; Lopresti-Goodman et al., 2015), and some individuals at Lola ya Bonobo and Chimfunshi do so too.

It is thus also possible that the emotional responsiveness of rescued individuals could be affected for their entire lives, including how they associate during periods of social tension. Those with more nervous dispositions brought on by years of trauma may be more likely to seek reassurance or engage in post-conflict affiliation. However, it is also possible that rescued individuals, particularly subadults and adults, may find it more difficult to integrate into a community and form social relationships, therefore influencing tendencies to engage in social contact affiliation broadly.

Furthermore, as much as sanctuaries attempt to mimic naturalistic environments, individuals are still confined to large but restricted enclosures and largely dependent on human provisioning. Groups are diverse in age and sex compositions but limited to a certain social spacing. Thus, whilst groups fission-fusion as they do in the wild, crowding is more likely than in the wild, and during regulated feeding protocols it is common for entire groups to congregate in a relatively small space. Thus, we can investigate certain pressures on *Pan* social behaviour, such as how crowding may influence tendencies to engage in reassurance. However, these are driven by unnatural conditions, and that caveat is important to bear in mind, including for my research. Taking these finding and applying similar protocols to wild populations is needed for the most accurate depiction of natural *Pan* socio-emotional life.

9.6 General limitations and other further directions

The studies included in this thesis provide relevant, novel contributions to the fields of comparative psychology and primatology. However, they come with their own limitations, which are addressed here. I have already highlighted some possible future empirical directions in this line of research, and I build on those here.

9.6.1 Species-specific rank assessments

Social dominance and rank relationships are central issues in many studies of animal behaviour, particularly primates (Bernstein, 1981). In chimpanzees, hierarchies are complex but typically purported to be strict and linear, headed by an alpha male with his closest allies occupying the next highest positions (Boesch, 2009; Goodall, 1986; Nishida, 2011). Chimpanzee hierarchies have been assessed through multiple methods, including rankings according to dyadic conflict outcomes using the ELO method (Kaburu & Newton-Fisher, 2015; Neumann et al., 2011; Newton-Fisher, 2017) and comparing the directionality of pant-grunts, a vocal greeting behaviour that has been demonstrated to communicate subordinacy in chimpanzees (Bygott 1979; Goodall 1986; Hayaki et al. 1989; Boesch & Boesch-Achermann 2000). Bonobo hierarchies appear harder to determine. Whilst male bonobos appear to follow a chimpanzee-like linear structure (Surbeck et al., 2011; Surbeck et al., 2012), clusters of females typically occupy the highest positions in non-linear, flexible patterns (Douglas et al., 2017; Paoli et al., 2006; Vervaecke et al., 2000; but see Stevens et al., 2007). Thus far, the most accurate method for assessing agonistic dominance in bonobos appears to be measuring 'fleeing from aggression' (Vervaecke et al., 2000; Stevens et al., 2007).

In order to obtain a universal, systematic assessment of rank position across species, I decided to analyse dyadic conflict outcomes to categorise individuals in high, medium, and low rank categories according to agonistic dominance based on ELO scores (Kaburu & Newton-Fisher, 2015; Newton-Fisher, 2017). I chose this method as it would be applicable across both species and complement our observations of periods of social tension. However, the ELO outcomes for bonobos appeared to have inaccuracies in some of their placements, particularly for the most dominant females. These inaccuracies may be due to applying a short-term dataset to reflect nonlinear bonobo hierarchies, general low observances of contact aggression, as well as some issues with group stability (see *Section 9.7.4*). In addition, using conflicts also limited the data we could collect on certain individuals—notably the eldest and youngest—for both species. To overcome these issues, I combined the ELO scores with categorical rankings provided by the onsite keepers and care staff, as well as personal observations from researchers. Thus, whilst likely capturing an accurate categorisation for both species, my measure of rank is less objective than desired.

These issues could have been addressed in several ways. Firstly, ELO scores could have been expanded to include less overt forms of submission, such as displacement and avoidance (Ballesta et al., 2021; Terburg & van Honk, 2013). Inclusion of these behaviours may have provided my hierarchical matrices with enough information to accurately represent the dominance ranks for both species. Otherwise, it may have been more suitable to use species-specific measures to assess dominance in these groups of sanctuary-living bonobos and chimpanzees. Whilst conflict was by no means rare in the chimpanzee groups, pant grunt greetings were considerably more common and, unlike conflict, was typically performed by each individual multiple times per day. In addition, contact aggression was comparatively rare in the bonobo groups compared to the chimpanzee groups, however chasing was common. Limiting the ELO analysis to instances of chasing and other forms of aggression that facilitated fleeing may have yielded a more representative hierarchy for each group. In addition, though it can occur, pant grunting is not a typical expression of subordinacy in bonobos (Furuichi, 1997; Ihobe & Furuichi, 1994). Thus, it may be more suitable for future systematic between-species comparisons of *Pan* groups to assess hierarchies based on species-specific dominance behaviours—'fleeing from aggression' data in bonobos and 'pant grunt greetings' in chimpanzees—rather than one overlapping behaviour.

However, I consider it important to note that accurately assessing hierarchies in non-human primates is a difficult endeavour (Neumann et al., 2011), particularly alongside other rich observations, such as post-conflict encounters. For both species, and all groups, many greetings and conflicts occur out of view, instances which cannot be included in ranking assessments. Moreover, during greeting periods for the chimpanzees, for example, ZG and I were focused on all-occurrence post-conflict/post-distress recordings and observing pre-feeding affiliation directed towards dominant individuals for a subproject for this thesis. Unfortunately, it was not possible to include the data for that subproject in the thesis due to time constraints. As a collective, we intend to analyse and publish this study in the future.

Furthermore, whilst not possible for my research, it appears crucial to possess prior knowledge of dominance ranks to achieve the most accurate assessment of current hierarchical statuses (Newton-Fisher, 2017). Access to prior rank relationships may have improved the accuracy of my ELO analysis for all groups, but especially the bonobo groups. Fortunately, my dataset on agonistic encounters could be applied to develop more accurate future hierarchical assessments in these groups.

Finally, due to the intensity of the data collection programme, it was also not possible to collect objective rank data for groups B3 or C1, which limited my ability to analyse the influence of rank on pre-feeding affiliation during the peanut swing experiment. However, the highest rank positions in *Pan* are typically occupied by socially bonded clusters of females in bonobos (Furuichi, 2011; Surbeck et al., 2012; Vervaecke et al., 2000; White & Wood, 2007) and an alpha male and his closest male allies in chimpanzees (Boesch, 2009; Nishida, 2011). My comparisons of increased contacts between female-female pairs in bonobos and male-male pairs in chimpanzees during pre-feeding periods provides some preliminary information on the role of these strong relationships during these periods (see *Chapter 5*). As rank may be influential for some measures of affiliation during periods of social tension (e.g., Romero et al., 2010), future studies of affiliative contact during tense contexts would benefit from comprehensive records of rank relationships.

9.6.2 Social affiliation

Social relationship strength has been demonstrated as a reliable predictor of consolation in bonobos, chimpanzees, and also humans (e.g., Clay & de Waal, 2013; Lindegaard et al., 2017; Palagi et al., 2013; Romero et al., 2010; Webb et al., 2017). Empathy and related responses are purported to be adaptively biased towards close social partners, becoming less likely the more unfamiliar an individual is to oneself (Eisenberg et al., 1989; Preston & de Waal, 2002). Primates, including humans, typically invest in long-term social cooperative relationships with kin and non-kin, and a social bias in empathy offers a selective explanation for how this costly behaviour emerged in our species and that of our close genetic relatives (Anderson & Keltner, 2002; Preston & de Waal, 2002).

For all groups in both sites, I had access to detailed records of maternal kin relationships, which I was able to include in my analyses for consolation (see *Chapter 4* and *Chapter 7*) and pre-feeding affiliation (see *Chapter 5* and *Chapter 7*). Only limited paternity associations are known in each field site, and thus I was unable to include paternal kin as a predictor in my models. However, whilst there are indications that some male chimpanzees form grooming relationships with their fathers (Sandel et al., 2020), females mate with multiple males in each species to confuse paternity (Gruber & Clay, 2016). It is thus generally expected that bonobos and chimpanzees are not certain who their fathers are (Langergraber et al., 2007; Gruber & Clay, 2016), and so including paternal kin in these analyses would be unnecessary.

For three groups (B1, B2, and C2), we were able to collect a substantial set of social focal follows to measure dyadic relationship strength to include in my consolation analysis. However, due to time constraints at Chimfunshi and Lola ya Bonobo, we were unable to collect social focal follows at groups B3 and C1. Whilst the inclusion of kin did provide some control for social relationship strength in my pre-feeding affiliation analyses, I was unable to control for non-kin social relationship strength. Nonetheless, my analyses provide valuable insights into the possible role of sex-bonding and tension management with social tolerance in bonobos and chimpanzees. Future studies may apply global social scan methods to more easily acquire substantial data on social relationships over a short period of time.

9.6.3 A mixed methods approach to empathy and reassurance

Throughout this thesis, I have highlighted the importance of investigating the socio-emotional capacities of great apes via multiple methods across multiple groups to gather the most comprehensive picture of intra- and interspecific tendencies and trends. Furthermore, I have also described the lack of clear function testing present in my research of reassurance. To uncover the mechanisms that may link consolation and other forms of reassurance, future studies could seek a comparative investigation of whether victim-directed reassurance and pre-competition reassurance associate with arousal reduction and other functions, such as protective (as in bonobo consolation: Palagi & Norscia, 2013) or selfish motivations (Batson, 2010). Studies of captive and wild primates have shown that the use of physiological measures to assess arousal is possible (e.g., Chotard et al., 2018; Dezecache et al., 2017), and anxiety is often also measured via recording self-directed behaviours (Baker & Aureli, 1997).

Furthermore, comparisons across groups would allow researchers to explore associations between group-level social factors, such as social tolerance (de Waal & Aureli, 1996), and how these behaviours are expressed. Combining these methods would provide a broader and more comprehensive view of how forms of reassurance are promoted or inhibited by physiological, social, and individual factors. In addition, the motivations and functions for consolation can vary (Romero & de Waal, 2010; Romero et al., 2011; Wittig & Boesch, 2003), and a comparative investigation of *Pan* could yield fascinating insights into shared and varied mechanisms that drive empathy in our closest living relatives.

9.7 Conclusion

As comparative science continues to reveal, we share a multitude of behaviours and capacities with other species, particularly the great apes. The use of reassuring body contact is no exception. Bonobos and chimpanzees are highly flexible and adaptable and particular conditions and pressures may influence tendencies to express socio-emotional behaviours. As the field of animal behaviour—including the subfield of animal empathy—has progressed, so too has our understanding that the building blocks of moral concepts may be embedded in animal societies, including reciprocity, cooperation, and conflict management. Through this thesis, I have argued for the significance of comparing multiple groups of bonobos and chimpanzees to gain the widest, and most inclusive picture of socio-emotional and cognitive behaviour of our closest relatives. I have shown that these species overlap considerably in their use of affiliative contacts during two contexts of social tension; as consolation and pre-feeding interactions. I have further shown that the most revealing variation in *Pan* lay at the group level. This within-species variation parallels with the stark cultural variation we see in humans regarding many aspects of socio-emotional behaviours. Thus, there is support for the notion that a capacity for empathy along with individual- and group-level variation was present in the last common ancestor of humans and the *Pan* lineage.

Whilst previously assumed to have emerged only in humans, empathy and its various behavioural components are observable across the animal kingdom. However, when investigating how empathy and related behaviours emerged, we must look beyond species comparisons and dig deeper into between- and within- community variation. The future of animal empathy research should include the systematic comparison of groups of the same species to explore within-community drivers and possible cultural flexibility in emotional responsiveness. Instead of approaching the evolution of human behaviour from a top-down perspective, it would be more revealing to acknowledge species- and group-specific abilities from a bottom-up approach. Studying socio-cognitive and socio-emotional behaviours through identifying their manifestation from bottom-up processes would help us understand the ancient emergence of human behaviour across our nonlinear evolutionary ancestry.

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Appendices

Appendix A: Ethograms

A.1: Contact-affiliation ethogram

Ethogram for contact-affiliation behaviours recorded during consolation and pre-feeding affiliation coding (*Chapters 4-8*). Based on Nishida et al. (2010), Goodall (1986), de Waal (1988), and Kano (1992).

Behaviour	Description
**Body kiss	Kiss or soft gnaw on the recipient's body, or burying face in other's fur. Not within a play context.
Contact sit	Sitting in physical contact with another individual. Not engaged in any other social behaviour.
Embrace	Gently placing one arm around the other's shoulder, back or waist, or putting both arms around the other. May include pulling him or her closer. Includes lateral, ventral and side hugging/embracing.
**Finger/hand in mouth	Placement of one's finger or hand in another individual's mouth (actor is one who extends hand/finger).
*Genito-genital contact[a]	Ventro-ventral embrace. Individuals swing their hips laterally, while keeping vulvae in contact. Not common in chimpanzees.
Genital inspection	Individual touches genitals of another with hand or foot. May sniff finger or sniff genitals directly but only code if contact occurs. Do not code sniffing without contact. May groom. May shake penis. Includes poking.
Grasp hand	Individual grasps hand of another individual, usually without shaking motion.
Groom	Pushing the hair of another individual back with the thumb or index finger of one hand and holding it back while picking at the exposed skin with the nail of the thumb, index finger, teeth, or lips of the other. ≥ 5sec duration; score only first interaction per grooming session; new event only after 30sec w/o grooming.
Hunch-over	One arm or the entire upper body is moved over or briefly pressed on the crouching partner. Not hugging/embracing.
Mount	Dorsal-ventral embrace. Individual touches or holds another's back or sides with or without intromission. May include thrusting pelvis movements. May include body kissing.
Mouth kiss	Kissing in mouth-nose region.
*Mount walk[b]	Resting head, arms or chest on the back of another individual while moving forward.
Pat[e]	Repeatedly tapping a hand on another individual's body.
Play	Any instances of playful behaviour solo or with a partner (including wrestling and tickling). May or may not be accompanied by play faces and/or laughter.
**Rump-rump touch[c]	Individuals face away from each other while putting their rumps in contact. Usually, no swinging or rubbing.
Touch	Other gentle hand or foot contact, including holding. Laying palm or fingers on another individual.

** Typically, only seen in bonobos*

*** Typically, only seen in chimpanzees*

[a] *"Genito-genital contact" and "Rump-rump touch" merged due to similarity in form*

[b] *Coded separately but merged with "Mount" due to rarity of occurrences*

[c] *Coded separately but merged with "Touch" due to rarity of occurrences*

A.2: Non-contact-affiliation ethogram

Ethogram for non-contact-affiliation behaviours recorded during pre-feeding affiliation coding (*Chapter 5*). Based on Nishida et al. (2010), Goodall (1986), de Waal (1988), and Kano (1992).

Behaviour	Description
**Bob	Body bobs up and down as elbows are flexed and straightened. Sequence usually repeats rapidly. Can be bipedal.
**Bow/crouch	Bow: Approaching another individual and flexing elbows to a greater extent than flexing knees. Usually associated with soft panting. Crouch: Legs flexed equally or more than the arms, occurs in a similar context to that in which bowing is seen.
Hold out hand	Actor, either sitting or standing, extends its arm roughly horizontally towards a fellow generally with the palm facing up.
Hold out hand bent	Same as "Hold out hand" but hand bent and palm-down.
Peering	Individual stares directly into the face of another individual with a distance of about 30cm or closer.
Sexual invitation	Male = concave back, penile erection; Female = crouch present (include rump turning). Some young males may present their rumps to other individuals. Includes successful and unsuccessful requests for contact.
**Submissive greeting	Individual directs ≥ 2 pant-grunts towards other individual, may approach them.

*** Typically, only seen in chimpanzees.*

A.3: Conflict ethogram

Ethogram for non-contact-affiliation behaviours recorded during pre-feeding affiliation coding (*Chapter 5*). Based on Nishida et al. (2010), Goodall (1986), de Waal (1988), and Kano (1992).

Behaviour	Description
Bluff display (directed)	A combination of any of the following: piloerection, bang on doors, drag hands on ground, wield sticks/stones, charge, stamp ground, swagger walk, rock, pant-hoot.
Chase	Aggressor chases victim. Victim runs at full speed.
High-contact aggression	Any of the following: slap, hit, stamp, kick, grab, bite.
Low-contact aggression	Any of the following: light-push, poke, shove.
Threat	Anticipatory gesture or movement to suggest aggression may initiate. Behaviours include head tip, throw at, threat bark, compressed lips, hunch, raise arm quickly. Does not include bluff behaviours.

Appendix B: *Chapter 4* supplementary

***Model 1.1*: Random slope estimates and stability output**

Term	Estimate	Min	Max
aggressor@(Intercept)@NA	0.626	0.407	0.723
aggressor@z.bystanders@NA	0.314	0.215	0.416
aggressor@(Intercept)@z.bystanders	-1.000	-1.000	-1.000
victim@(Intercept)@NA	0.709	0.233	0.797
victim@z.bystanders@NA	0.155	0.041	0.618
victim@(Intercept)@z.bystanders	1.000	0.775	1.000

***Model 1.2*: Random slope estimates and stability output**

Term	Estimate	Min	Max
aggressor@(Intercept)@NA	0.404	0.253	0.449
aggressor@z.bystanders@NA	0.207	0.141	0.272
aggressor@(Intercept)@z.bystanders	-1.000	-1.000	-1.000
victim@(Intercept)@NA	0.367	0.282	0.439
victim@z.bystanders@NA	0.153	0.086	0.203
victim@(Intercept)@z.bystanders	1.000	1.000	1.000

***Model 2.1*: Random slope estimates and stability output**

Term	Estimate	Min	Max
bystander@(Intercept)@NA	0.000	0.000	0.000
bystander@z.victim_age@NA	0.620	0.000	0.764
bystander@victim_sex.M@NA	0.983	0.000	1.347
victim@(Intercept)@NA	0.000	0.000	0.067
victim@z.bystander_age@NA	0.522	0.293	0.703

***Model 2.2*: Random slope estimates and stability output**

Term	Estimate	Min	Max
bystander@(Intercept)@NA	0.854	0.694	0.921
bystander@victim_sex.M@NA	0.328	0.000	1.162
victim@(Intercept)@NA	0.575	0.460	0.733
victim@kinship.nonkin@NA	0.599	0.000	1.698
victim@z.bystander_age@NA	0.261	0.000	0.427
victim@bystander_rank.low@NA	0.951	0.769	1.281
victim@bystander_sex.M@NA	0.622	0.105	1.118
victim@z.proxaff@NA	0.318	0.000	0.456

Appendix C: *Chapter 5* supplementary

C.1: *Model 2* with group B3 included

Summary of *Model 2* (with group B3 included), a Bayesian generalised linear mixed model for group comparisons of pre-feeding affiliation in sanctuary-living groups of bonobos and chimpanzees. This Bernoulli distribution model included group B3, which revealed great uncertainty due to no observations of male-male dyads in group B3 engaging in any pre-feeding affiliative contact across all observations. Thus, in *Chapter 5*, I present *Model 2* with an identical model structure on a reduced dataframe with group B3 removed. The credibility and robustness of all other effects match those in the version of *Model 2* without group B3. Robust effects of predictors (i.e., in the frequentist approach, "significant" effects) are highlighted in italic-bold font. Dependent variable listed in header line. Abbreviations: F-F = Female-Female; F-M = Female-Male; MM = Male-Male.

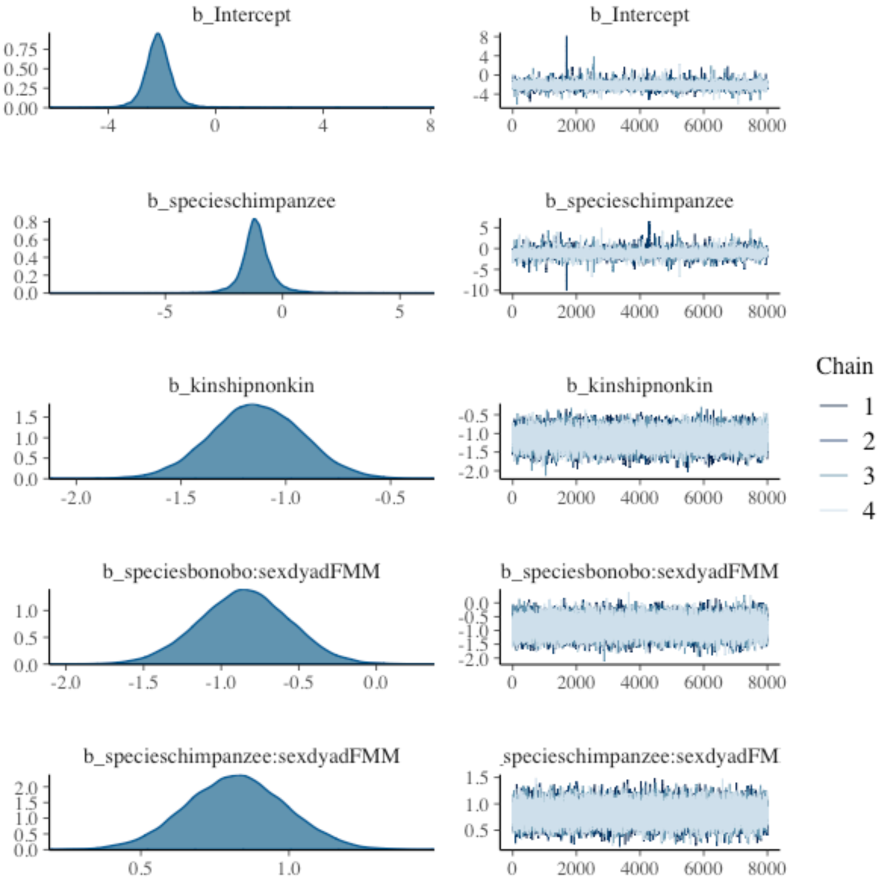
Model 2 Group differences in pre-feeding contact-affiliation tendencies [including group B3] (observations *N* = 12694), binary variable (0 = no contact, 1 = 1+ contacts)

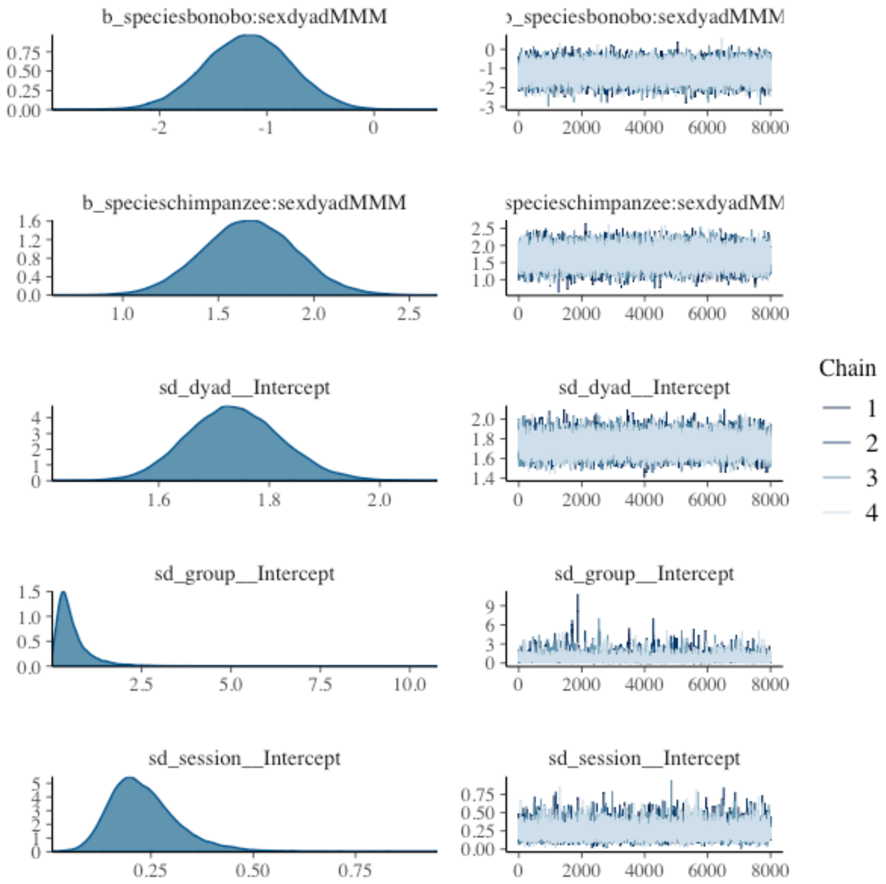
	eff. *N*	$\hat{R}$	*b*	*S.D.*	2.50%	97.50%	Default Prior
Intercept	1145	1	-2.90	0.41	-3.72	-2.09	student_t(3, 0, 2.5)
Group[a]							
[B2]	1069	***1***	***1.47***	***0.53***	***0.43***	***2.51***	***(flat)***
[B3]	***1069***	1	0.93	0.55	-0.13	2.01	(flat)
[C1]	1091	1	-0.20	0.53	-1.04	0.65	(flat)
[C2]	1131	1.01	-0.65	0.38	-1.38	0.11	(flat)
Kinship [nonkin][b]	1485	***1***	***-1.08***	***0.22***	***-1.51***	***-0.66***	***(flat)***
Group [B1] x Sex-dyad [F-M][c]	***1089***	1	-0.06	0.43	-0.88	0.78	(flat)
Group [B2] x Sex-dyad [F-M][c]	1448	***1***	***-1.30***	***0.52***	***-2.33***	***-0.29***	***(flat)***
Group [B3] x Sex-dyad [F-M][c]	***1570***	***1***	***-1.86***	***0.63***	***-3.12***	***-0.66***	***(flat)***
Group [C1] x Sex-dyad [F-M][c]	***1750***	***1***	***0.75***	***0.34***	***0.09***	***1.44***	***(flat)***
Group [C2] x Sex-dyad [F-M][c]	***2308***	***1***	***0.84***	***0.20***	***0.46***	***1.24***	***(flat)***
Group [B1] x Sex-dyad [M-M][c]	1608	1	-0.24	0.57	-1.39	0.86	(flat)
Group [B2] x Sex-dyad [M-M][c]	***1930***	***1***	***-1.51***	***0.68***	***-2.86***	***-0.21***	***(flat)***
Group [B3] x Sex-dyad [M-M][c]	***651***	***1***	***-298.67***	***412.90***	***-1408.94***	***-9.36***	***(flat)***
Group [C1] x Sex-dyad [M-M][c]	2133	1	0.87	0.55	-0.22	1.94	(flat)
Group [C2] x Sex-dyad [M-M][c]	***1684***	***1***	***1.87***	***0.28***	***1.32***	***2.43***	***(flat)***
Dyad Intercept	2615	1	1.74	0.09	1.58	1.92	student_t(3, 0 ,2.5)
Session Intercept	3178	1	0.24	0.09	0.11	0.44	student_t(3, 0, 2.5)

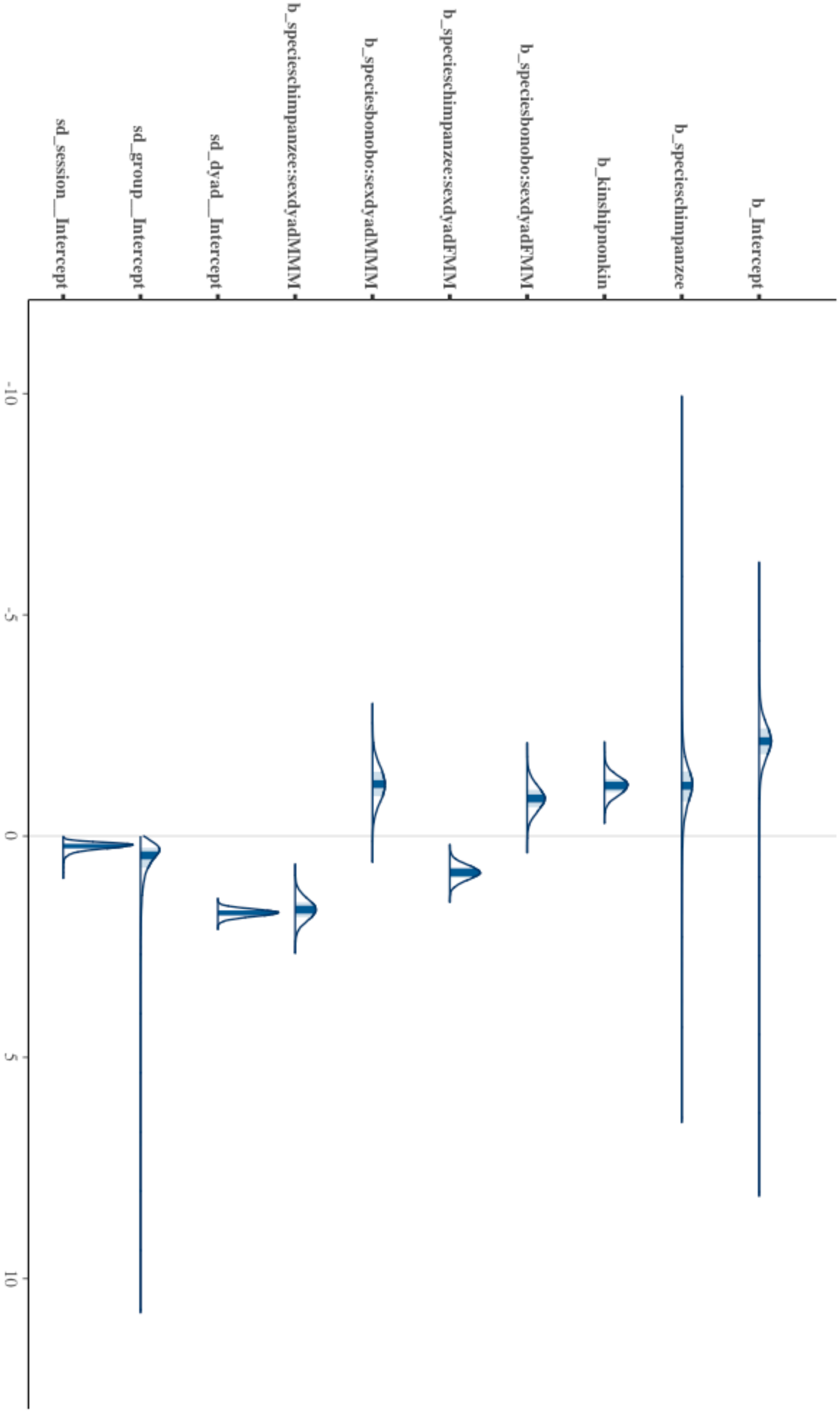
[a] *Reference level = B1*
[b] *Reference level = Kin*
[c] *Reference level = B1 Female-Female*

C.2: *Model 1* diagnostics checks

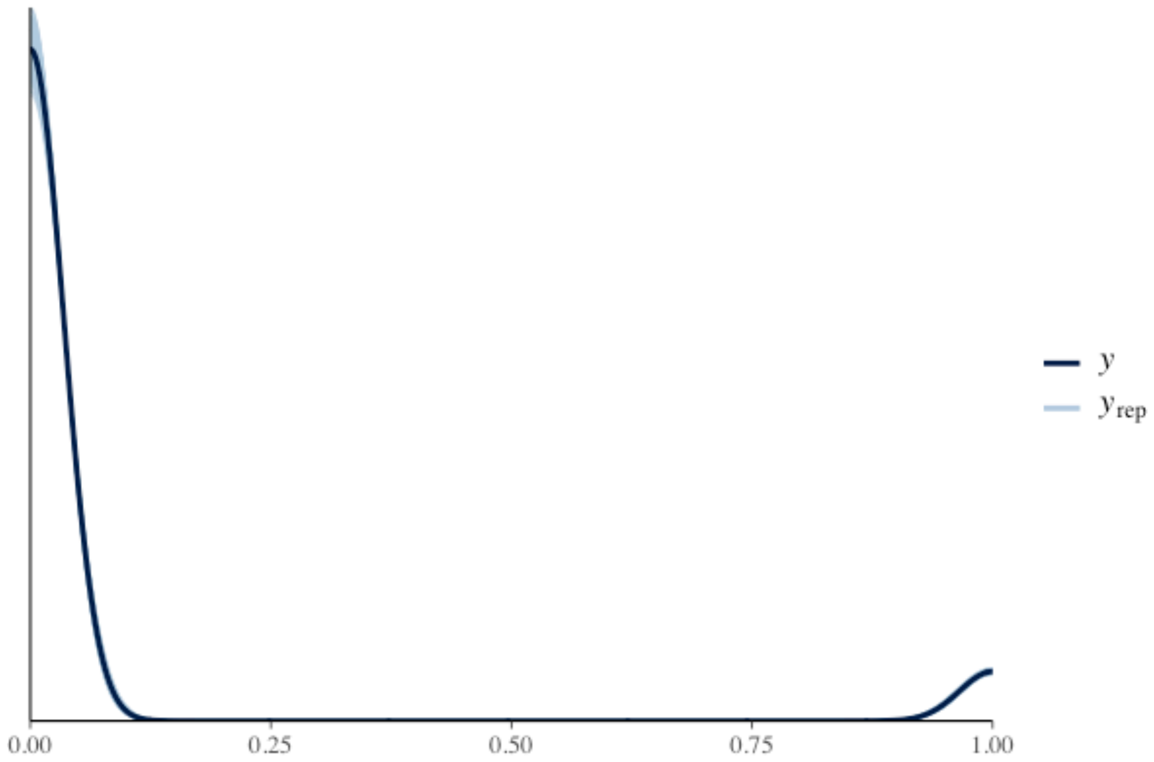
***Model 1*: Trace plots of MCMC chains and posterior distributions.**




b_speciesbonobo:sexdyadMMM
b_specieschimpanzee:sexdyadMMM
sd_dyad__Intercept
sd_group__Intercept
sd_session__Intercept
Chain
1
2
3
4
0
2000
4000
6000
8000


b_Intercept
b_specieschimpanzee
b_kinshipnonkin
b_speciesbonobo:sexdyadFMM
b_specieschimpanzee:sexdyadFMM
b_speciesbonobo:sexdyadMMM
b_specieschimpanzee:sexdyadMMM
sd_dyad__Intercept
sd_group__Intercept
sd_session__Intercept
-10
-5
0
5
10

***Model 1*: Posterior predictive check.**



C.3: *Model 2* pairwise comparisons and diagnostics checks

Summary of pairwise contrasts for *Model 2*, comparing pre-feeding contact-affiliation tendencies across sex-dyads within- and between-group (excluding group B3). Parameter estimates are on the logit scale and were obtained through the hpd.summary function of the package emmeans. Abbreviations: F-F = Female-Female; F-M = Female-Male; M-M = Male-Male.

***Model* 2. Within-group pairwise comparisons for group:sex-dyad**

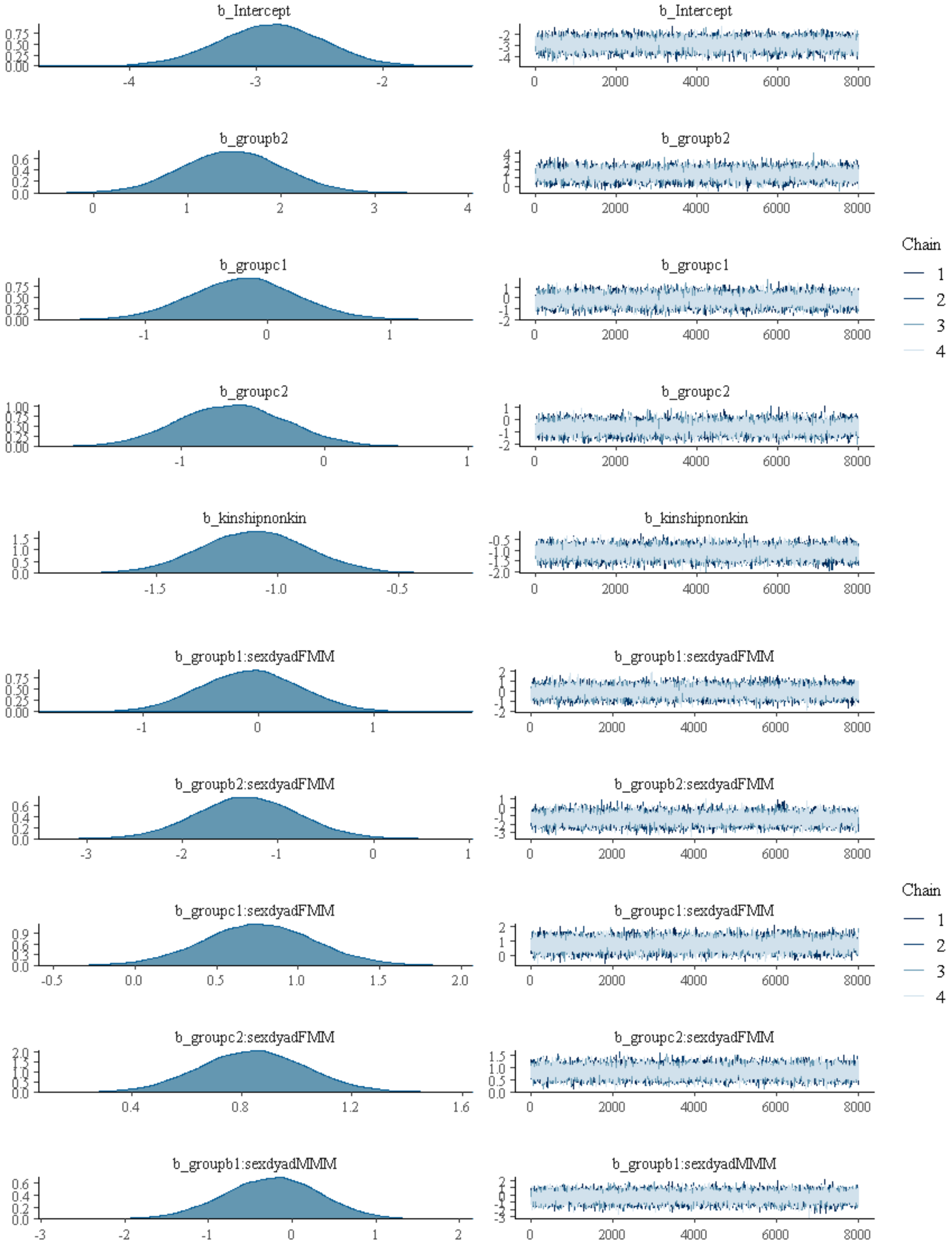
Contrasts	*b*	*S.D.*	*Lower HPD*	*Upper HPD*
(B1 F-F) - (B1 F-M)	0.07	0.44	-0.78	0.92
(B1 F-F) - (B1 M-M)	0.25	0.57	-0.86	1.37
(B1 F-M) - (B1 M-M)	0.17	0.53	-0.88	1.19
(B2 F-F) - (B2 F-M)	***1.32***	***0.53***	***0.28***	***2.37***
(B2 F-F) - (B2 M-M)	***1.50***	***0.68***	***0.17***	***2.85***
(B2 F-M) - (B2 M-M)	0.17	0.64	-1.08	1.43
(C1 F-F) - (C1 F-M)	***-0.76***	***0.34***	***-1.43***	***-0.08***
(C1 F-F) - (C1 M-M)	-0.87	0.55	-1.91	0.22
(C1 F-M) - (C1 M-M)	-0.11	0.53	-1.13	0.95
(C2 F-F) - (C2 F-M)	***-0.84***	***0.19***	***-1.21***	***-0.45***
(C2 F-F) - (C2 M-M)	***-1.86***	***0.28***	***-2.42***	***-1.32***
(C2 F-M) - (C2 M-M)	***-1.02***	***0.27***	***-1.54***	***-0.49***

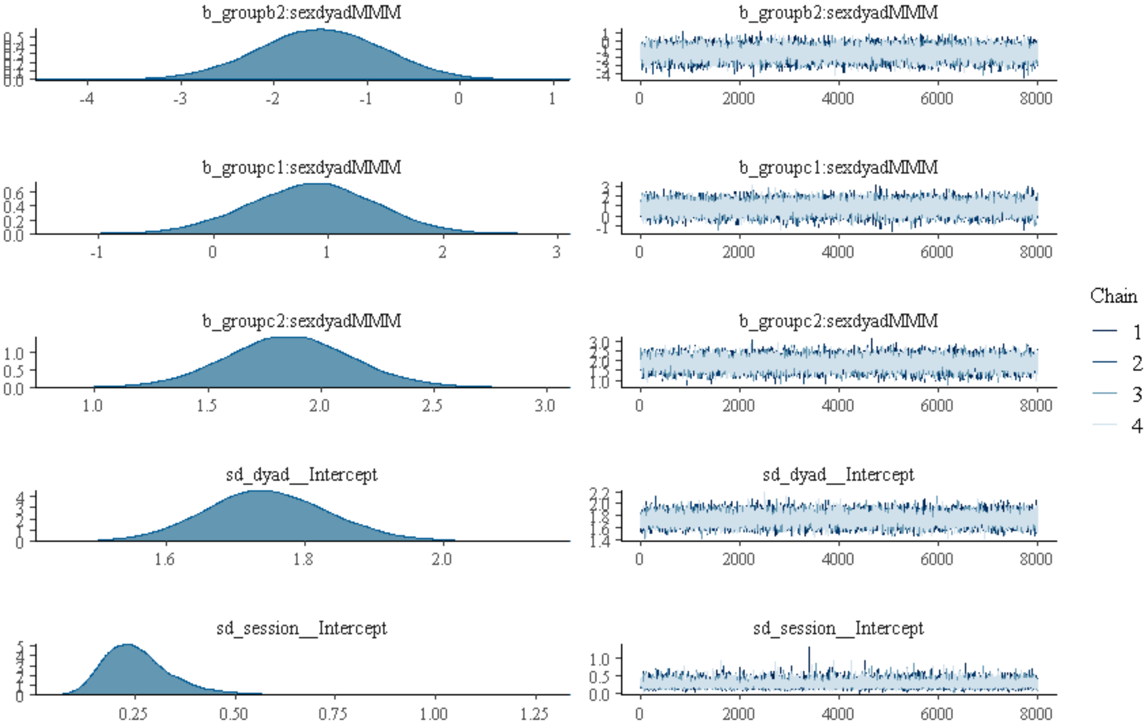
***Model* 2. Between-group pairwise comparisons for group:sex-dyad**

Contrasts	*b*	*S.D.*	*Lower HPD*	*Upper HPD*
(B1 F-F) - (B2 F-F)	***-1.48***	***0.54***	***-2.54***	***-0.42***
(B1 F-F) - (C1 F-F)	0.19	0.43	-0.65	1.05
(B1 F-F) - (C2 F-F)	0.64	0.38	-0.11	1.36
(B1 F-F) - (B2 F-M)	-0.16	0.48	-1.10	0.77
(B1 F-F) - (C1 F-M)	-0.57	0.42	-1.38	0.25
(B1 F-F) - (C2 F-M)	-0.20	0.37	-0.91	0.55
(B1 F-F) - (B2 M-M)	0.02	0.65	-1.24	1.30
(B1 F-F) - (C1 M-M)	-0.67	0.60	-1.82	0.51
(B1 F-F) - (C2 M-M)	***-1.22***	***0.42***	***-2.04***	***-0.40***
(B2 F-F) - (C1 F-F)	***1.67***	***0.49***	***0.73***	***2.65***
(B2 F-F) - (C2 F-F)	***2.12***	***0.44***	***1.23***	***2.96***
(B2 F-F) - (B1 F-M)	***1.55***	***0.49***	***0.58***	***2.51***
(B2 F-F) - (C1 F-M)	***0.91***	***0.48***	***0.00***	***1.86***
(B2 F-F) - (C2 F-M)	***1.28***	***0.44***	***0.43***	***2.14***
(B2 F-F) - (B1 M-M)	***1.73***	***0.62***	***0.55***	***2.99***
(B2 F-F) - (C1 M-M)	0.81	0.64	-0.47	2.07
(B2 F-F) - (C2 M-M)	0.26	0.48	-0.65	1.22
(C1 F-F) - (C2 F-F)	0.45	0.30	-0.13	1.05
(C1 F-F) - (B1 F-M)	-0.12	0.37	-0.86	0.60
(C1 F-F) - (B2 F-M)	-0.35	0.43	-1.16	0.51

(C1 F-F) - (C2 F-M)	-0.39	0.29	-0.97	0.18
(C1 F-F) - (B1 M-M)	0.06	0.53	-0.95	1.12
(C1 F-F) - (B2 M-M)	-0.17	0.61	-1.38	1.00
(C1 F-F) - (C2 M-M)	***-1.41***	***0.35***	***-2.11***	***-0.73***
(C2 F-F) - (B1 F-M)	-0.58	0.31	-1.18	0.02
(C2 F-F) - (B2 F-M)	***-0.80***	***0.37***	***-1.51***	***-0.08***
(C2 F-F) - (C1 F-M)	***-1.21***	***0.27***	***-1.75***	***-0.68***
(C2 F-F) - (B1 M-M)	-0.40	0.48	-1.34	0.56
(C2 F-F) - (B2 M-M)	-0.62	0.57	-1.74	0.48
(C2 F-F) - (C1 M-M)	***-1.32***	***0.51***	***-2.29***	***-0.31***
(B1 F-M) - (B2 F-M)	-0.22	0.43	-1.07	0.60
(B1 F-M) - (C1 F-M)	-0.63	0.35	-1.32	0.05
(B1 F-M) - (C2 F-M)	-0.26	0.30	-0.87	0.32
(B1 F-M) - (B2 M-M)	-0.05	0.61	-1.26	1.12
(B1 F-M) - (C1 M-M)	-0.74	0.55	-1.81	0.34
(B1 F-M) - (C2 M-M)	***-1.28***	***0.36***	***-1.99***	***-0.58***
(B2 F-M) - (C1 F-M)	-0.41	0.40	-1.18	0.40
(B2 F-M) - (C2 F-M)	-0.04	0.36	-0.76	0.65
(B2 F-M) - (B1 M-M)	0.41	0.57	-0.68	1.53
(B2 F-M) - (C1 M-M)	-0.51	0.59	-1.68	0.62
(B2 F-M) - (C2 M-M)	***-1.06***	***0.41***	***-1.86***	***-0.26***
(C1 F-M) - (C2 F-M)	0.37	0.27	-0.15	0.89
(C1 F-M) - (B1 M-M)	0.82	0.51	-0.16	1.84
(C1 F-M) - (B2 M-M)	0.59	0.59	-0.59	1.74
(C1 F-M) - (C2 M-M)	***-0.65***	***0.33***	***-1.31***	***-0.02***
(C2 F-M) - (B1 M-M)	0.44	0.48	-0.47	1.40
(C2 F-M) - (B2 M-M)	0.22	0.56	-0.87	1.33
(C2 F-M) - (C1 M-M)	-0.47	0.50	-1.42	0.55
(B1 M-M) - (B2 M-M)	-0.23	0.71	-1.58	1.19
(B1 M-M) - (C1 M-M)	-0.92	0.66	-2.22	0.39
(B1 M-M) - (C2 M-M)	***-1.46***	***0.52***	***-2.48***	***-0.45***
(B2 M-M) - (C1 M-M)	-0.69	0.73	-2.12	0.74
(B2 M-M) - (C2 M-M)	***-1.24***	***0.60***	***-2.39***	***-0.06***
(C1 M-M) - (C2 M-M)	***-0.55***	***0.54***	***-1.61***	***0.52***

***Model 2*: Trace plots of MCMC chains and posterior distributions.**

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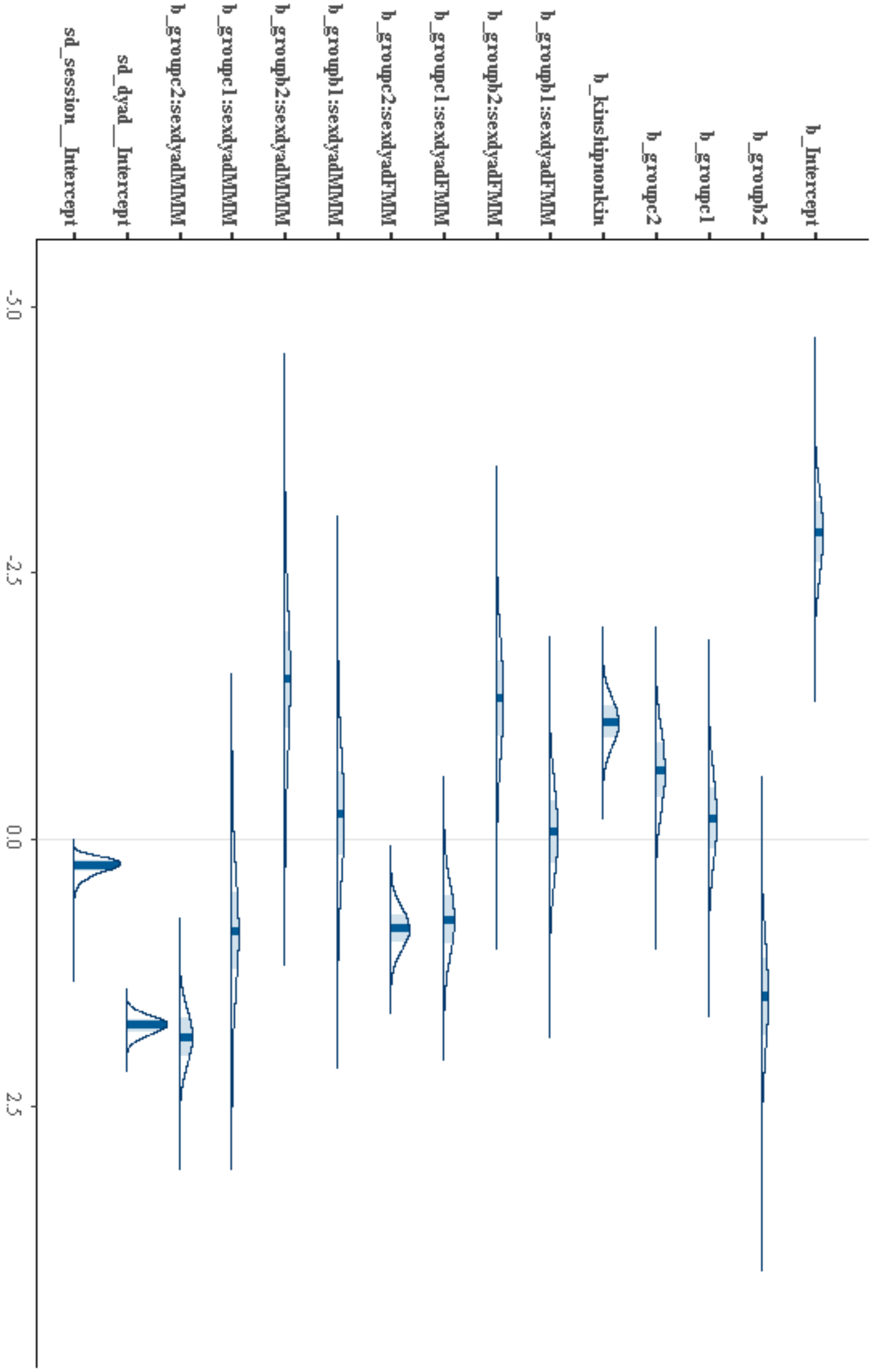
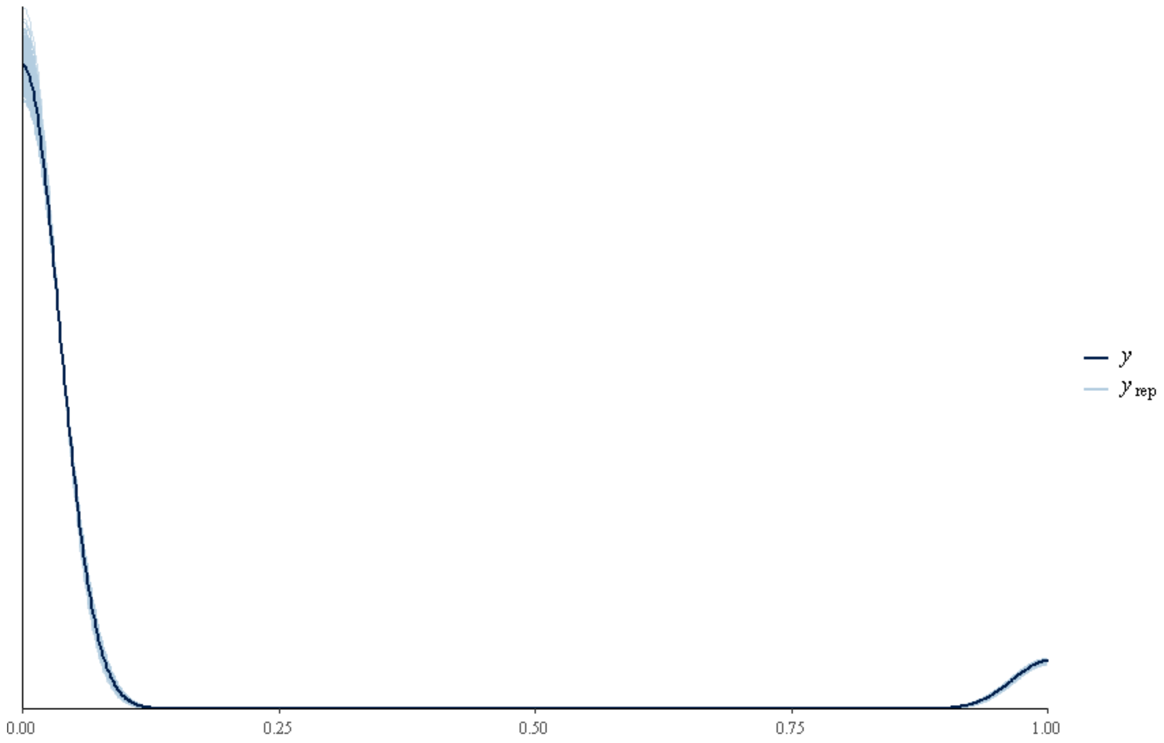
0.0
-4
-3
-2
-1
0
1
b_groupb2:sexdyadMMM
1
0
-4
0
2000
4000
6000
8000
b_groupc1:sexdyadMMM
0.6
0.4
0.2
0.0
-1
0
1
2
3
b_groupc1:sexdyadMMM
3
0
-1
0
2000
4000
6000
8000
b_groupc2:sexdyadMMM
1.0
0.5
0.0
1.0
1.5
2.0
2.5
3.0
b_groupc2:sexdyadMMM
3.0
2.0
1.0
0
2000
4000
6000
8000
sd_dyad__Intercept
4
0
1.6
1.8
2.0
sd_dyad__Intercept
2.2
2.0
1.8
1.6
1.4
0
2000
4000
6000
8000
sd_session__Intercept
5
0
0.25
0.50
0.75
1.00
1.25
sd_session__Intercept
1.0
0.5
0.0
0
2000
4000
6000
8000
Chain
1
2
3
4


b_Intercept
b_groupb2
b_groupc1
b_groupc2
b_kinshipnonkin
b_groupb1:sexdyadFMM
b_groupb2:sexdyadFMM
b_groupc1:sexdyadFMM
b_groupc2:sexdyadFMM
b_groupb1:sexdyadMMM
b_groupb2:sexdyadMMM
b_groupc1:sexdyadMMM
b_groupc2:sexdyadMMM
sd_dyad__Intercept
sd_session__Intercept
-5.0
-2.5
0.0
2.5

***Model 2*: Posterior predictive check.**



C.4: Statistical output for *Models 3.1–3.2*

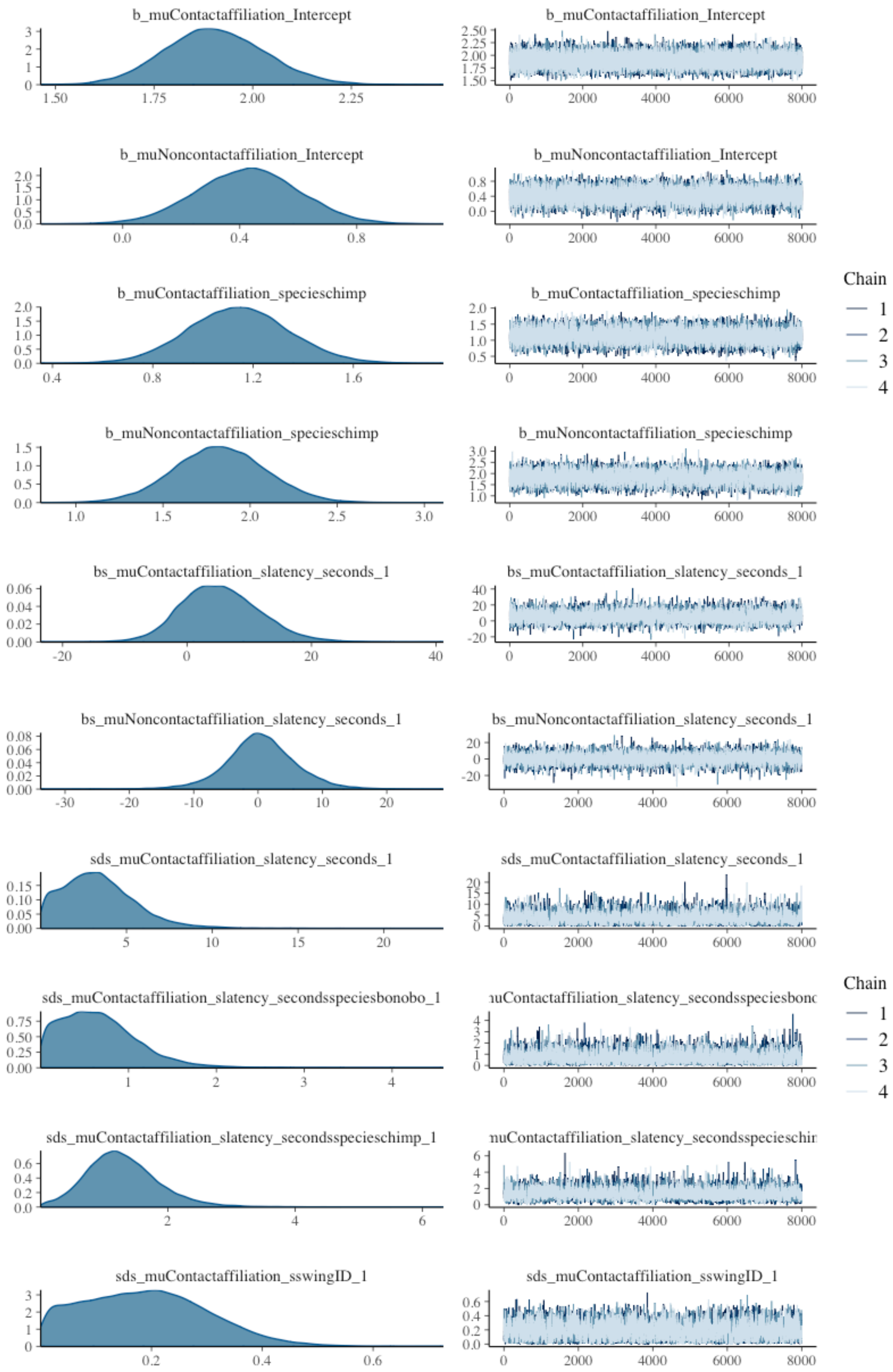
Model 3.1

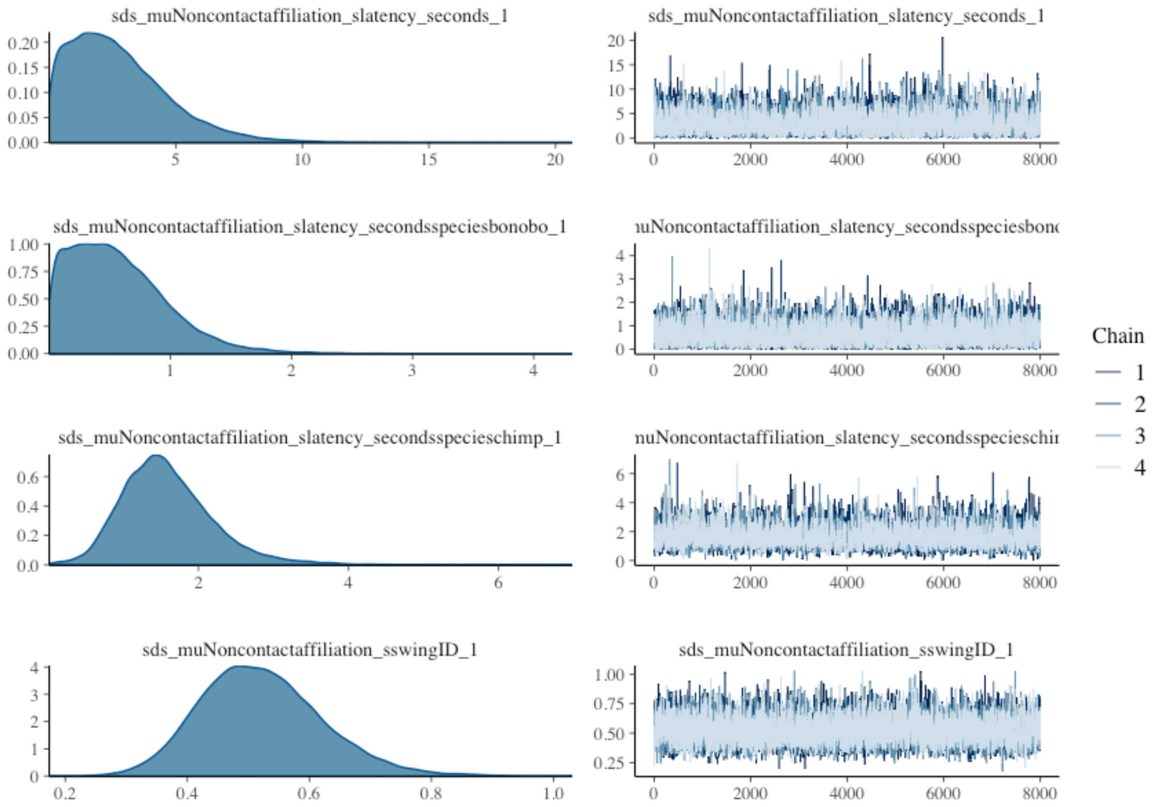
Summary of Bayesian Generalized Additive Model for species comparisons on the use of contact-affiliation, non-contact-affiliation, and conflict behaviour across sessions. The reference level for behaviour type is "Conflict". All population-level effects are on the logit scale and bonobo are the reference category.

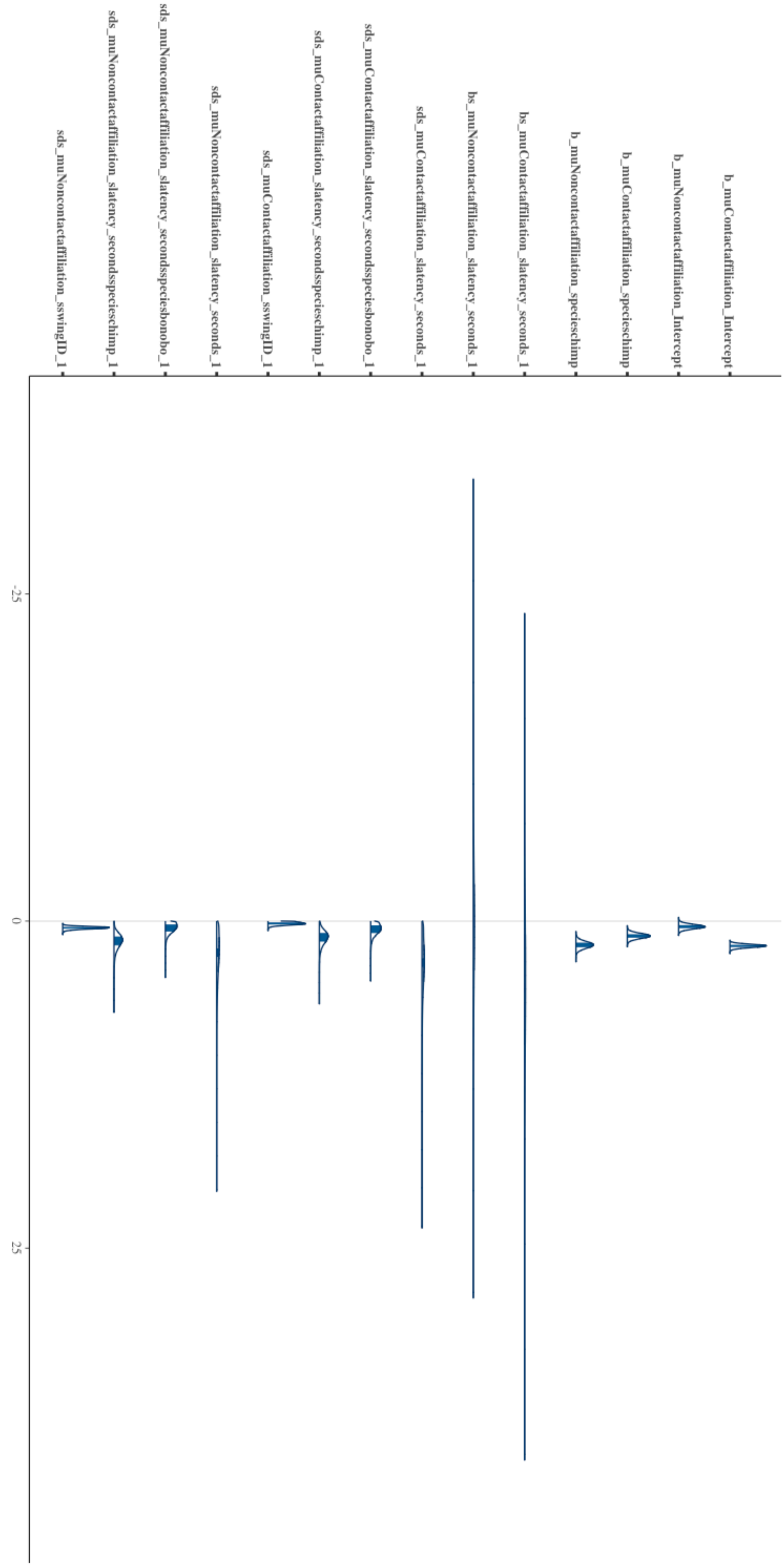
Model 3.1 Species variation in use of behaviour types across sessions

	eff. N	*b*	*S.D.*	*2.50%*	*97.50%*
Smooth Terms					
Contact-Affiliation_Latency_1	4,627	3.40	2.14	0.22	8.33
Contact-Affiliation_Latency_Species-Bonobo_1	5,206	0.66	0.44	0.03	1.68
Contact-Affiliation_Latency_Species-Chimpanzee_1	4,984	1.29	0.57	0.30	2.57
Contact-Affiliation_SwingID_1	4,175	0.19	0.11	0.01	0.42
Non-Contact-Affiliation_Latency_1	5,814	2.76	1.98	0.14	7.50
Non-Contact-Affiliation_Latency_Species-Bonobo_1	8,369	0.57	0.40	0.03	1.52
Non-Contact-Affiliation_Latency_Species-Chimpanzee_1	5,938	1.59	0.62	0.58	3.04
Non-Contact-Affiliation_SwingID_1	9,275	0.52	0.10	0.35	0.74
Population-Level Effects					
Contact-Affiliation_Intercept	32,000	1.90	0.13	1.66	2.16
Non-Contact-Affiliation_Intercept	16,151	0.43	0.18	0.08	0.77
Contact-Affiliation_Species-Chimpanzee	10,927	1.14	0.20	0.75	1.54
Non-Contact-Affiliation_Species-Chimpanzee	8,170	1.83	0.26	1.31	2.35
Contact-Affiliation_Latency_Seconds_1	7,715	5.41	6.29	-5.94	18.62
Non-Contact-Affiliation_Latency_Seconds_1	11,180	0.45	5.47	-10.63	11.52

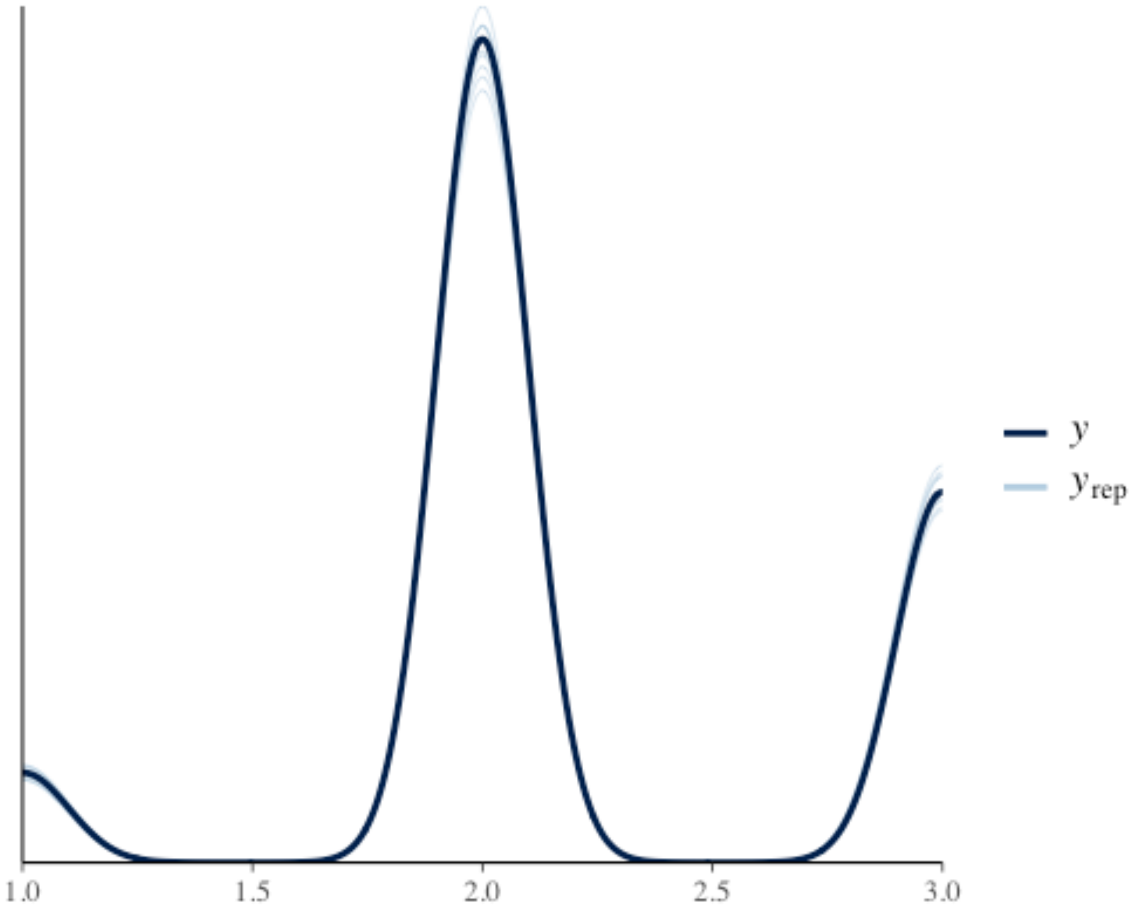
***Model 3.1*: Trace plots of MCMC chains and posterior distributions.**




sds_muNoncontactaffiliation_slatency_seconds_1
0.20
0.15
0.10
0.05
0.00
5
10
15
20
sds_muNoncontactaffiliation_slatency_seconds_1
20
15
10
5
0
0
2000
4000
6000
8000
sds_muNoncontactaffiliation_slatency_secondsspeciesbonobo_1
1.00
0.75
0.50
0.25
0.00
1
2
3
4
uNoncontactaffiliation_slatency_secondsspeciesbon
4
3
2
1
0
0
2000
4000
6000
8000
Chain
1
2
3
4
sds_muNoncontactaffiliation_slatency_secondsspecieschimp_1
0.6
0.4
0.2
0.0
2
4
6
nuNoncontactaffiliation_slatency_secondsspecieschi
6
4
2
0
0
2000
4000
6000
8000
sds_muNoncontactaffiliation_sswingID_1
4
3
2
1
0
0.2
0.4
0.6
0.8
1.0
sds_muNoncontactaffiliation_sswingID_1
1.00
0.75
0.50
0.25
0
2000
4000
6000
8000


b_muContactaffiliation_Intercept
b_muNoncontactaffiliation_Intercept
b_muContactaffiliation_specieschimp
b_muNoncontactaffiliation_specieschimp
bs_muContactaffiliation_slatency_seconds_1
bs_muNoncontactaffiliation_slatency_seconds_1
sds_muContactaffiliation_slatency_seconds_1
sds_muContactaffiliation_slatency_secondsspeciesbonobo_1
sds_muContactaffiliation_slatency_secondsspecieschimp_1
sds_muContactaffiliation_sswingID_1
sds_muNoncontactaffiliation_slatency_seconds_1
sds_muNoncontactaffiliation_slatency_secondsspeciesbonobo_1
sds_muNoncontactaffiliation_slatency_secondsspecieschimp_1
sds_muNoncontactaffiliation_sswingID_1
-25
0
25

***Model 3.1*: Posterior predictive check.**

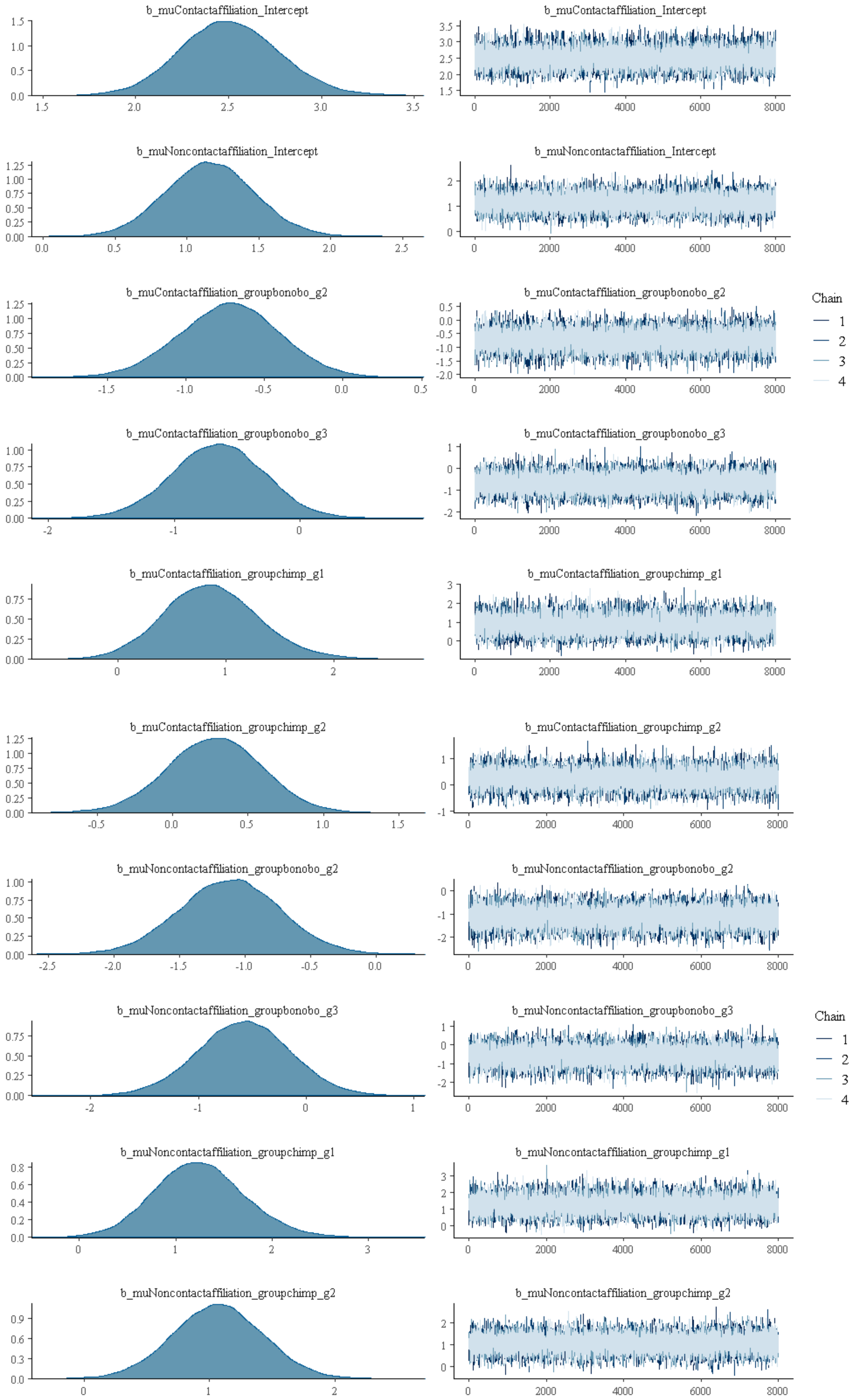


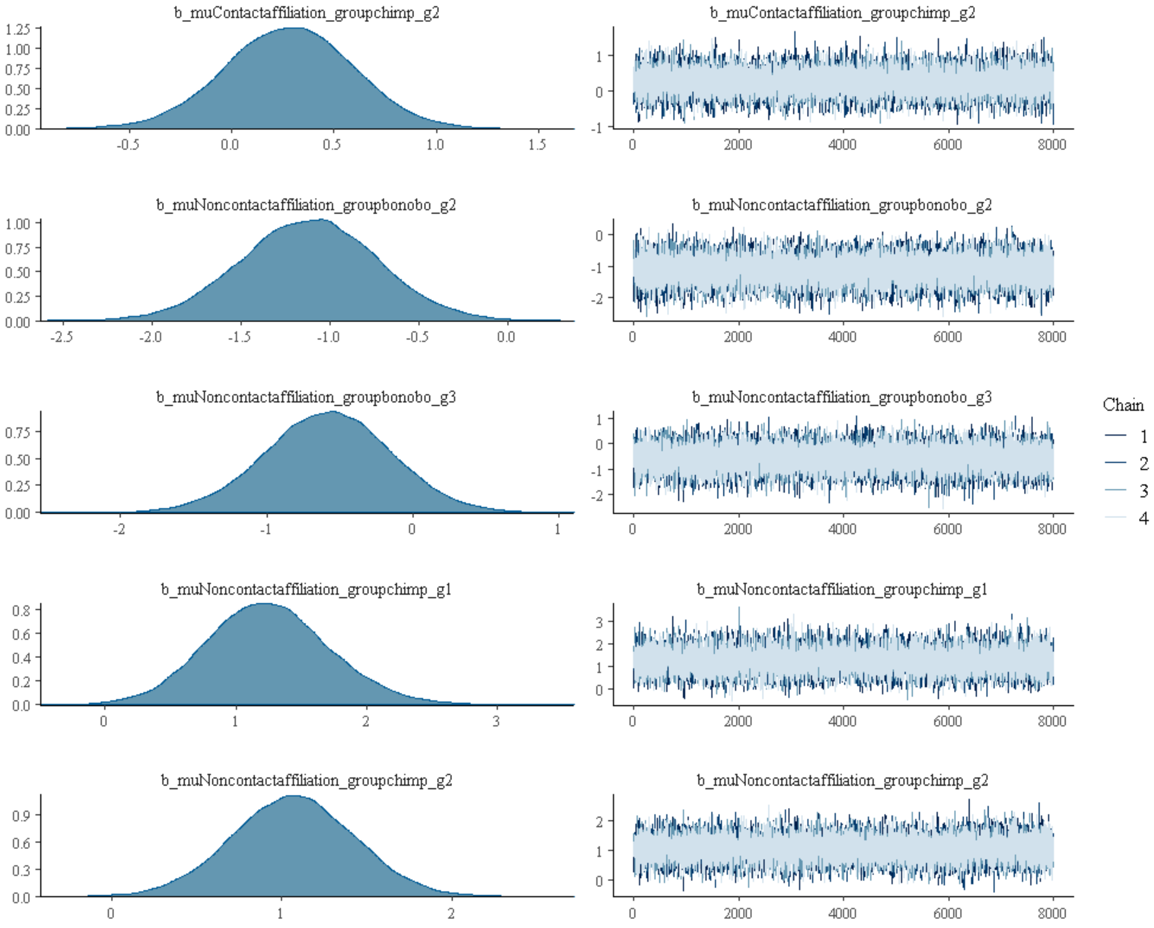
Model 3.2

Summary of Bayesian Generalized Additive Model for group comparisons on the use of contact-affiliation, non-contact-affiliation, and conflict behaviour across sessions. The reference level for behaviour type is "Conflict". All population-level effects are on the logit scale and group B1 are the reference category.

Model 3.2 Group variation in use of behaviour types across sessions					
	eff. N	*b*	*S.D.*	*2.50%*	*97.50%*
Smooth Terms					
Contact-Affiliation_Latency_1	7,821	5.13	1.87	2.46	9.72
Contact-Affiliation_Latency_Group-B1_1	9,727	0.45	0.37	0.02	1.39
Contact-Affiliation_Latency_Group-B2_1	13,334	0.30	0.26	0.01	0.97
Contact-Affiliation_Latency_Group-B3_1	10,560	0.50	0.43	0.02	1.59
Contact-Affiliation_Latency_Group-C1_1	5,460	1.28	0.62	0.34	2.73
Contact-Affiliation_Latency_Group-C2_1	6,322	0.34	0.30	0.01	1.12
Contact-Affiliation_SwingID_1	4,131	0.16	0.10	0.01	0.39
Non-Contact-Affiliation_Latency_1	5,720	5.26	2.13	1.89	10.22
Non-Contact-Affiliation_Latency_Group-B1_1	8,559	0.58	0.44	0.03	1.65
Non-Contact-Affiliation_Latency_Group-B2_1	8,204	0.53	0.41	0.02	1.52
Non-Contact-Affiliation_Latency_Group-B3_1	7,431	0.79	0.64	0.03	2.37
Non-Contact-Affiliation_Latency_Group-C1_1	3,884	0.88	0.59	0.05	2.29
Non-Contact-Affiliation_Latency_Group-C2_1	3,681	0.69	0.45	0.04	1.76
Non-Contact-Affiliation_SwingID_1	8,141	0.47	0.10	0.29	0.69
Population-Level Effects					
Contact-Affiliation_Intercept	5,501	2.50	0.25	2.03	3.00
Non-Contact-Affiliation_Intercept	5,139	1.14	0.32	0.52	1.77
Contact-Affiliation_Group-B2	6,156	-0.74	0.30	-1.33	-0.17
Contact-Affiliation_Group-B3	7,293	-0.67	0.34	-1.33	-0.01
Contact-Affiliation_Group-C1	4,787	0.96	0.44	0.14	1.90
Contact-Affiliation_Group-C2	5,861	0.32	0.29	-0.25	0.89
Non-Contact-Affiliation_Group-B2	5,862	-1.15	0.41	-1.95	-0.35
Non-Contactaffiliation_Group-B3	6,217	-0.61	0.45	-1.49	0.26
Non-Contactaffiliation_Group-C1	4,705	1.22	0.51	0.26	2.27
Non-Contactaffiliation_Group-C2	4,653	1.12	0.39	0.36	1.88
Contact-Affiliation_Latency_1	7,769	8.56	6.18	-3.68	20.73
Non-Contact-Affiliation_Latency_1	7,242	1.42	6.55	-12.04	14.09

Model 3.2: Trace plots of MCMC chains and posterior distributions.

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0.50
0.25
0.00
-0.5
0.0
0.5
1.0
1.5
b_muContactaffiliation_groupchimp_g2
1
0
-1
0
2000
4000
6000
8000
b_muNoncontactaffiliation_groupbonobo_g2
1.00
0.75
0.50
0.25
0.00
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
b_muNoncontactaffiliation_groupbonobo_g2
0
-1
-2
b_muNoncontactaffiliation_groupbonobo_g3
0.75
0.50
0.25
0.00
-2
-1
0
1
b_muNoncontactaffiliation_groupbonobo_g3
1
0
-1
-2
Chain
1
2
3
4
b_muNoncontactaffiliation_groupchimp_g1
0.8
0.6
0.4
0.2
0.0
0
1
2
3
b_muNoncontactaffiliation_groupchimp_g1
3
2
1
0
b_muNoncontactaffiliation_groupchimp_g2
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0.3
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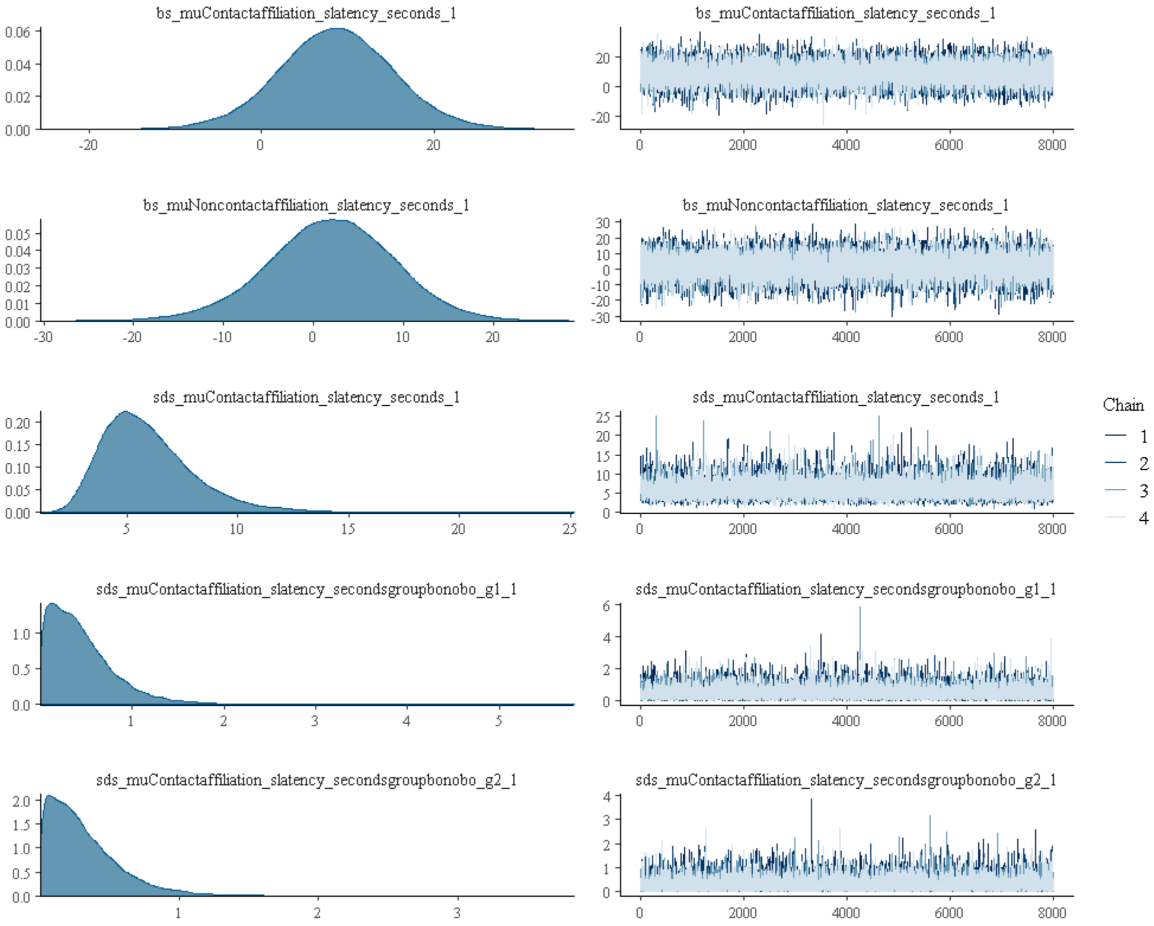
1
2
b_muNoncontactaffiliation_groupchimp_g2
2
1
0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-20
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20
0
-20
0
2000
4000
6000
8000
bs_muNoncontactaffiliation_slatency_seconds_1
0.05
0.04
0.03
0.02
0.01
0.00
-30
-20
-10
0
10
20
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30
20
10
0
-10
-20
-30
sds_muContactaffiliation_slatency_seconds_1
0.20
0.15
0.10
0.05
0.00
5
10
15
20
25
sds_muContactaffiliation_slatency_seconds_1
25
20
15
10
5
0
Chain
1
2
3
4
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0.5
0.0
1
2
3
4
5
sds_muContactaffiliation_slatency_secondsgroupbonobo_g1_1
6
4
2
0
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2.0
1.5
1.0
0.5
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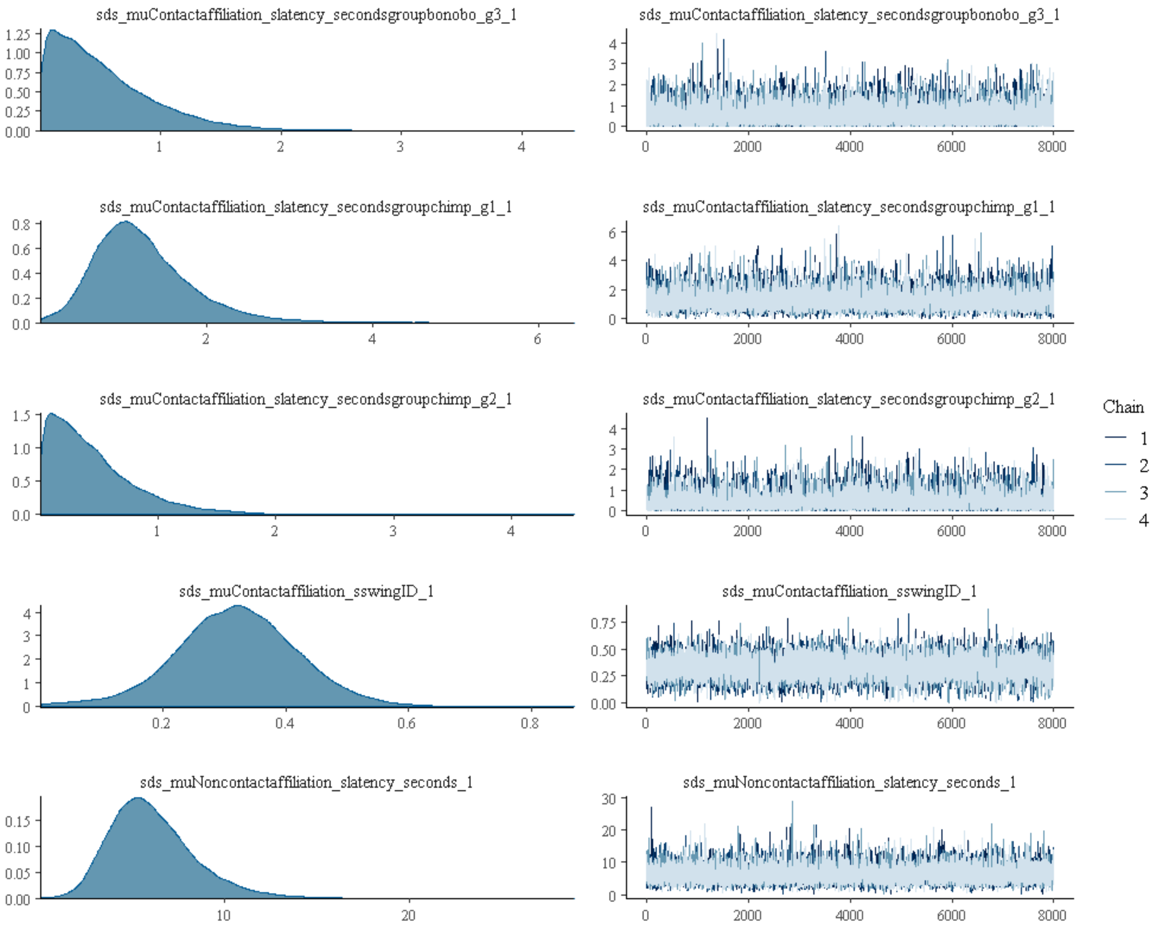
1
2
3
sds_muContactaffiliation_slatency_secondsgroupbonobo_g2_1
4
3
2
1
0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0.75
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0.25
0.00
1
2
3
4
sds_muContactaffiliation_slatency_secondsgroupbonobo_g3_1
4
3
2
1
0
0
2000
4000
6000
8000
sds_muContactaffiliation_slatency_secondsgroupchimp_g1_1
0.8
0.6
0.4
0.2
0.0
2
4
6
sds_muContactaffiliation_slatency_secondsgroupchimp_g1_1
6
4
2
0
0
2000
4000
6000
8000
sds_muContactaffiliation_slatency_secondsgroupchimp_g2_1
1.5
1.0
0.5
0.0
1
2
3
4
sds_muContactaffiliation_slatency_secondsgroupchimp_g2_1
4
3
2
1
0
0
2000
4000
6000
8000
Chain
1
2
3
4
sds_muContactaffiliation_sswingID_1
4
3
2
1
0
0.2
0.4
0.6
0.8
sds_muContactaffiliation_sswingID_1
0.75
0.50
0.25
0.00
0
2000
4000
6000
8000
sds_muNoncontactaffiliation_slatency_seconds_1
0.15
0.10
0.05
0.00
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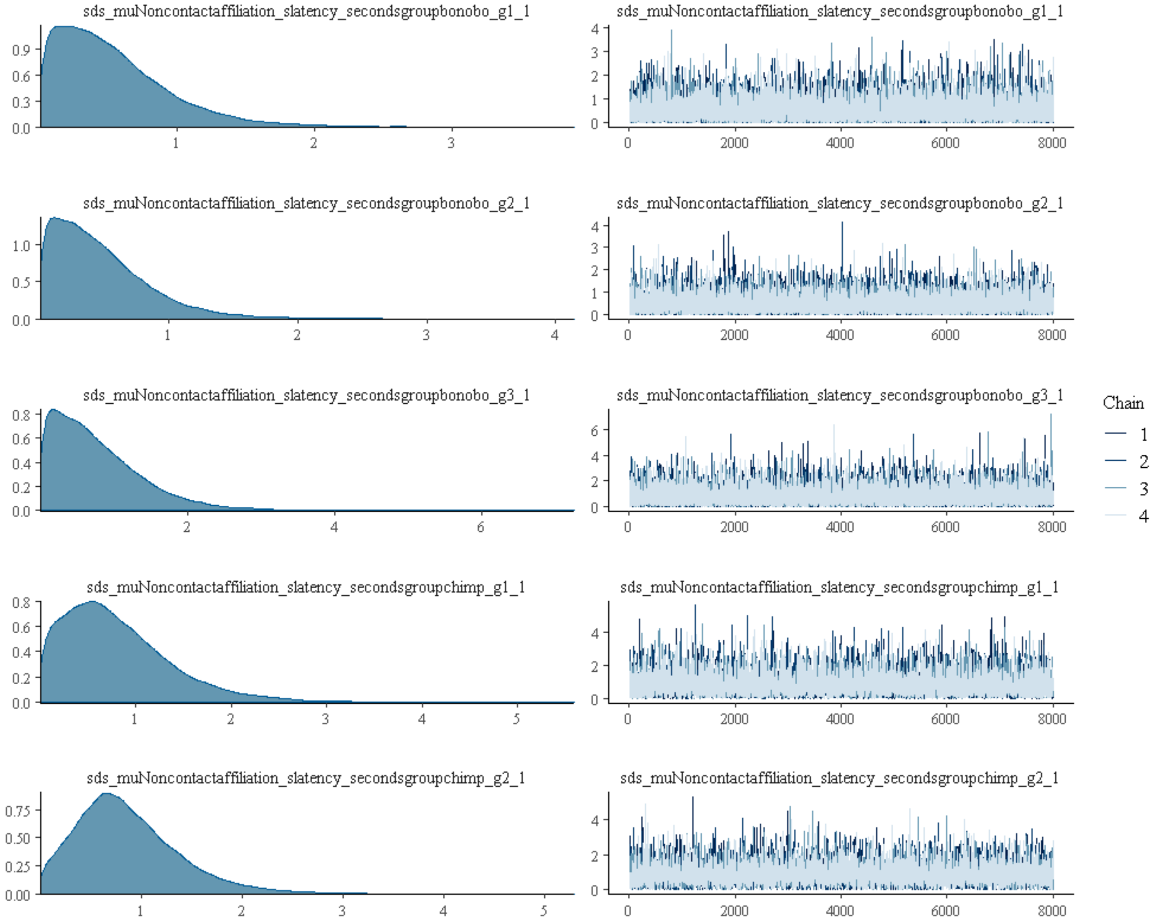
20
sds_muNoncontactaffiliation_slatency_seconds_1
30
20
10
0
0
2000
4000
6000
8000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1
2
3
sds_muNoncontactaffiliation_slatency_secondsgroupbonobo_g1_1
4
3
2
1
0
0
2000
4000
6000
8000
sds_muNoncontactaffiliation_slatency_secondsgroupbonobo_g2_1
1.0
0.5
0.0
1
2
3
4
sds_muNoncontactaffiliation_slatency_secondsgroupbonobo_g2_1
4
3
2
1
0
0
2000
4000
6000
8000
sds_muNoncontactaffiliation_slatency_secondsgroupbonobo_g3_1
0.8
0.6
0.4
0.2
0.0
2
4
6
sds_muNoncontactaffiliation_slatency_secondsgroupbonobo_g3_1
6
4
2
0
0
2000
4000
6000
8000
Chain
1
2
3
4
sds_muNoncontactaffiliation_slatency_secondsgroupchimp_g1_1
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
sds_muNoncontactaffiliation_slatency_secondsgroupchimp_g1_1
4
2
0
0
2000
4000
6000
8000
sds_muNoncontactaffiliation_slatency_secondsgroupchimp_g2_1
0.75
0.50
0.25
0.00
1
2
3
4
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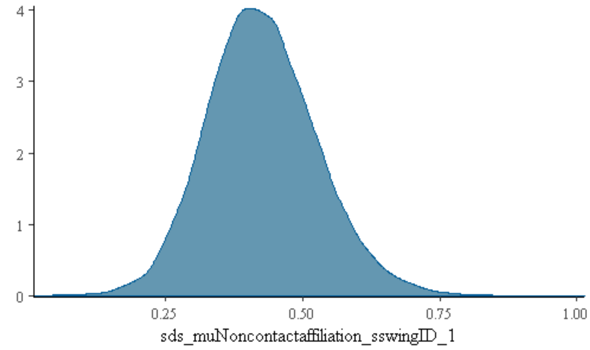
sds_muNoncontactaffiliation_slatency_secondsgroupchimp_g2_1
4
2
0
0
2000
4000
6000
8000


4
3
2
1
0
0.25
0.50
0.75
1.00
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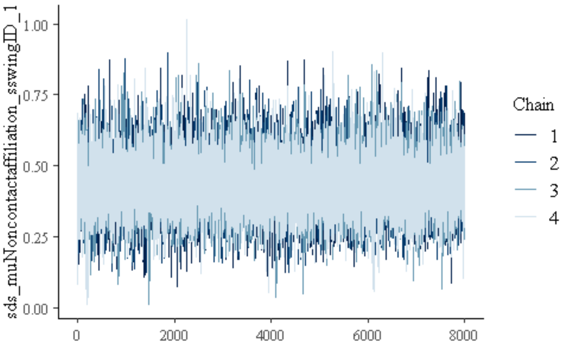
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0.50
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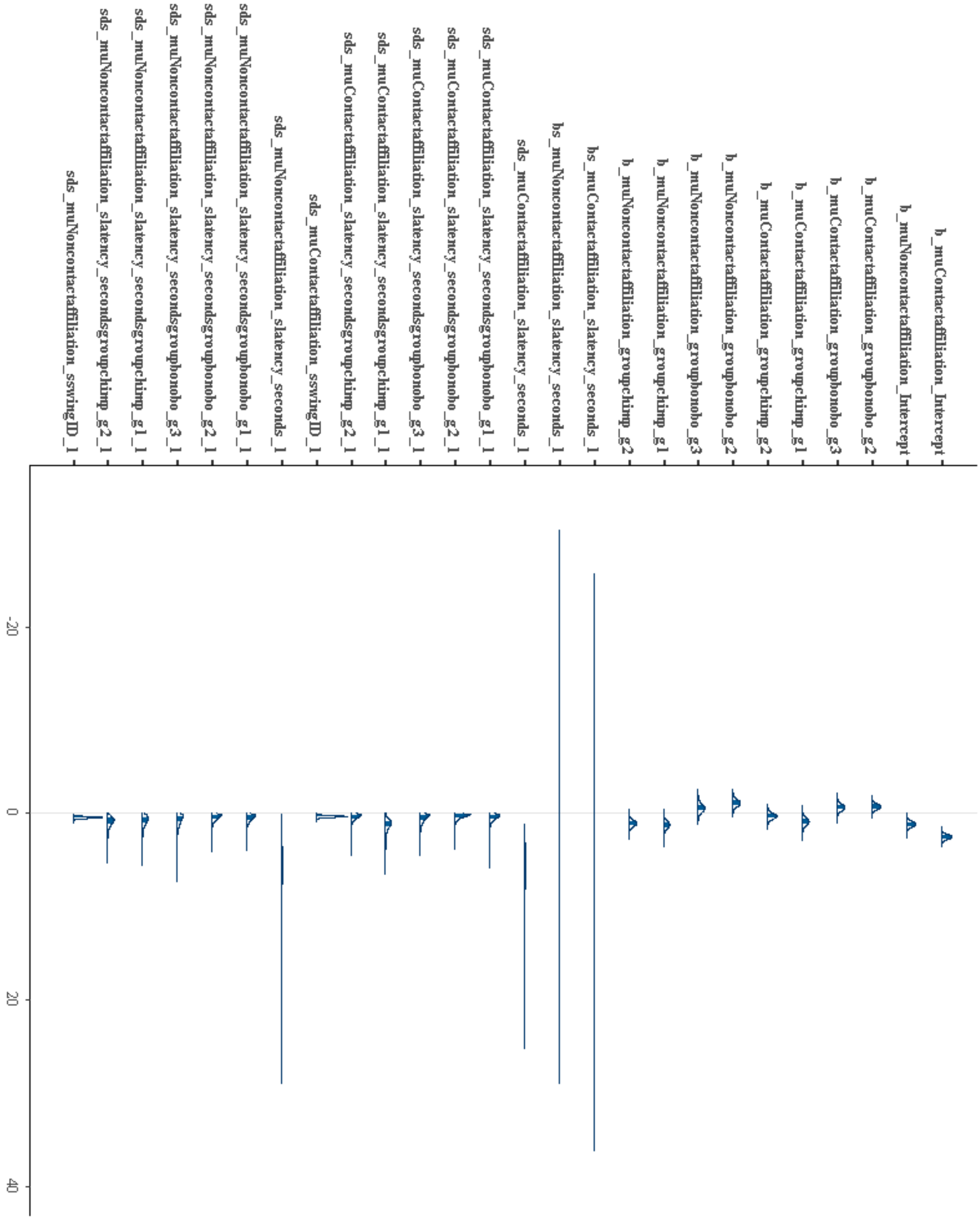
0
2000
4000
6000
8000
Chain
1
2
3
4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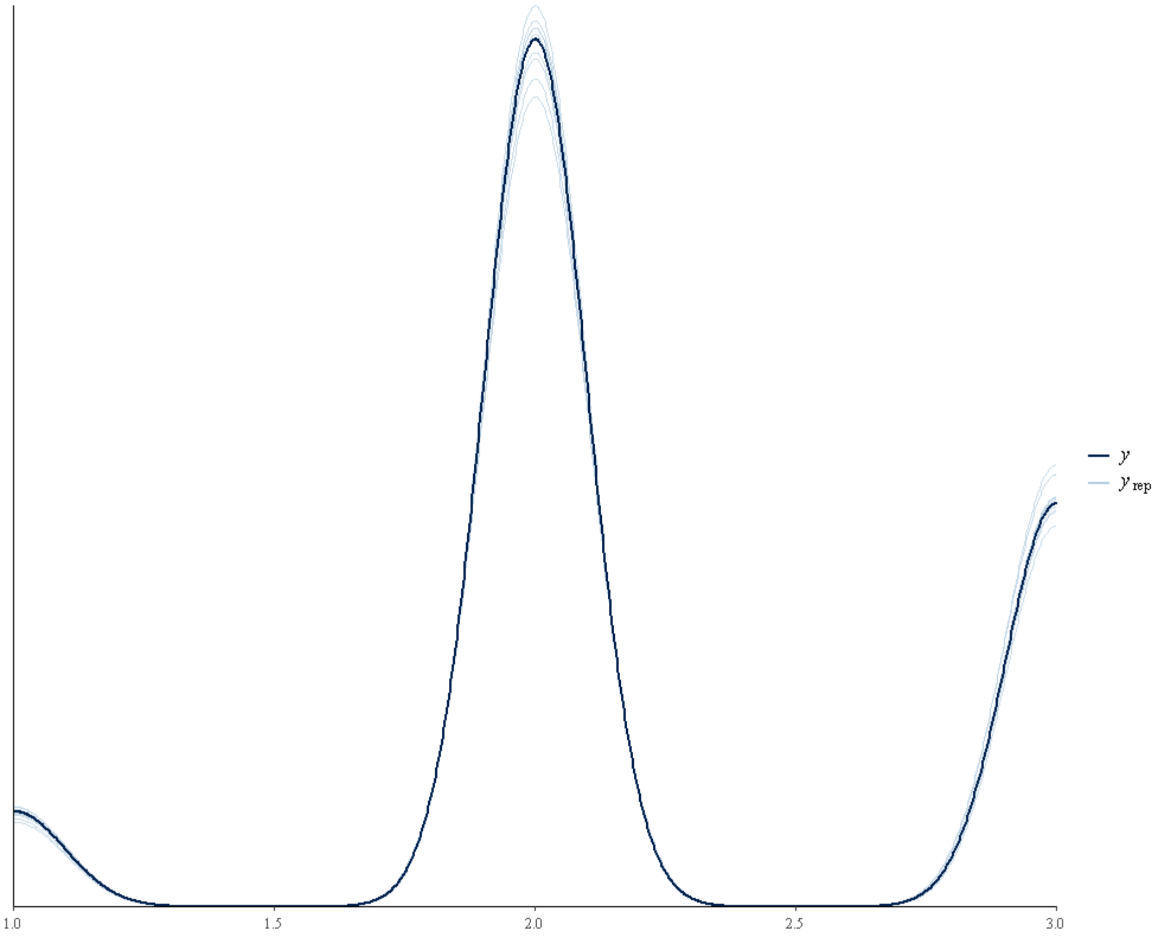
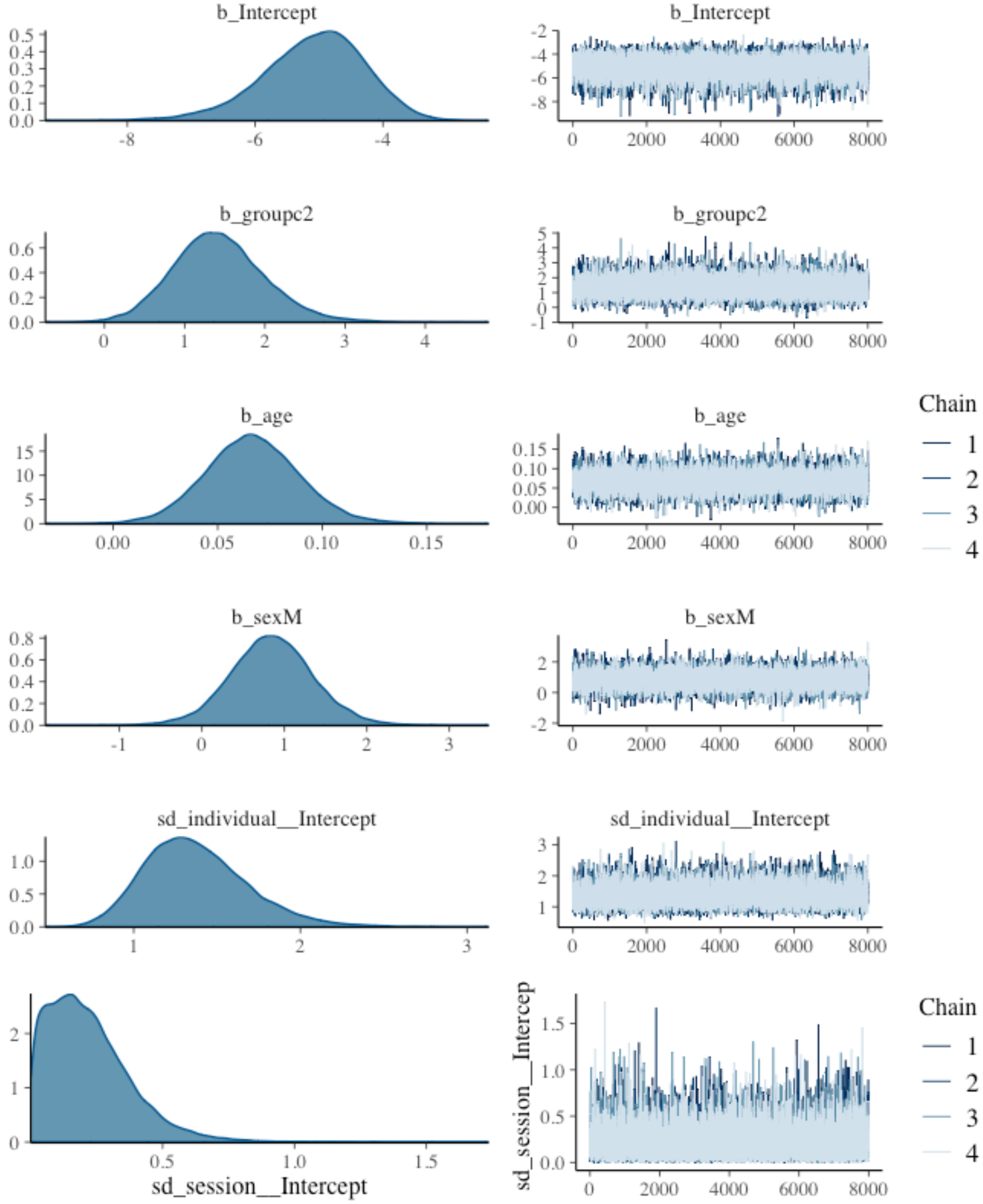
sds_muNoncontactaffiliation_slatency_secondsgroupchimp_g1_1
sds_muNoncontactaffiliation_slatency_secondsgroupbonobo_g3_1
sds_muNoncontactaffiliation_slatency_secondsgroupbonobo_g2_1
sds_muNoncontactaffiliation_slatency_secondsgroupbonobo_g1_1
sds_muNoncontactaffiliation_slatency_seconds_1
sds_muContactaffiliation_sswingID_1
sds_muContactaffiliation_slatency_secondsgroupchimp_g2_1
sds_muContactaffiliation_slatency_secondsgroupchimp_g1_1
sds_muContactaffiliation_slatency_secondsgroupbonobo_g3_1
sds_muContactaffiliation_slatency_secondsgroupbonobo_g2_1
sds_muContactaffiliation_slatency_secondsgroupbonobo_g1_1
sds_muContactaffiliation_slatency_seconds_1
bs_muNoncontactaffiliation_slatency_seconds_1
bs_muContactaffiliation_slatency_seconds_1
b_muNoncontactaffiliation_groupchimp_g2
b_muNoncontactaffiliation_groupchimp_g1
b_muNoncontactaffiliation_groupbonobo_g3
b_muNoncontactaffiliation_groupbonobo_g2
b_muContactaffiliation_groupchimp_g2
b_muContactaffiliation_groupchimp_g1
b_muContactaffiliation_groupbonobo_g3
b_muContactaffiliation_groupbonobo_g2
b_muNoncontactaffiliation_Intercept
b_muContactaffiliation_Intercept
-20
0
20
40

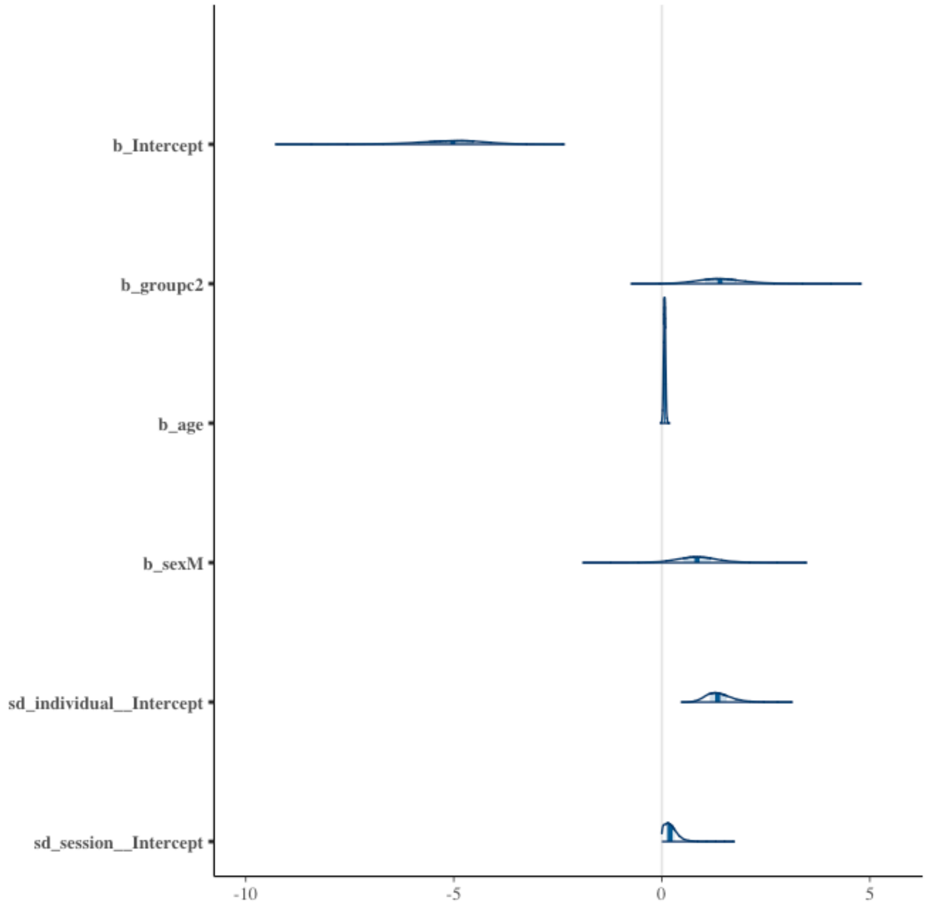
Model 3.2: **Posterior predictive check.**



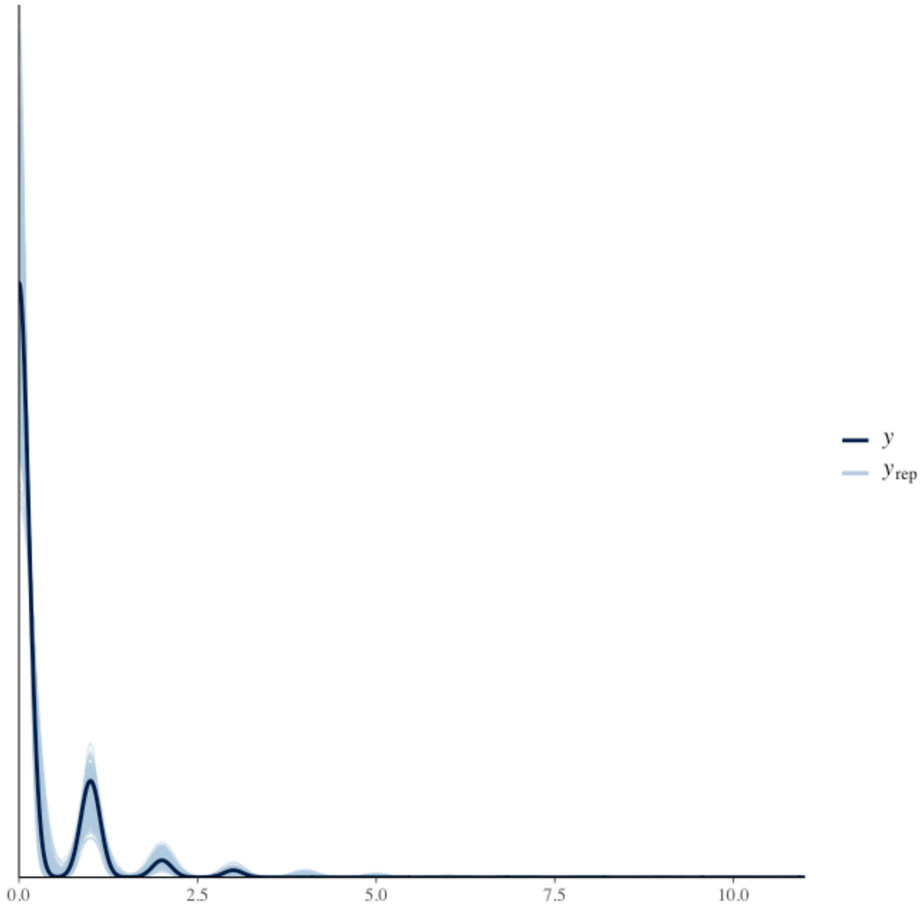
C.5: *Model 4.1.1* and *Model 4.1.2* diagnostics checks

***Model 4.1.1*: Trace plots of MCMC chains and posterior distributions.**

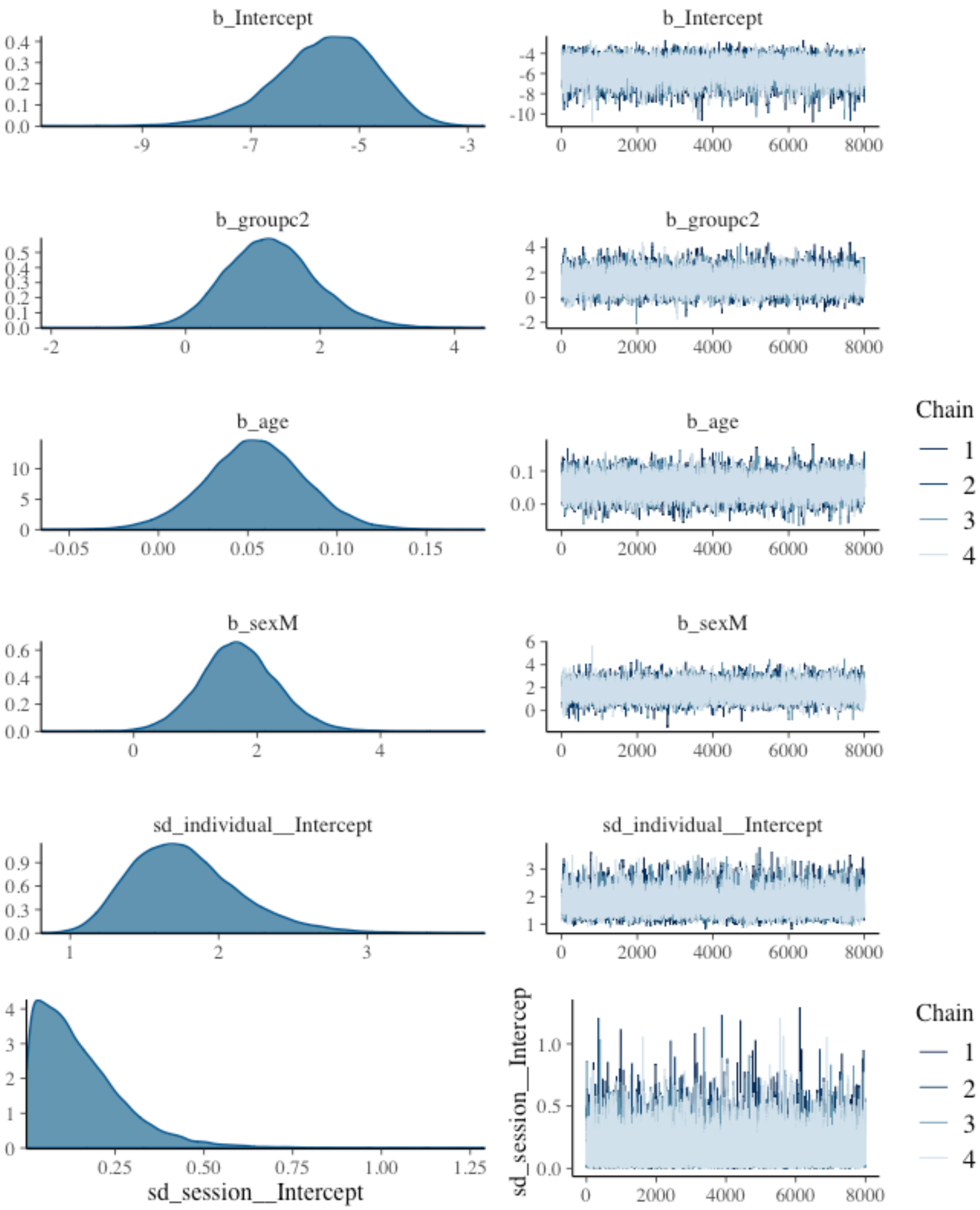


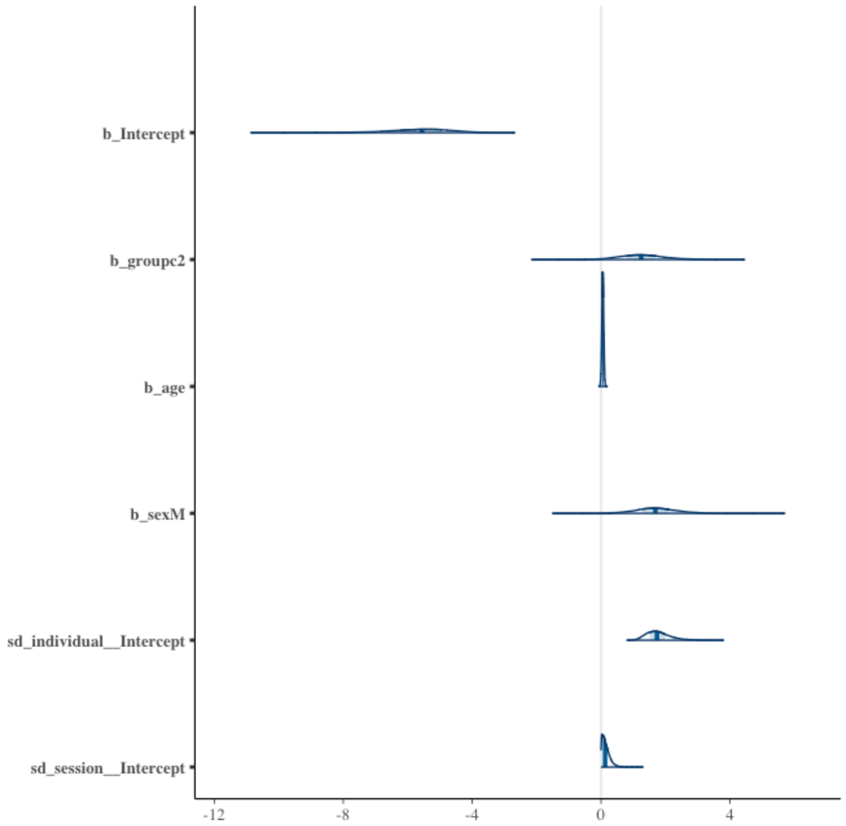


Model 4.1.1: **Posterior predictive check.**

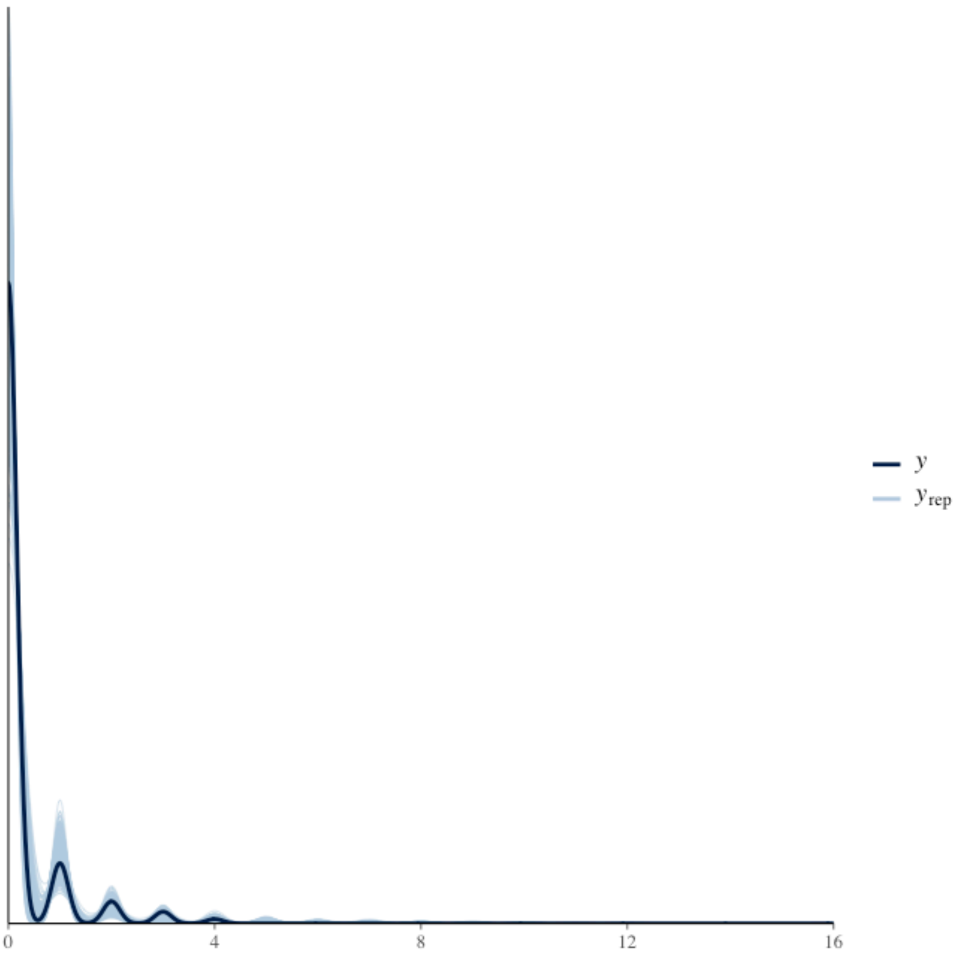


Model 4.1.1: **Trace plots of MCMC chains and posterior distributions.**



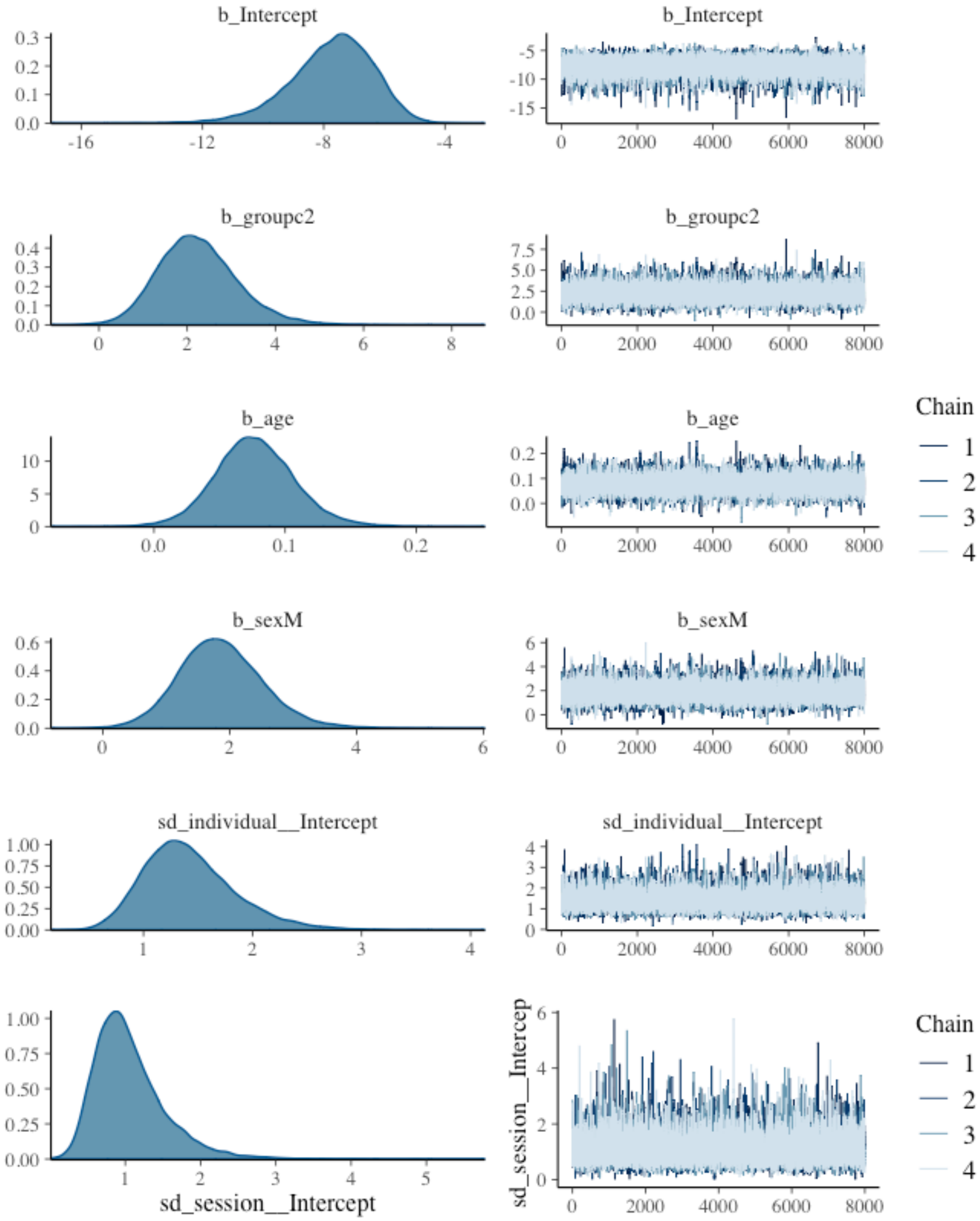


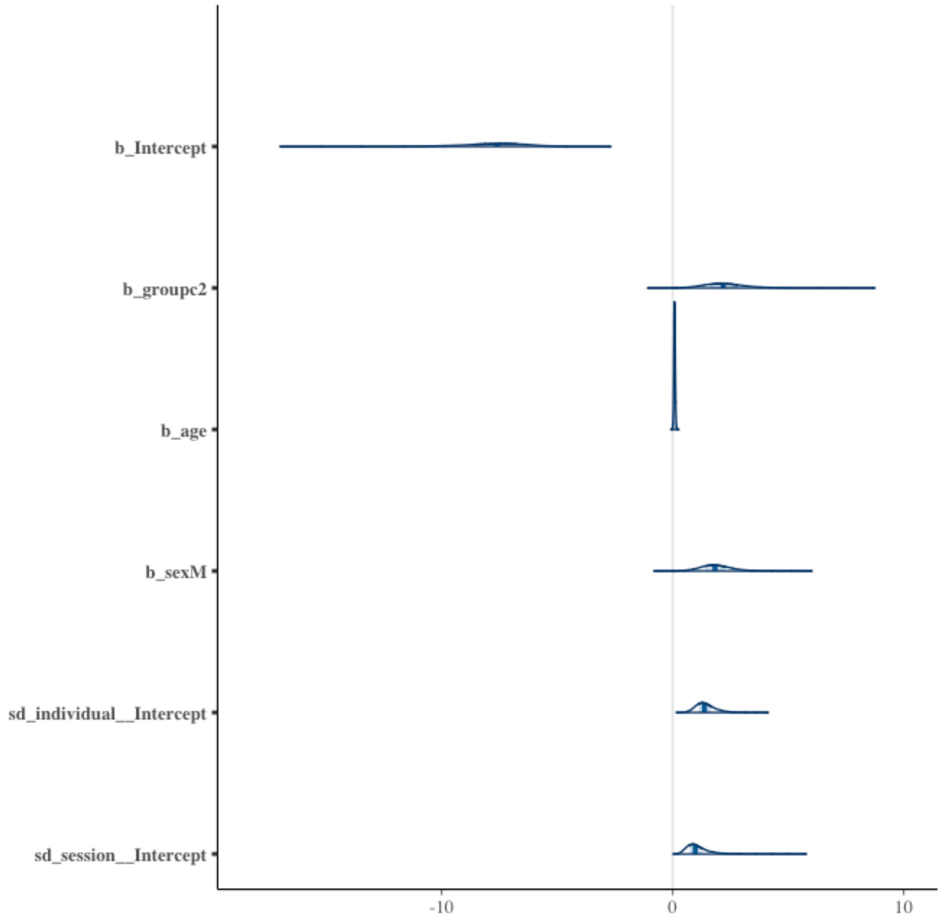
Model 4.1.2: **Posterior predictive check.**



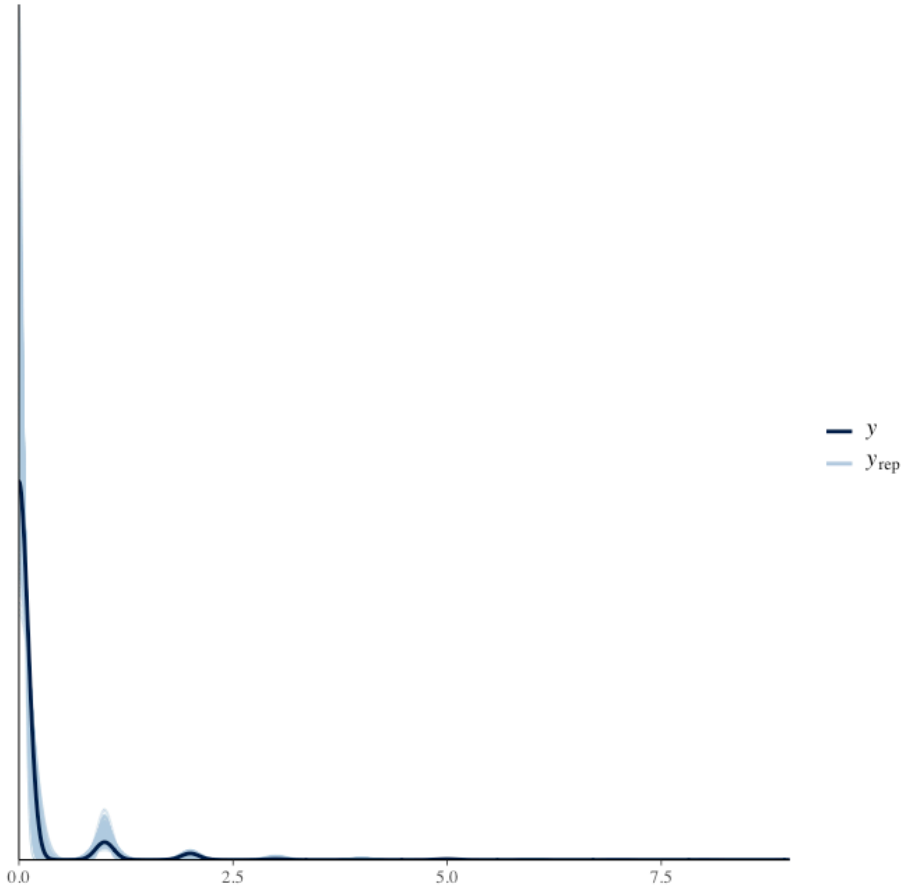
C.6: *Model 4.2.1* and *Model 4.2.2* diagnostics checks

***Model 4.2.1*: Trace plots of MCMC chains and posterior distributions.**

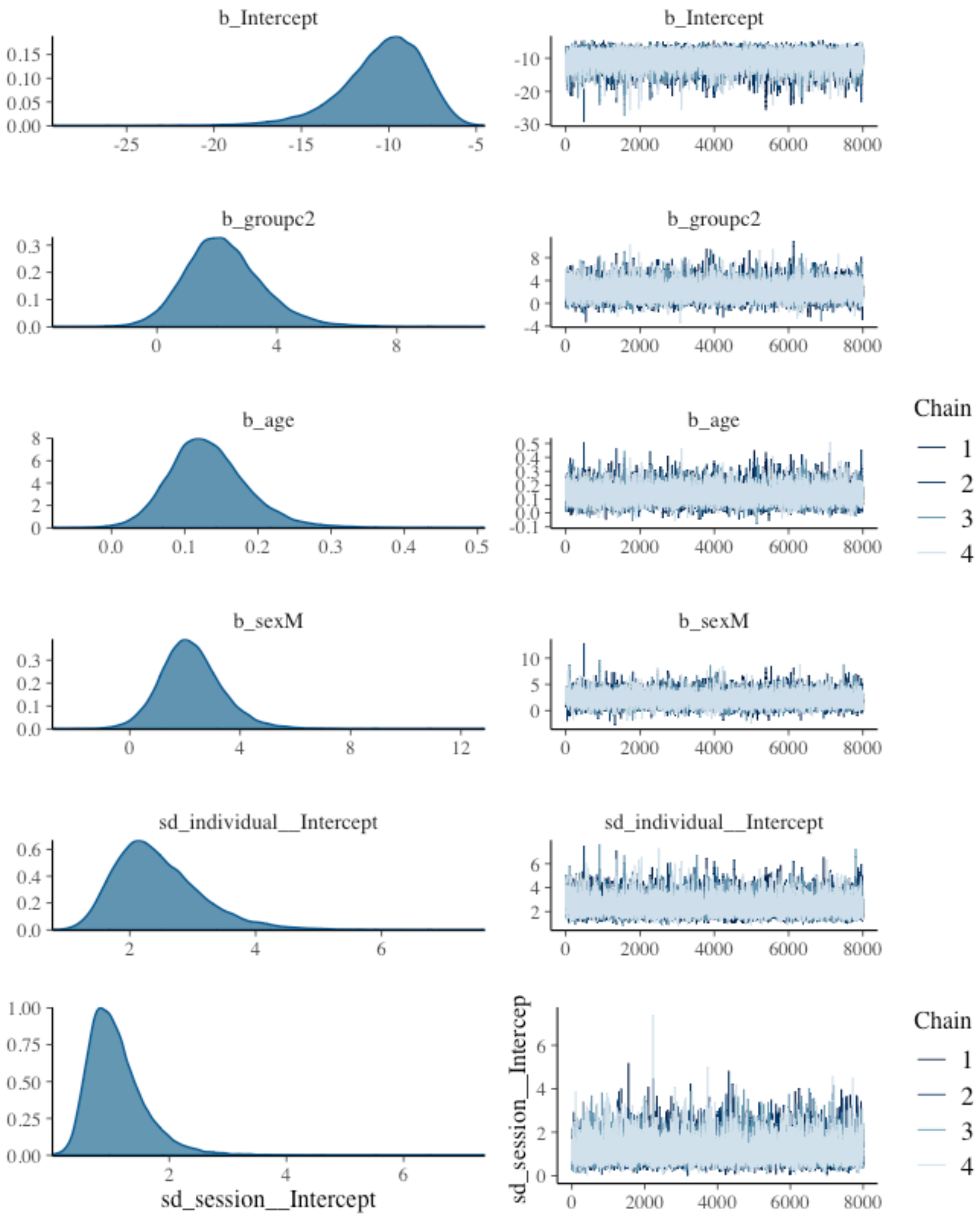


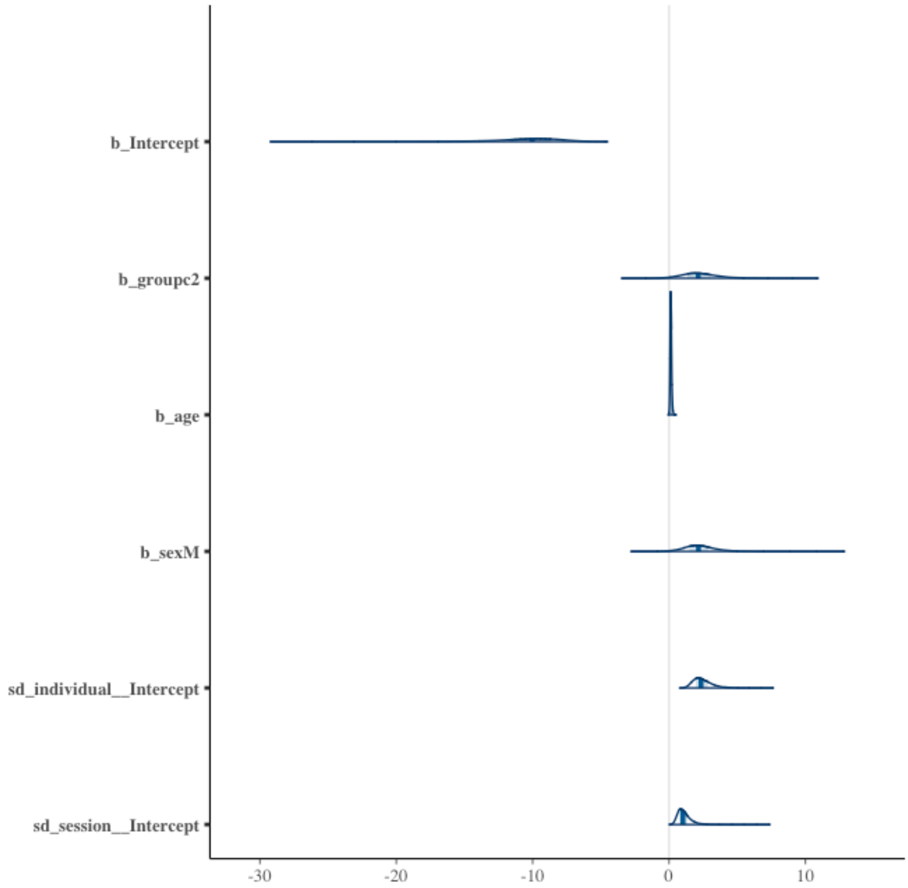


Model 4.2.1: **Posterior predictive check.**

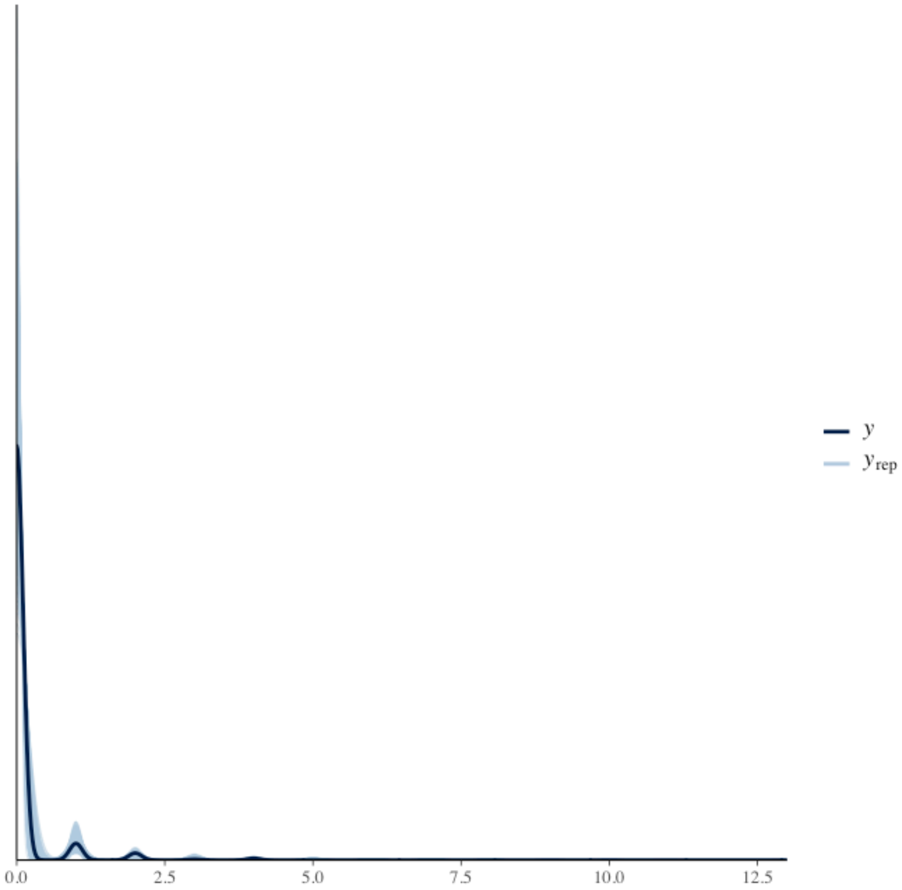


Model 4.2.2: **Trace plots of MCMC chains and posterior distributions.**





Model 4.2.2: **Posterior predictive check.**



Appendix D: *Chapter 6* supplementary

D.1 Full-null model comparisons

Results for full-null comparison of *Model 1.1*. Full version included an interaction and respective main effects of species and pre-feeding contact affiliation partners, alongside control variables of sex and age of the individual, with random effects for the identities of the group, individual, and session number. Null model included the same structure, except dropped species and pre-feeding contact affiliation partners from the fixed effect structure entirely.

Model 1.1

Model	**AIC**	**BIC**	**logLik**	**Deviance**	**Chi^2**	**Df**	***P*-value**
Null	3827.980	3973.626	-1882.990	3765.980			
Full	3824.200	3983.941	-1878.100	3756.200	9.780	3	.021

Results for full-null comparison of *Model 1.2*. Full version included an interaction and respective main effects of group and pre-feeding contact affiliation partners, alongside control variables of sex and age of the individual, with random effects for the identity of the individual and session number. Null model included the same structure, except dropped group and pre-feeding contact affiliation partners from the fixed effect structure entirely.

Model 1.2

Model	**AIC**	**BIC**	**logLik**	**Deviance**	**Chi^2**	**Df**	***P*-value**
Null	3834.207	4031.534	-1875.103	3750.207			
Full	3821.704	4061.316	-1859.852	3719.704	30.502	9	< .001

Results for full-null comparison of *Model 2.1*. Full version included an interaction and respective main effects of species and pre-feeding contacts, alongside control variables of sex and age of the individual, with random effects for the identities of the group, individual, and session number. Null model included the same structure, except dropped species and pre-feeding contacts from the fixed effect structure entirely.

Model 2.1

Model	**AIC**	**BIC**	**logLik**	**Deviance**	**Chi^2**	**Df**	***P*-value**
Null	3834.548	3980.194	-1886.274	3772.548			
Full	3828.925	3988.666	-1880.463	3760.925	11.622	3	.009

Results for full-null comparison of *Model 2.2*. Full version included an interaction and respective main effects of group and pre-feeding contacts, alongside control variables of sex and age of the individual, with random effects for the identity of the individual and session number. Null model included the same structure, except dropped group and pre-feeding contacts from the fixed effect structure entirely.

Model 2.2

Model	**AIC**	**BIC**	**logLik**	**Deviance**	**Chi^2**	**Df**	***P*-value**
Null	3840.755	4038.083	-1878.378	3756.755			
Full	3822.836	4062.448	-1860.418	3720.836	35.919	9	< .001

D.2 Random slope estimates and stability

***Model 1.1*: Random slope estimates and stability output**

Term	Estimate	Min	Max
group@(Intercept)@NA	0.233	0.000	0.521
group@sex.M@NA	0.454	0.188	0.642
group@z.partners@NA	0.044	0.027	0.073
group@z.age@NA	0.483	0.202	0.619
group@(Intercept)@sex.M	-0.611	-1.000	1.000
group@(Intercept)@z.partners	0.753	-1.000	0.941
group@(Intercept)@z.age	-0.112	-0.990	0.800
group@sex.M@z.partners	-0.981	-1.000	-0.100
group@sex.M@z.age	-0.718	-0.980	-0.401
group@z.partners@z.age	0.570	-0.663	1.000
individual@(Intercept)@NA	0.812	0.700	0.940
individual@z.partners@NA	0.122	0.094	0.221
individual@(Intercept)@z.partners	-1.000	-1.000	-0.654
session@(Intercept)@NA	0.097	0.053	0.321
session@species.chimpanzee@NA	0.078	0.037	0.358
session@z.partners@NA	0.028	0.022	0.078
session@z.age@NA	0.036	0.025	0.053
session@sex.M@NA	0.026	0.013	0.050
session@(Intercept)@species.chimpanzee	0.964	-0.118	1.000
session@(Intercept)@z.partners	-0.997	-1.000	-0.158
session@(Intercept)@z.age	-0.996	-1.000	-0.829
session@(Intercept)@sex.M	-0.931	-1.000	-0.357
session@species.chimpanzee@z.partners	-0.981	-1.000	-0.109
session@species.chimpanzee@z.age	-0.984	-1.000	-0.318
session@species.chimpanzee@sex.M	-0.800	-1.000	0.611
session@z.partners@z.age	1.000	0.566	1.000
session@z.partners@sex.M	0.901	-0.372	1.000
session@z.age@sex.M	0.894	0.217	1.000

Model 1.2: **Random slope estimates and stability output**

Term	Estimate	Min	Max
individual@(Intercept)@NA	0.858	0.786	0.933
individual@z.partners@NA	0.175	0.123	0.240
individual@(Intercept)@z.partners	-0.833	-1.000	-0.700
session@(Intercept)@NA	0.116	0.000	0.130
session@group.b2@NA	0.318	0.246	0.367
session@group.b3@NA	0.361	0.192	0.424
session@group.c1@NA	0.256	0.180	0.316
session@group.c2@NA	0.239	0.199	0.283
session@z. partners@NA	0.059	0.045	0.070
session@z.age@NA	0.031	0.015	0.037
session@sex.M@NA	0.059	0.044	0.081
session@(Intercept)@group.b2	-0.169	-0.474	0.180
session@(Intercept)@group.b3	-0.280	-0.446	-0.087
session@(Intercept)@group.c1	0.800	0.637	0.987
session@(Intercept)@group.c2	-0.434	-0.771	-0.145
session@(Intercept)@z.partners	-0.818	-0.930	-0.620
session@(Intercept)@z.age	-0.828	-0.934	-0.602
session@(Intercept)@sex.M	0.093	-0.219	0.572
session@group.b2@group.b3	0.867	0.680	0.955
session@group.b2@group.c1	0.429	0.101	0.817
session@group.b2@group.c2	0.914	0.772	0.954
session@group.b2@z.partners	-0.368	-0.368	0.090
session@group.b2@sex.M	0.269	-0.360	0.806
session@group.b2@z.age	0.581	0.172	0.833
session@group.b3@group.c1	0.165	-0.127	0.533
session@group.b3@group.c2	0.970	0.861	0.992
session@group.b3@z.partners	-0.074	-0.074	0.453
session@group.b3@sex.M	-0.242	-0.817	0.465
session@group.b3@z.age	0.442	0.183	0.862
session@group.c1@group.c2	0.089	-0.215	0.568
session@group.c1@z.partners	-0.995	-1.000	-0.788
session@group.c1@sex.M	0.412	0.094	0.745
session@group.c1@z.age	-0.345	-0.810	0.996
session@group.c2@z.partners	-0.008	-0.489	0.556
session@group.c2@sex.M	-0.071	-0.700	0.717
session@group.c2@z.age	0.642	0.291	0.845
session@z.partners@sex.M	-0.470	-0.825	-0.227
session@z.partners@z.age	0.360	-0.836	0.636
session@sex.M@z.age	0.375	-0.209	0.763

Model 2.1: **Random slope estimates and stability output**

Term	Estimate	Min	Max
group@(Intercept)@NA	0.338	0.000	0.349
group@sex.M@NA	0.263	0.141	0.532
group@z.contact@NA	0.053	0.020	0.085
group@z.age@NA	0.340	0.140	0.462
group@(Intercept)@sex.M	1.000	-1.000	1.000
group@(Intercept)@z.contact	-0.926	-0.999	0.160
group@(Intercept)@z.age	-0.777	-0.978	0.700
group@sex.M@z.contact	-0.926	-1.000	0.777
group@sex.M@z.age	-0.777	-1.000	0.221
group@z.contact@z.age	0.958	-0.954	1.000
individual@(Intercept)@NA	0.800	0.664	0.889
individual@z.contact@NA	0.164	0.130	0.301
individual@(Intercept)@z.contact	-1.000	-1.000	-1.000
session@(Intercept)@NA	0.084	0.052	0.295
session@species.chimpanzee@NA	0.071	0.039	0.329
session@z.contact@NA	0.012	0.008	0.058
session@z.age@NA	0.035	0.021	0.057
session@sex.M@NA	0.022	0.011	0.053
session@(Intercept)@species.chimpanzee	0.915	-0.356	1.000
session@(Intercept)@z.contact	-1.000	-1.000	0.648
session@(Intercept)@z.age	-0.988	-1.000	-0.724
session@(Intercept)@sex.M	-0.842	-1.000	-0.286
session@sex.M@species.chimpanzee	-0.554	-1.000	0.714
session@sex.M@z.contact	0.829	-0.907	1.000
session@sex.M@z.age	0.751	-0.018	1.000
session@species.chimpanzee@z.contact	-0.925	-1.000	0.577
session@species.chimpanzee@z.age	-0.966	-1.000	-0.127
session@z.contact@z.age	0.992	-0.212	1.000

Model 2.2: **Random slope estimates and stability output**

Term	Estimate	Min	Max
individual@(Intercept)@NA	0.838	0.780	0.906
individual@z.contact@NA	0.202	0.171	0.271
individual@(Intercept)@z.contact	-1.000	-1.000	-1.000
session@(Intercept)@NA	0.106	0.000	0.128
session@group.b2@NA	0.322	0.232	0.367
session@group.b3@NA	0.364	0.209	0.445
session@group.c1@NA	0.280	0.165	0.346
session@group.c2@NA	0.226	0.190	0.269
session@z.contact@NA	0.048	0.033	0.055
session@z.age@NA	0.034	0.021	0.040
session@sex.M@NA	0.045	0.030	0.058
session@(Intercept)@group.b2	-0.072	-0.420	0.268
session@(Intercept)@group.b3	-0.160	-0.399	0.047
session@(Intercept)@group.c1	0.810	0.723	0.983
session@(Intercept)@group.c2	-0.261	-0.719	-0.013
session@(Intercept)@z.contact	-0.617	-0.868	-0.363
session@(Intercept)@z.age	-0.755	-0.854	-0.515
session@(Intercept)@sex.M	-0.005	-0.316	0.546
session@group.b2@group.b3	0.923	0.772	0.980
session@group.b2@group.c1	0.506	0.286	0.858
session@group.b2@group.c2	0.912	0.760	0.963
session@group.b2@z.contact	-0.725	-0.983	-0.453
session@group.b2@sex.M	0.197	-0.719	0.996
session@group.b2@z.age	0.638	0.325	0.960
session@group.b3@group.c1	0.332	0.122	0.676
session@group.b3@group.c2	0.995	0.917	0.999
session@group.b3@z.contact	-0.551	-0.801	-0.052
session@group.b3@sex.M	-0.184	-0.943	0.961
session@group.b3@z.age	0.545	0.342	0.832
session@group.c1@group.c2	0.241	-0.168	0.622
session@group.c1@z.contact	-0.960	-0.992	-0.823
session@group.c1@sex.M	0.257	-0.091	0.711
session@group.c1@z.age	-0.236	-0.620	0.919
session@group.c2@z.contact	-0.476	-0.877	0.195
session@group.c2@sex.M	-0.176	-0.960	0.952
session@group.c2@z.age	0.613	0.337	0.842
session@z.contact@sex.M	-0.298	-0.889	0.282
session@z.contact@z.age	-0.030	-0.991	0.340
session@sex.M@z.age	0.409	-0.169	0.696

Appendix E: *Chapter 7* supplementary

***Model* 3: Random slope estimates and stability output**

Term	Estimate	Min	Max
group@(Intercept)@NA	0.000	0.000	0.000
group@initiator_sex.M@NA	1.027	0.000	1.316
initiator@(Intercept)@NA	0.615	0.491	0.751
initiator@z.recipient_age@NA	0.395	0.126	0.544
recipient@(Intercept)@NA	0.826	0.683	0.941
session@(Intercept)@NA	0.000	0.000	0.000
session@recipient_sex.M@NA	0.161	0.000	0.379
session@z.recipient_age@NA	0.211	0.000	0.280
session@kinship.nonkin@NA	1.196	0.816	1.396
session@initiator_sex.M@NA	1.027	0.000	1.316

***Model 4.1*: Random slope estimates and stability output**

Term	Estimate	Min	Max
initiator@(Intercept)@NA	1.216	0.900	1.842
recipient@(Intercept)@NA	1.215	0.843	1.872
session@(Intercept)@NA	0.433	0.000	0.726
session@recipient_sex.M@NA	0.761	0.000	1.589
session@kinship.nonkin@NA	1.388	0.000	2.946
session@initiator_sex.M@NA	1.960	1.294	2.819

***Model 4.2*: Random slope estimates and stability output**

Term	Estimate	Min	Max
initiator@(Intercept)@NA	0.477	0.306	0.585
initiator@z.recipient_age@NA	0.166	0.000	0.404
recipient@(Intercept)@NA	0.752	0.557	0.841
recipient@initiator_sex.M@NA	0.631	0.000	0.928
session@(Intercept)@NA	0.000	0.000	0.000
session@z.recipient_age@NA	0.292	0.193	0.364
session@kinship.nonkin@NA	0.996	0.754	1.214