Navigating personal space: Investigating the relationship between risk and signalling in baboon approach behaviour

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Abstract

Entering physical proximity to a conspecific is a resource; it can give an individual opportunities for social learning or affiliative interactions and could provide safety from threats through association. How individuals access this space and the interactions that follow are important aspects of primate signalling and social behaviour. Within the primate signalling literature, there has been much discussion of how species-level signalling repertoires and their complexity may be affected by social complexity and risk (e.g., despotic versus egalitarian species). However, research on how signalling in individual interactions may be affected by similar factors, for example the interpersonal risk posed by an interaction to a signaller, remains limited. This thesis re-examines approach behaviour in baboons, first taking a species-level approach investigating male-male stereotyped greetings in chacma baboons (*Papio ursinus griseipes)* in the larger context of *Papio*, then examining the content, outcome, and structure of baboon approach interactions more generally across sex combinations in olive baboons (*Papio anubis)* and chacma baboons.

The first chapter provides an introduction to the signalling and risk literature and provides a theoretical background for the remainder of the thesis. Chapter 2 discusses the relevance of baboons as a study genus and reviews the existing approach literature in baboons, in particular the male-male greeting and infant approach grunting literatures. An overview of the overall thesis methods, materials, and the two field sites (Gorongosa National Park, Mozambique and Gombe National Park, Tanzania) is provided in Chapter 3. The following three chapters are the empirical chapters, addressing different aspects of baboon approach behaviour. Chapter 4 compares male-male greeting behaviour of chacma baboons in Gorongosa National Park, to that observed in other *Papio* species. Chacma baboons are often referred to as exhibiting no stereotyped male-male greeting behaviour, unlike the other *Papio* species, and it has been suggested that this is related to their lack of coalition formation. We provide evidence that similar male-male greetings are seen in chacma baboons, contrary to expectation. Chapter 5 uses a network-analysis approach to study how individual signals are combined during approach interactions in chacma and olive baboons. We compare these across sex combinations and between interactions where infants of the recipient are present or absent. The relevance of how signalling between sex combinations may differ

due to philopatry or rank is discussed. The results of the network-analysis are then used to develop hypotheses regarding how identified signal combinations are associated with changes in the outcomes of those interactions. We identified several clusters of signals used together and discuss their relevance to whether contact is made with the recipient or recipient's infant where applicable. The focus of Chapter 6 is how signalling complexity relates to the level of interpersonal risk faced by the approacher. We use two proxies of risk - first, the sex of the recipient (approaches towards males being higher risk than towards females) and second, where the approacher is a female, whether she has a natal coat infant with her or not. Complexity is assessed using entropy and event size, with a third set of models investigating whether the likelihood of physical contact differs by these proxies for risk. We found weak evidence for differences in event size and physical contact by sex combination and infant presence. Contrary to expectation, differences in entropy ratio were found by approacher sex, but not recipient sex. Chapter 7 provides a final discussion of the thesis findings, key implications, limitations, and future directions.

Contents

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Authorship Contributions

This thesis follows an integrated thesis format, with each empirical chapter presented as an independent paper. The following three papers are included in this thesis.

1. Muschinski, J. (preprint). Male-male greeting behaviour in chacma baboons (*Papio ursinus griseipes)* in Gorongosa National Park, Mozambique. *bioRxiv.*

   Plans for submission: This paper has been submitted to the American Journal of Biological Anthropology for the special issue "Primate adaptations in a highly seasonal and heterogenous African ecosystem" and is awaiting review.
   Contributions: I completed all video coding, data analysis, and writing for this chapter.

2. Muschinski, J., Mielke, A., Collins, A., & Carvalho, S. (preprint). Signal combinations during approach interactions in chacma and olive baboons.

   Plans for submission: This paper will be resubmitted following revision in response to reviewer comments, possibly to eLife or Animal Behaviour and Cognition.
   Contributions: I completed video coding, data analysis, and writing for this chapter. Susana Carvalho and Alexander Mielke provided project design and statistical feedback, in addition to editing the paper draft. Anthony Collins assisted with designing the data collection protocol, coordinated filming in Gombe, and provided editorial input.

3. Muschinski, J., Mielke, A., Collins, A., & Carvalho, S. (in prep). Complexity, risk, and physical contact in chacma and olive baboon approach interactions.

   Plans for submission: This paper will be preprinted on bioRxiv and will be considered for submission following the publication of the above two papers.
   Contributions: I completed video coding, data analysis, and writing for this chapter. Susana Carvalho and Alexander Mielke provided project design and statistical feedback, in addition to editing the paper draft. Anthony Collins assisted with designing the data collection protocol, coordinated filming in Gombe, and will provide editorial input prior to submission for publication.

Authorship Contributions

Co-author	Signature	Date
Susana Carvalho		11 December 2023
Anthony Collins		17 December 2023
Alexander Mielke		15 January 2024

Other collaborators and funders

Gorongosa National Park video archive

Two thirds of the Gorongosa video archive was collected by Lucy Baehren during her DPhil research in Gorongosa National Park from October through November 2018 and the other third by me. She collected the videos for her DPhil research on leave-taking behaviours and has published on the dataset (Baehren & Carvalho, 2022). After the start of the Covid-19 pandemic, as my supervisors and I redeveloped my dissertation topic, she kindly allowed for me to use them for my own research, with acknowledgement in resulting papers. Video recording in Gorongosa National Park was completed under permit numbers PNG/DSCi/C145/2019 (Jana Muschinski) and PNG/DSCi/C110/2018 (Lucy Baehren) and was cleared by the University of Oxford Animal Welfare and Ethical Review Board (APA/1/5/ACER/10Dec2018).

Gombe National Park video archive

The data set from Gombe National Park was created through a collaboration with Anthony Collins and Nuhu Buke. The videography was completed by research technician Nuhu Buke, with coordination by Anthony Collins. This work was funded by the St John's College Special Grant, the Owen Aldis Scholarship awarded by the International Society for Human Ethology, and the Boise Trust Fund Research Grant. It was completed as part of long-term data collection in the park under research permit numbers 2020-287-NA-1990-170, and 2021-447-NA-1990-170 (Anthony Collins) and will remain a part of the long-term archive locally. The long-term baboon research at the field site is supported by the Jane Goodall Institute - US's Africa Programs.

Inter-observer reliability checks

Reece Hammond (undergraduate/MPhil student) completed video coding for inter-observer reliability checks. This work was completed between October 2022 - February 2023 and December 2023 - January 2024. This work was funded by a Boise Trust Fund Research Grant.

Additional academic outputs

The following papers were also written or contributed to during the course of my DPhil, but were not directly related to the material presented in my DPhil. The first is the result of research during my time as a student with the Koobi Fora Field School in 2015, the second from work contributed to during my MPhil, and the final two written over the last year and a half during my time with Dogs Trust. Asterisk denotes joint first-authorship.

1. Cutts, R. B., Hlubik, S., Campbell, R., **Muschinski, J. M.**, Akuku, P., Braun, D.R., Patterson, D.B., O'Brien, J.J., Garrison, E. and Harris, J.W.K. (2019). Thermal curved-fragments: A method for identifying anthropogenic fire in the archaeological record. *Journal of Archaeological Science, 106*, 10-22.

2. Lightfoot, E., Jones, P. J., Joglekar, P. P., Tames-Demauras, M., Smith, E., **Muschinski, J.**, Shinde, V., Singh, R.N., Jones, M.K., O'Connell, T.C. and Petrie, C.A. (2020). Feeding the herds: Stable isotope analysis of animal diet and its implication for understanding social organisation in the Indus Civilisation, Northwest India. *Archaeological Research in Asia, 24,* p.100212.

3. Samet, L. E.*, **Muschinski, J. M.***, Harvey, N. D., Giragosian, K., Upjohn, M., Murray, J., Owczarczak-Garstecka, S. (In internal review). Public perceptions of dog behaviour in videos: A cross-sectional analysis. To be submitted 2024.

4. **Muschinski, J. M.**, Samet, L. E., Harvey, N. D., Upjohn, M., Murray, J., Owczarczak-Garstecka, S. (In internal review). Exploring relationships between knowledge of dog behaviour and perception of dog emotional and motivational states. To be submitted 2024.

Covid-19 Impact Statement

I started my DPhil in 2018 and completed my first year and a half of work prior to the Covid-19 pandemic. My original DPhil project was fieldwork based and addressed questions regarding the evolution of cultural behaviour in non-human primates, involving in person observation of wild baboons, measurement and recording of archaeological traces of primate culture, and non-invasive social transmission experiments, all to take place in Gorongosa National Park, Mozambique. I finished my 4-month pilot season in November 2019 and was scheduled to return to Gorongosa after the flooding of the wet season receded in March 2020, with 2020 being my principal year of data collection (approximately 9 months of fieldwork planned). As a result of the Covid-19 pandemic, all 2020 fieldwork plans were cancelled, and we worked to change my project so that it would not rely on fieldwork but would still incorporate my previous work wherever possible. We worked to repurpose existing video footage of the troop I had studied and reached out to other field sites to develop collaborations. As a result of the pandemic, additional data collection opportunities were extremely limited and I was unable to conduct additional filming in Gorongosa or collect further rank or social affiliation data, meaning I had to work within the constraints of the original video data set. We developed a collaboration with Anthony Collins to collect further video data of olive baboons in Gombe National Park, Tanzania. Overall, the Covid-19 pandemic resulted in a complete change of DPhil topic, a significantly extended timeline due to this change, and several insurmountable limitations to data collection which have resulted in limited sample sizes and unavailability of rank and social affiliation data. The extended timeline also meant that my funding expired before I finished analysing data for my DPhil. I took on a part-time research officer role with Dogs Trust in June 2021 to financially support myself while finishing the DPhil, moving to four days per week in September 2023 and full-time in January 2024.

1 Introduction

Communication is shaped by and facilitates interactions, and very often these interactions begin with an approach between one individual and a conspecific. Interactions and access to proximity are themselves resources, with interactions providing opportunities to build or strengthen bonds (Dal Pesco & Fischer, 2020; Lehmann et al., 2007; Silk et al., 2009), to groom (Dunbar, 2010; Jablonski, 2021), or solicit social support (Henzi & Barrett, 2003; Noë & Sluijter, 1995), and proximity allowing for potential safety through association (Smuts, 1985), access to resources (Marshall et al., 2012; Marshall et al., 2015) and opportunities for transfer of social information (Claidière et al., 2013; Kendal et al., 2010; Pays et al., 2013). Interactions are facilitated by the signals used during the approach and during the interaction itself (Fedurek et al., 2015). Signals provide information to both intended and unintended recipients, and are shaped by evolutionary pressures linked to social behaviour (Johnstone, 2009).

Particularly in group-living primates, the ability to successfully navigate social encounters and social space are critical (Taborsky & Oliveira, 2012). While a larger group size can provide benefits, such as increased predator detection or the ability to displace other groups from valuable resources, it also comes with trade-offs from an energetic and reproductive perspective (Dunbar & Shultz, 2021b; Janson &

Schaik, 1988; Markham & Gesquiere, 2017; Van Schaik & Hooff, 1983). A larger group size is associated with more within-group competition, leading to a balance between the pressures of within-group competition and external pressures such as between-group competition or predation (Janson & Goldsmith, 1995; Majolo et al., 2008; Van Schaik & Hooff, 1983). Larger group sizes are also associated with costs relating to reproduction, such as reduced female fecundity (Dunbar & Mac Carron, 2019; Dunbar & Shultz, 2021b; Majolo et al., 2008). Social cohesion is furthermore influenced by environmental risk, with inter-group interactions and threats from predators increasing in-group cohesion (LaBarge et al., 2020; Samuni et al., 2020). Where social groups grow in size, bonds must be maintained to avoid fissioning. Grooming and social touch often serve this purpose (Dunbar, 2010), but signalling and eventually language may serve to fill this social maintenance gap where social groups are too large (Dunbar, 2017, 2012).

As such, understanding how communication in primates has evolved to help reduce the stressors of group living is highly relevant to understanding the evolution of more complex social structures and social cohesion (Corballis, 2009; Freeberg et al., 2012). In humans, language has been proposed as a social glue of sorts, that facilitates the impressive degree of high-density living and larger overlapping and intersecting social groups we see today (Dunbar, 2017, 2012). Brain size and cognitive capacity have been found to be associated with social complexity (Dunbar, 1998; Dunbar & Shultz, 2007; Dunbar & Shultz, 2021a; Meguerditchian et al., 2021) and also with communicative complexity (Dunn & Smaers, 2018). There is furthermore a relationship between communicative and social complexity (Freeberg et al., 2012; Peckre et al., 2019), suggesting there is a three-way relationship between these factors, potentially involving several feedback loops (see Figure 1.1). Studying signalling in primates can give insight into the selective pressures that shape communication and have played a role in the evolution of the underlying cognitive processes necessary for both language and social complexity.

Approach behaviour, or "greeting", has been a popular area of study both in humans and non-human primates for decades (Dal Pesco & Fischer, 2020; Knuf,

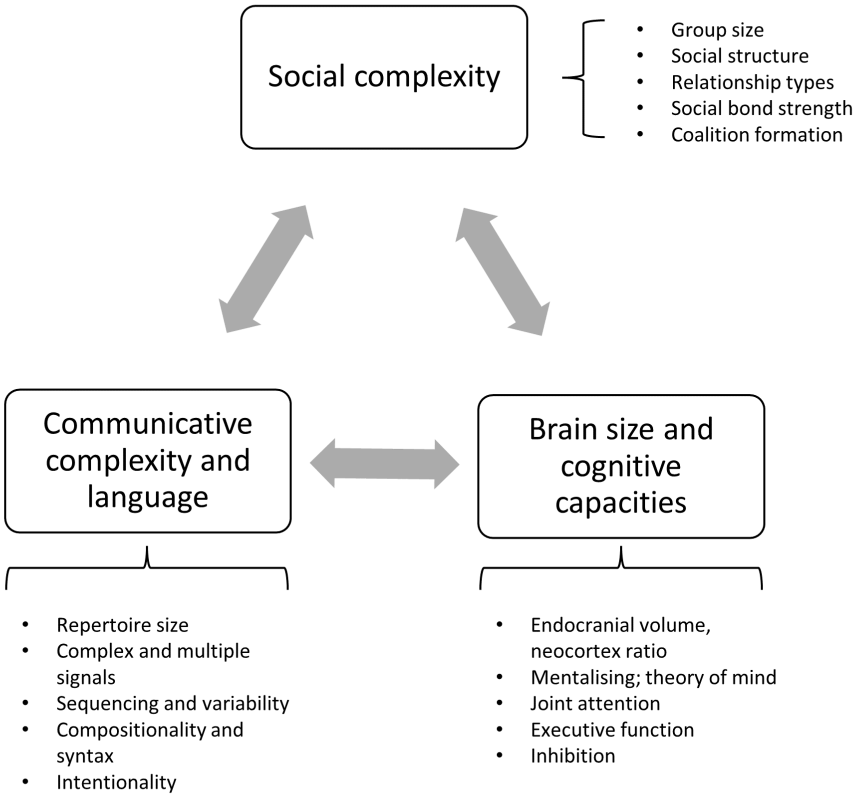

Figure 1.1: The relationships between social complexity, communicative complexity, and brain size as outlined in the social complexity hypothesis and social complexity hypothesis for communicative complexity

1990). It is a universal human behaviour that acts as the "opener" of interactions, often determining what actions may follow. In many human societies, greetings follow specific structures and social rules, taking a ritualized form, and may assist with social cohesion (Bell, 1997; Duranti, 1992; Frith, 1972; Rossano, 2012, 2015; H. Whitehouse & Lanman, 2014). Research on human greeting is approached from many angles including ethology, proxemics, and linguistics (Duranti, 1997; Greenbaum & Rosenfeld, 1980; Schmidt, 2016; Walsh, 1982). It has also been studied broadly in the animal world, with subjects ranging from sea horses (Vincent, 1995), marmots (Barash, 1973), and hyaenas (Mills, 1983), to primates (Dal Pesco & Fischer, 2020), among others. However, greeting is a broad term encompassing

an array of potential interaction types – for example in humans a greeting could occur between two individuals at a cocktail party continuing a conversation from earlier, it could happen between two strangers meeting for the first time, or it could occur when someone welcomes a close family member after a long separation (similar to the zones of separation described in farewell - see Baehren, 2022). This complicates the study of greeting, with it being investigated under many names across the zoological and social sciences resulting in unstandardised methods and difficult cross-study comparison.

While the term "greeting" has a number of implied immediate functions, for example opening an interaction or alerting someone to your presence, in practice it often has more nuanced functions such as confirming or re-establishing relationships, negotiating social status, signalling benign intent, coordinating with a group, and determining risk of aggression (Dal Pesco & Fischer, 2020; Mercier et al., 2017). Matters are made more difficult by the broad use of the term; often it is used to refer to any time an individual approaches and comes in close contact with a conspecific while displaying non-agonistic behaviour (Kutsukake et al., 2006; Mercier et al., 2017). Alternatively, it has been used to denote a specific set of signal combinations used within a single sex (Corewyn & Setchell, 2019; Dal Pesco & Fischer, 2020). In primates "greeting" is often defined as "ritualized, nonaggressive interactions that serve as a form of tactile communication between two individuals," typically focusing on male-male interactions (Corewyn & Setchell, 2019, p. 630; De Marco, 2017; Dias & Rangel-Negrín, 2017). Elsewhere it refers to behaviours exhibited after periods of separation (De Marco et al., 2011; Luef & Pika, 2019; Okamoto et al., 2001). The one consistency across all uses lies in the analysis of signals exhibited during an approach of one individual towards another.

1.1 Overall thesis objective

This thesis focuses on that critical part of interactions where the tone is set and access to personal space is negotiated: the approach (Greenbaum & Rosenfeld,

1980). In particular, the empirical studies presented address the relationship between risk and signalling. The work is based on studies relating social complexity to communicative complexity at a species level (Dobson, 2012; Kavanagh et al., 2021; Rincon et al., 2023) and the risk or uncertainty of an interaction with communicative complexity at an individual level (Clark et al., 2022). However, defining complexity is difficult, both for sociality and for communication (Bergman & Beehner, 2015). In practice, many previous studies have compared signalling repertoires between closely related despotic (less complex) and egalitarian (more complex) species, finding those which are more egalitarian, and therefore have a greater variability in the relationships between individuals, exhibit more complicated communicative repertoires (Kavanagh et al., 2021; Maestripieri, 2005; Rincon et al., 2023). One of the drivers contributing to the differentiation in communicative complexity between more egalitarian and more despotic species may be selective pressure within more despotic species for reducing the risk of miscommunication in interactions which could be tense and pose personal risk to the approacher (see Section 1.2.2).

As such, the overall research question of this thesis is as follows:

> *How does interpersonal risk shape signalling by an approacher, both at a species and individual level, in baboons?*

This thesis uses data from baboons, specifically chacma baboons (*Papio ursinus griseipes)* and olive baboons (*Papio anubis).* Baboons have frequently been proposed as a useful model for studying links between communication, cooperation, and social organisation and structure (Dal Pesco & Fischer, 2020). While not as closely related to humans as the great apes are, baboons are a useful model organism due to their parallel evolutionary history with early hominins (Elton, 2006). *Papio's* expansion across Africa and divergence of the six species occurred from 2.5 mya to 1 mya, with the highest rate of divergence between 1.5 and 1.3 mya (Roos et al., 2021). This period also saw a radiation of hominins, encompassing first appearance dates for multiple *Australopithecus*, *Paranthropus*, and *Homo* species

(Hockings et al., 2015; van Holstein & Foley, 2022). The evolutionary parallels between *Papio* and hominids make baboons a useful analogous model for studying behavioural diversity across a number of closely related species and interactions with social organisation, structure, communication and tolerance (see Chapter 2).

Throughout the thesis I focus on signalling during approaches between individuals, as this is a period of interaction that can be clearly defined and is relevant for all interaction contexts. Within baboons, approach behaviour has been studied primarily from two angles, the first being male-male "greeting" behaviour (see Section 2.3.1) and the second being grunting during female approaches (see Section 2.3.2) (Dal Pesco & Fischer, 2020; Rendall et al., 1999). These two fields exist in parallel, but remain separate, only intersecting occasionally during discussions of affiliative behaviour and friendships (Smuts, 1985). A comprehensive cross-sex study of approach signals does not exist for baboons, limiting the greater context available for the discussions on both male and female approach behaviour. By focusing solely on male-male encounters when studying greeting in baboons, we premise interpretations of the data on the assumption that such encounters are special in comparison to the other sex combinations and are uniquely placed to provide insight on larger evolutionary questions about connections between communication and social cohesion. The signals exhibited in male-male greetings are observed across all sex combinations (male-male, female-female, female-male, male-female), and thereby have not evolved in response solely to male-biased selection pressures. Studying approach behaviour systematically across all sex combinations would provide a comprehensive view of how and when signals are used and combined, thereby improving understanding of signal function and evolution.

The thesis starts with a species-level perspective, situating chacma baboons within the larger baboon male greeting literature (Chapter 4). Very little of the existing baboon male greeting literature has addressed chacma baboons, even though they present a critical data point being both the most sexually dimorphic and the only species reported to show no male-male coalitionary behaviour (Kalbitzer et al., 2015; Saayman, 1971). As such, they are arguably the most despotic of the baboons

and would therefore be expected to have a more limited greeting repertoire. I then reconsider approach behaviour more broadly, considering how signals across modalities are used together and how differences in signal combination are associated with different outcomes, using approach data from both chacma and olive baboons (Chapter 5). Signalling combinations are compared across sex combinations and by presence and absence of infants, considering how these types of relationships differ. The final empirical chapter develops and tests hypotheses regarding how interpersonal risk to the approacher may act as a selective pressure reducing the complexity and increasing the predictability of the approacher's signalling. The thesis aims to inform our understanding of what baboon approach behaviour looks like, how different contexts and goals may result in different types of approach behaviour, and how social complexity and risk are related to communication within individual interactions and across baboon species.

In previous studies, signals used during approaches are at times referred to as "greeting" in both the human and non-human primate literature, but this term has a fuzzy definition at best, so it is avoided throughout the empirical chapters of the thesis except when in reference to "male greetings" which constitute a specific interaction type between adult males observed in several primate species (see Chapter 4). Shifting away from these more murky "greeting" definitions and using a proximity-based definition of "approach behaviour" is one of the key strengths of this thesis, along with the inclusion of signals across visual, audible, and tactile modalities, the use of network-based methods to consider how these signals co-occur, and the use of video footage to collect detailed behavioural data. These strengths are discussed in more detail at the end of this chapter.

This introductory chapter provides first a brief introduction to signalling and communicative complexity, followed by a review of the approach and greeting literature in humans and non-human primates. Finally, I provide a brief overview of the specific aims and novel aspects of this thesis. A more in depth review of baboons and baboon approach behaviour is found in Chapter 2.

1.2 Signalling and selective pressures

Signalling is critical for the management of inter-individual and inter-group relationships, and as such is heavily influenced by selective pressures tied to social behaviour. Signals are typically defined as behaviours or traits which provide information to a receiver and influence that receiver's behaviour (Hebets & Papaj, 2005; Higham & Hebets, 2013). Aspects of signaller behaviour or physiology may be informative to receivers, but not be under selection for their communicative function, making them a cue instead of a signal (Higham & Hebets, 2013). Signals can be classified using different frameworks, for example unimodal versus multimodal and single versus multicomponent signals. Modality refers to the number of sensory channels a signal may engage in a receiver, for example auditory, visual, tactile, and olfactory (Higham & Hebets, 2013). A signal is considered multicomponent if it is made up of multiple components which do not elicit a response on their own, whereas multiple signalling occurs when multiple signals are used together, but each signal also influences receiver behaviour on its own (Hebets & Papaj, 2005; Rowe, 1999).

Signals used together may be redundant or non-redundant, with redundant being further split into equivalent signals or enhancement signals, where intensity is increased (Higham & Hebets, 2013; Johnstone, 1996; Partan & Marler, 1999). Non-redundant signals can similarly be further classified into sub-categories depending on how the receiver's response is influenced (e.g., modulating the responses versus causing an entirely new response) (Higham & Hebets, 2013). The classification and identification of signals is further complicated by the issue of gradation. Many vocalisations and facial expressions vary continuously along a range, known as gradation, which makes differentiating between expressions difficult (Arbib et al., 2008). The defining of and measuring of signal use and intensity is challenging, but necessary for the study of signal use and evolution.

Studying signalling in non-human species, in particular primates, provides opportunities to identify the origins of the building blocks required for human

language (Arbib, 2017; Arbib et al., 2008; Armstrong, 2008; Rodrigues et al., 2021). The evolution of language is difficult to study due to the ephemeral nature of language and its lack of preservation in the archaeological record. As such, the general approach has been to triangulate evidence through the use of the fossil record, comparative study of behaviour and neurology in extant primates and modern humans, and philosophical or theoretical considerations (Armstrong, 2008). Debates regarding the defining features of language and the order of their evolutionary origin have been lively since the 1970s, though also considered earlier on by philosophers and scientists alike (see Armstrong, 2008 for a historical review). While some approaches have focused heavily on the possibility of a direct evolutionary path between primate vocalisations and human language, others have instead considered the possibility of a gestural origin for language (Arbib, 2017; Arbib et al., 2008; Armstrong, 2008; Corballis, 2017, 2009; Hewes et al., 1973). Instead of viewing human language as a sudden shift characterised by a "jump" that enabled or reflected the evolution of complex thought, those who favour a gestural origin hypothesis focus on the evolution of language as a communicative tool, with many of the underlying building blocks having evolved earlier (Corballis, 2017). Language in humans uses multiple modalities, consisting of signals beyond speech alone, such as gesture and body language (Arbib et al., 2008). Gesture, possibly evolving from imitation and then pantomime, could have provided the scaffolding for proto-linguistic communication that eventually evolved into more complex language (Armstrong, 2008; Corballis, 2009). This again emphasises the importance of considering communication across modalities, rather than focusing on single signalling streams.

Beyond identifying the phylogenetic origins of the components underlying linguistic behaviour, comparative work on communication also helps identify the selective pressures which shape communication more broadly (McComb & Semple, 2005). At a general level, signalling faces selective pressures from both the signaller's perspective and the receiver's perspective, sometimes referred to as

"efficacy based" and "strategic" pressures (Johnstone, 2009). For signallers, selective pressures include the energetic costliness, the risk incurred (e.g., attracting attention from predators), and the effectiveness (e.g., was a mate successfully attracted) (Johnstone, 2009). Receiver-based elective pressures include, for example, a receiver's ability to detect a signal, to determine whether a signal is genuine, and to respond in a way that benefits them (Johnstone, 2009). These pressures at the individual signaller level can also lead to larger patterns at a species level, depending upon environmental and social conditions. As mentioned previously, evidence from comparative studies suggests that socioecological factors such as group size often correlate with aspects of communication. For example, primate species with larger group sizes tend to also have more facial mobility, possibly due to the importance of facial expressions in conflict management and in social bonding, both of which contribute to social cohesion (Dobson, 2009). Facial expression repertoire was also found to be correlated with the level of social tolerance across macaque species (Dobson, 2012). Similarly, vocal repertoire size across 42 primate species was found to be positively associated with group size and time spent grooming (McComb & Semple, 2005). The relationship between social factors and communicative repertoire characteristics has been formalised in the social complexity for communicative complexity hypothesis (Freeberg et al., 2012).

1.2.1 Social complexity hypothesis for communicative complexity

The social complexity for communicative complexity hypothesis suggests that in species where social complexity is higher, signalling repertoires will be larger and signal use more variable (Freeberg et al., 2012; Peckre et al., 2019; Dunbar, 1998; Humphrey, 1976; an extension of the more general social complexity hypothesis or social brain hypothesis A. Jolly, 1966). The communicative complexity hypothesis has been tested in a variety of species including primates (Bouchet et al., 2013; Kavanagh et al., 2021; Rebout et al., 2020; Thierry, 2007), birds (Freeberg, 2006), and rodents (Blumstein & Armitage, 1997; Pollard & Blumstein, 2012). However,

defining social complexity is difficult, and the lack of standardised, comprehensive measures makes it easy to use oversimplified measures or retrofit measures to align with hypotheses (Bergman & Beehner, 2015; Kavanagh et al., 2021). Group size for example, which is a commonly used measure, does not account for the many types of social structure or relationship types that exist and that can differ even between groups of the same size (Bergman & Beehner, 2015). Bergman and Beehner suggested using a measure based on the number of differentiated relationships that exist (e.g., dominance hierarchies, kinship structure, pair bonding, mate preference) (2015). Dominance style has often been used as a measure of social complexity in primate communication studies, with the assumption that species which are more egalitarian are more complex as they would have a wider variety of interactions and relationships that may occur between individuals, with the constant potential for rank reversal (Freeberg et al., 2012). However, it could also be argued that linear dominance hierarchies are more complex as they require the ability for transitive inference (MacLean et al., 2008; Peckre et al., 2019). Other suggested measures of social complexity include the number of distinct social roles, group density, home range size, and stability of subunits (Freeberg et al., 2012).

Similarly, the complexity of communication is difficult to capture (Fischer, Wadewitz, et al., 2017; Peckre et al., 2019). At the simplest level, the complexity of a species' communicative repertoire could be measured by the repertoire size. However, even this poses difficulties, as signals are often graded, meaning that two signals may be variations of each other, making it difficult to know how many signals are in a repertoire (Fischer, Wadewitz, et al., 2017). Studies measuring complexity by repertoire size often also focus on single signalling modalities, such as vocalisations, again ignoring that complexity may be contained in how signals of different modalities are used together (Pika, 2017). The complexity of a system is not just defined by the number of parts it contains (i.e., repertoire size), but also the types of those parts (i.e., modalities), the connections between them, the higher structure of those connections, and the variability in how they are combined (Pika, 2017; Pollard & Blumstein, 2012). Developing measures that encompass all

of these aspects of flexibility is difficult, which is why often multiple measures will be used within one study to capture these different layers of complexity. Measures such as entropy (Mielke et al., 2021; Shannon, 1948), measures of multimodality (Stange et al., 2017), typicality coefficients from fuzzy clustering of signals (Fischer, Wadewitz, et al., 2017), or the number of transitions between signals (Clark et al., 2022) are often used as measures for these varying levels of complexity.

In primates, most of the studies on how communicative complexity relates to social complexity focus on single modalities, for example facial expressions (Dobson, 2009), vocalisations (Bouchet et al., 2013; Gustison et al., 2012; Kavanagh et al., 2021; Rebout et al., 2020), or gestures (Maestripieri, 2005). The largest such study considered vocalisations in 111 populations across 26 species of non-human primates and considered the relationship between the steepness of dominance hierarchies and the species' overall vocal repertoires (Kavanagh et al., 2021). Contrary to what may be expected based on the social complexity hypothesis, there was no difference in overall repertoire size based on dominance style. However, despotic species exhibited larger repertoires of hierarchy-related vocalisations. Kavanagh et al. also looked at signalling differences in individual signalling bouts by dominant individuals, finding that in tolerant species dominant individuals had a higher rate of vocalisation compared to in more despotic species (2021). This was not reflected in the rate of vocalisations by subordinate individuals, however. These findings highlight the need to consider how such selection pressures may reflect differently across levels of analysis (i.e., individual interactions versus species level) and how they may differ depending upon signal type (Kavanagh et al., 2021). When comparing across studies, it also becomes evident that there are issues with the definition of social complexity, as highlighted earlier. For example, when comparing De Brazza's monkeys, Campbell's monkeys, and red-capped mangabeys, Bouchet et al. characterise mangabeys, who live in multi-male, multi-female groups with strong dominance hierarchies, as more socially complex than Campbell's monkeys who live in medium–sized harems with discrete hierarchies (2013). They found red-capped mangabeys exhibited greater repertoire complexity and more vocal

activity, aligning with the social complexity hypothesis (Bouchet et al., 2013). When Gutison et al. compared chacma baboons, who live in multi-male, multi-female groups with geladas, who live in harem-like reproductive units with long-term bonds, they argued geladas were more socially complex (2012), in opposition to Bouchet's interpretation of harem versus multi-male, multi-female groups. Geladas were found to have the larger vocal repertoire (Gustison et al., 2012). As demonstrated by these two studies, the complexity of a given type of social system can be interpreted differently, making it difficult to evaluate the social complexity hypothesis for communicative complexity.

It may be easier to identify how different aspects of social complexity relate to communicative complexity when considering closely related species who primarily differ in one major feature. Across species of macaques for example, which are closely related but differ in their level of despotism (Thierry, 2007), the evidence across signal modalities indicates there is a positive association between communicative complexity and a species' level of tolerance or egalitarianism as opposed to despotism (Maestripieri, 2005; Rebout et al., 2020). Rebout et al. compared female vocalisations in four macaque species, considering affiliative, agonistic, and neutral contexts. While no difference was found in neutral contexts, tolerant macaque species exhibited higher diversity and flexibility in aggressive and agonistic contexts compared to intolerant macaques (Rebout et al., 2020). Comparisons of facial expressions across macaque species have similarly shown that species with more tolerant social styles were likely to have larger facial expression repertoires (Dobson, 2012) and to show more complexity and flexibility in their signal use (Rincon et al., 2023). When comparing across rhesus macaques, stumptail macaques and pigtails macaques, gestural communication repertoires were similarly found to be smallest in the most despotic species and largest in the most tolerant (Maestripieri, 2005), with the same pattern also present in frequency of gesturing (Maestripieri, 1999). While gestures related to dominance and submission were very similar across the three species, the greatest species differences were found in affiliative and bonding gestures (Maestripieri, 2005). These repeatedly found patterns in closely related

macaque species highlight the benefit of comparisons which focus on differences in a single aspect (i.e., tolerance versus despotism) of social complexity. It may be that increased social tolerance acts as a selective pressure driving communication to be more flexible and variable, but that the risk associated with interactions in a highly despotic species also constrains signalling, driving selection for clearer, less complex, and more predictable signalling that is less likely to be misunderstood.

1.2.2 Risk and signalling

In the relationship between risk and signalling, the extremeness of the potential negative outcome should be related with the strength of the selective pressure. Where the negative outcomes of potential miscommunication are stronger, the pressure to reduce miscommunication in turn is expected to be higher (Clark et al., 2022). We see this in species which modify signals to ensure environmental interference or noise does not obscure signals. Wolf spiders, for example, use signals across multiple modalities to ensure their courtship messages are transmitted (Uetz et al., 2009). Male wolf spiders use both visual and seismic signals in courtship displays, adapting displays to environmental conditions (Gordon & Uetz, 2011; Uetz et al., 2013). Similarly in the case of vocalisations, multiple species of birds have been shown to modify the intensity or auditory frequency of their signals to overcome habitat interference (Brumm, 2004; Hart et al., 2015; Kroodsma, 1977). A metanalysis of 73 studies spanning 82 species of insects, anurans, and birds showed that both anurans and birds account for environmental noise during signalling (Gomes et al., 2022). However, miscommunication can also be the result of misunderstanding between signaller and recipient more generally, rather than being due to environmental interference.

In signalling bouts between individuals where a misunderstanding could present a high risk to the signaller, this should lead to clearer, easier to interpret signalling (Clark et al., 2022). Determining what it means for something to be "clearer" however, is difficult, just as it is difficult to measure complexity (Pika, 2017). Studies focusing on differences in signalling behaviour on the interaction level,

rather than on the species level, have also posed the question of how uncertainty in interpersonal relationships relates to signalling complexity (Clark et al., 2022; Grampp et al., 2023). Clark et al. compared crested macaque facial movement intensity and variability in high risk (i.e., individuals close in rank) and low risk (far apart in rank) interactions across affiliative, submissive, aggressive, and copulatory contexts (2022). They found that facial movements in affiliative contexts were least intense and most variable compared to other contexts and that signalling was more intense when individuals were close in rank, supporting the idea that risky social situations were associated with reduced ambiguity in facial behaviour (Clark et al., 2022). Sex combination differences were also found, with same sex interactions exhibiting more variability than between sex interactions (Clark et al., 2022). A study of signalling complexity across different interaction contexts in chimpanzees and sooty mangabeys, however, found that the most complex signals (multisensory or combined signals) were used in post-conflict approaches or, in the case of chimpanzees, during subgroup fusions (Grampp et al., 2023).

The different measures (complexity versus variability) used make these studies difficult to compare; while more combined signals may have been used in more tense contexts in sooty mangabeys and chimpanzees, this more complex signal use may not necessarily result in greater variability. In other words, more complex signals may be used, but they may be used very predictably, leading to low variability. Using more signals in the form of redundant or backup signals could be a method for reducing miscommunication (Johnstone, 1996). This could then appear as more complex communication due to the use of more signals in a single encounter. However, similar disambiguation can be seen in affiliative contexts. For example the addition of a play face in an interaction between chimpanzees can disambiguate the meaning of a signal (e.g., hitting or shoving) which may lead to different responses depending on the context (Palagi, 2008). Adding components to a signal may also strengthen or modify the meaning of the original signal. In crested macaques, a lip-smack together with a vocal component is more likely to result in affiliative contact than a lip-smack without the vocal component for example (Micheletta et

al., 2013). Across these studies, we can see that the potential for miscommunication and interpersonal risk (e.g., rank differential) can affect signalling on an interaction level, not just on a species level.

Interpersonal risk is itself influenced by a variety of factors, and these factors may differ by sex-combination, by individual, and by larger species characteristics such as levels of sexual dimorphism. Within any interaction, both the signaller and the recipient are exposed to potential risk through that interaction. Risk could be the result of a rank differential, or even closeness in rank; interactions with a larger rank differential may in fact be more predictable and secure for both participants as the likelihood of the lower ranking individual to challenge the dominant individual is so low (Clark et al., 2022). Other extra-pair relationships, such as the matriline the recipient belongs to or the coalitionary partners or friends they may have could also impact the risk posed to the approacher (Schaik et al., 2006).

We may also expect to see risk relating to more sex-based characteristics, such as infant presence, the possibility for infanticide, or sexual dimorphism. Several primate species, including chacma baboons, exhibit infanticide (Palombit, 2000), which may be a reproductive strategy to reduce the time until a female is cycling again, and sexual harassment/intimidation (Baniel et al., 2017; Palombit, 2014). The risk for this may be especially high in species with higher sexual dimorphism. Sexual dimorphism in body mass, canine tooth dimensions, and post-cranial skeletal shape has been recorded across many primate species and is influenced primarily by mate choice and mate competition, along with other influences such as predation, female competition, diet, female ontogeny, and niche dimorphism (Clutton-Brock et al., 1977; Plavcan, 2001; Plavcan, 2012). Higher levels of sexual dimorphism may alter the perceived risk levels in approaches between different sex combinations, resulting in differences in signal use compared to species with lower levels of sexual dimorphism.

1.3 Approach behaviour in primates

To manage well within a social group, individuals must be able to navigate social relationships and have a basic level of social competency given the social requirements of their species (Taborsky & Oliveira, 2012). Part of social competency is knowing how to successfully initiate an interaction. Within primates, there are many examples of how signalling during an approach can reduce the likelihood of a recipient exhibiting avoidance behaviour (Cheney & Seyfarth, 1997) or increase the likelihood of physical contact (Fedurek et al., 2015; Silk et al., 2018), which as mentioned previously, is critical to the development and maintenance of social bonds and greater social cohesion. Within humans, these types of approach signals are often referred to as "greetings", so the term will be used throughout this section in line with how it is used in the publications referred to.

1.3.1 Humans

In the human greeting literature, greeting is typically defined as a salutation occurring when people come together and is "the recognition of an encounter with another person as socially acceptable" (Frith, 1972, p. 1). Morris highlights the links between greeting, leave-taking and ritual, stating "We salute their comings, their goings and their transformations" (Morris, 1977, p. 77). Ritualised behaviours have long been suggested as a method of managing and avoiding aggression (Lorenz, 1963). In humans, proposed functions of greeting include signalling "readiness for social contact" (Eibl-Eibesfeldt, 1979, p. 18), confirming relationship condition, temporarily suppressing tension (Goffman, 1967), and recognising, but also negotiating, rank and status (Duranti, 1992).

While significant cultural variation exists within human greeting, certain behaviours have been reported across cultures. The head-toss and eyebrow flash greeting has been recorded across the globe, including in Polynesia, Japan, the United States, and Europe (Eibl-Eibesfeldt, 1979; Kendon & Ferber, 1973). Depending upon context, gaze aversion is used during greeting (Duranti, 1992; Kendon

& Ferber, 1973) and could function to avoid aggression (Eibl-Eibesfeldt, 1979). Cross-cultural studies on the physicality of greeting have declined in popularity recently, with interests refocusing on the social and personal effects of greeting, such as assisting immigrants adjusting to new countries, resolving work place stress, or improving greetings performed by robots (Elhami, 2020; Kristensen & Kristensen, 2020; Liu, 2016; Prasad et al., 2022). The Covid-19 pandemic provided an interesting case study, having resulted in attempts to change greeting culture through the passing of laws and highlighting how deeply embedded greetings are in social interactions, even when health may be at risk (Gopez et al., 2021).

While the focus of greeting research may change with time, several cross-cultural patterns can be identified. First, human greetings are typically multi-modal. Communication in greetings runs along several planes – bodily, spatial, and verbal – simultaneously (Kendon & Ferber, 1973). Second, they are usually predictably ordered (Duranti, 1992, 1997). Linguistic analysis across cultures suggests greetings are "inherently sequential," with a set of predetermined words/actions resulting in the selection of appropriate responses (Duranti, 1992, p. 658; Frith, 1972). Third, signal choice is affected by the individual's relationship with and relative rank compared to the recipient (Frith, 1972). Fourth, greeting within a culture or even a specific pairing of individuals can differ by function or intention (Kendon & Ferber, 1973).

Apart from written greetings, human greetings incorporate combinations of vocal/verbal (e.g., "hello"), visual (e.g., a wave), tactile (e.g., a hug), and spatial (e.g., staying at a distance) signals. Looking at one modality in isolation (e.g., verbal, as linguists might), limits interpretability. Other cues, for example body language or gaze, can add and modify the meaning of spoken language (Duranti, 1992). In Samoan ceremonial greetings, spatial choices by a participant determine the role they will play in the event (Duranti, 1992). An account of only the verbal or tactile signals used by participants would leave out this crucial information that explains much of what follows. A study of greetings at an American house party provides a clear example of how such components fit together – a visual distance

salutation, for example a wave or smile, is followed by gaze aversion during the approach, a verbal interaction, and at times a tactile interaction, for example a hug or handshake (Kendon & Ferber, 1973). In some countries the incorporation of tactile signals plays a strong enough role in greetings that this contributed to the spread of Covid-19. The "A Filipino Greeting for Health" Act was passed by the Philippine government to encourage members of the public to change their greeting style, reducing proximity and physical touch, for example (Gopez et al., 2021).

Sequence and predictable ordering of components has been highlighted as a common feature of greetings, both in physical and verbal modalities. Multiple authors highlight the role adjacency pairs play in greetings – one signal has an expected response (Duranti, 1997; Frith, 1972; Morris, 1977). The overall format of a greeting interaction involves first, encountering another individual, second, both participants recognising the other's presence, and third, a series of exchanges, often with relatively predictable content and structure. Once the encounter is finished, it has reduced the uncertainty of what type of interaction will follow (Frith, 1972). Kendon and Ferber detail a similar, but more concrete structure involving sighting of each other, orientation towards each other, initiation of the approach and/or a distance greeting, the approach, and finally arrival and close salutation (1973). Adjacency pairs and predetermined calls and responses can be identified throughout these stages. A study of airport greetings demonstrated that certain behaviours were more likely to occur at the beginning of an interaction (mutual-lip-kiss, face-kiss, and handshake), and others at the end (hand-to-upper-body contact) (Greenbaum & Rosenfeld, 1980). Choice of an initiating action may also determine what other actions follow – for example while most types of contact were seen to happen with other types of contact, travellers who greeted with a handshake were unlikely to perform another contact behaviour (Greenbaum & Rosenfeld, 1980). Violation of the expected response would often be considered a slight and can act to exclude an individual from an interaction (Frith, 1972). A study of the experience of nursing students on placements in Denmark demonstrated this. The hospital's registered nurses had a culture of ignoring and not greeting student

nurses, which made students feel alienated and unvalued (Kristensen & Kristensen, 2020). Both adherance to and violation of expected sequences are critical to shaping the outcome of greeting interactions.

Across cultures, we see that greetings vary intra-culturally based on context and personal relationship. In many instances, social status of participants determines who can greet and in what way (Atika, 2020; Frith, 1972; Kendon & Ferber, 1973; Oluyemi & Olumide, 2021; Rababah & Malkawi, 2012; Walsh, 1982). The lower ranking individual often changes their posture more, for example physically lowering oneself in a bow, and may move location more, for example approaching the higher ranking individual while they remain stationary (Frith, 1972; Kendon & Ferber, 1973). Beyond social status, the closeness of relationships and gender of participants affects greeting form. Often the distance between individuals during a greeting is reflective of the social distance between participants, with a closer distance indicative of a closer friendship (Frith, 1972). Personal relationship also affects the type of physical contact used, with bodily areas considered taboo to touch varying drastically by relationship type (Forsell & Åström, 2012; Suvilehto et al., 2015; Suvilehto et al., 2019). The gender of participants can affect any of the modalities. Male and female speakers of Persian use different linguistic forms, levels of formality, and discuss matters of differing levels of privacy (Dezhara et al., 2012). In the study of airport greetings, female-female pairs had longer bouts of physical contact than male-male pairs. Cross-sex and female-female physical contact was longer and more variable than in male-male interactions (Greenbaum & Rosenfeld, 1980). Greenbaum and Rosenfeld suggest that males perform a "highly formalised greeting consistent with culturally prescribed male sex-role behavior" (1980, p. 22). Finally, greetings may differ by function or intention, even within the same relationship. The type of distance greeting and eye gaze used may give permission for the partner to approach or indicate that no closer greeting is desired (Kendon & Ferber, 1973). Among the Yoruba in West Africa, greetings differ by function, event, and health condition (Oluyemi & Olumide, 2021). Greetings, while

often having similar functions, structures, and physical actions across cultures, are variable depending upon context, intention, and relationship.

1.3.2 Non-human Primates

In non-human primates, greeting and approach behaviour have been studied in chimpanzees, Tonkean macaques, vervets, sooty mangabeys, mantled howler monkeys, black-and-white colobus monkeys, and baboons (for baboons see Chapter 2), among others. Like human greetings, they are often multi-modal, have varying functions, and change based on personal relationship and context. While there are some approach signals seen across a number of taxa, for example grunting, embracing, and genital inspection, there is a large amount of inter-species and intra-species variation. What is even more difficult in research of non-human primate greetings than in human greeting research, is identifying what contexts and what behaviours should be classified as greetings. As mentioned previously, the term "greeting" is used to denote a wide range of encounter types in primates. This issue is compounded by the difficulty of identifying which behaviours relate specifically to reunion after separation, and which occur, for example, in every situation where signalling submission is needed (Rodrigues et al., 2022).

Approach and greeting behaviour across non-human primates exhibit both shared and species-specific signals. Embracing is seen across multiple species including chimpanzees, black-and-white colobus monkeys, baboons, Tonkean macaques, and mantled howler monkeys (Corewyn & Setchell, 2019; Dal Pesco & Fischer, 2020; De Marco et al., 2011; Kutsukake et al., 2006; Okamoto et al., 2001). Several species include mounting or some type of genital contact (Black-and-white colobus monkeys: Kutsukake et al., 2006; baboons: Dal Pesco & Fischer, 2020; mantled howler monkeys: Corewyn & Setchell, 2019). Other types of contact include kissing and crouching with an extended hand in chimpanzees (Fedurek et al., 2021; Luef & Pika, 2019; Okamoto et al., 2001), overhead mounting in black-and-white colobus monkeys (Kutsukake et al., 2006); various types of grasping and shoulder-clasping in Tonkean macaques and mantled howler monkeys (Corewyn &

Setchell, 2019; De Marco et al., 2011), hindquarter touches in baboons (Dal Pesco & Fischer, 2020), and armpit sniffing in mantled howler monkeys (Corewyn & Setchell, 2019). Vocalisations include pant-grunts and pant-barks in chimpanzees (Laporte & Zuberbühler, 2010; Nakamura, 2022; Okamoto et al., 2001), low-pitched grunts in baboons, sooty mangabeys, and vervets (Fedurek et al., 2019; Mercier et al., 2017), high-frequency twitters in sooty mangabeys (Fedurek et al., 2019), and sirena screams in black-horned capuchin monkeys (Alfaro, 2008).

These types of signals are often combined into multi-modal displays during approach. In chimpanzees for example, vocalisations such as the pant-grunt can be used together with physical touch incluing kissing or embracing (Okamoto et al., 2001). Fedurek et al. suggest that interactions with a greater rank difference should involve a higher signalling effort by the lower ranked individual to avoid aggression and would therefore be more likely to be multimodal (2021). This is supported in findings demonstrating that the level of multi-modality in chimpanzee greetings is affected by rank differential, with gesture-only communication (rather than multimodal) being less likely when the receiving partner was ranked higher (Rodrigues et al., 2022). Across primates, brief touch is often seen in greetings and is argued to be a signal of benign intent, used in relationships that are particularly risky or uncertain to reduce the risk of aggression and assess the social relationship (Aureli & Schino, 2022). While signals in primate encounters are often given by both participants, the level of reciprocity is very dependent on species and sequencing is not as clear as in human greetings. In chimpanzees, only 5% of greetings were found to be reciprocal, with reciprocity being more likely in gestural greetings than other modes (Luef & Pika, 2017). A stronger social bond was associated with more reciprocity, particularly in bimodal greetings (Luef & Pika, 2017). Reciprocity is also a common theme in the baboon greeting literature, with levels of reciprocity differing across the genus (see Section 2.3.1).

As in humans, rank, sex, and relationship affect approach signals in non-human primates. In many species, signals are displayed primarily by the lower ranking individual towards the higher ranking (Corewyn & Setchell, 2019; Fedurek et al.,

2019). In some species, a greater rank differential is associated with a higher likelihood of greeting behaviour (chimpanzees: Fedurek et al., 2019), while in others the reverse is observed (mantled howler monkeys: Dias et al., 2008; sooty mangabeys: Fedurek et al., 2019). In black-and-white colobus monkeys a similar relationship is seen between age and greeting, with greeting being more common in pairs with a greater age difference (Kutsukake et al., 2006). Signals during approach are less likely in pairs that are socially close or related in bonobos (Heesen et al., 2021), chimpanzees (Luef & Pika, 2019), and baboons (Silk et al., 2018), suggesting that exaggerated communication is not needed between individuals with strong bonds because the status of the relationship is known and secure. In chimpanzees, a stronger social bond is also associated with more greeting reciprocity, especially for bimodal greetings (Luef & Pika, 2017). The sex of the participants and audience members is associated with differences in the likelihood of greeting behaviour being exhibited by chimpanzees. If the alpha male is present, females are less like to pant-grunt at males (Laporte & Zuberbühler, 2010). Presence of a greater number of males also has an inhibitory effect (Laporte & Zuberbühler, 2010). Greeting behaviour between female chimpanzees is far less common than between males and females in the wild, and separation in a captive setting also had different results across sex combinations, with an increase in male-female affiliative interactions after reunion, but no change for male-male pairings (Okamoto et al., 2001). Some of these differences across contexts and relationship types may be reflective of the underlying function of different types of approach behaviour.

One of the difficulties with cross species and even within species comparisons of approach or greeting behaviour is that the definitions and inclusion criteria used vary so drastically. Even within only the study of male greetings in baboons, this effect is strongly felt (see Chapter 4). More generally, it would be useful to understand how signalling during approaches are used to initiate interactions, and whether different signalling clusters can be identified which may be associated with different behavioural outcomes.

1.4 Thesis scope and purpose

This thesis aims to broaden our understanding of how chacma baboons fit into the larger *Papio* male greeting picture, to consider how signals are combined and used to initiate interactions within baboons, and to test hypotheses regarding the relationship between signalling complexity and interpersonal risk in baboons. Signals across vocal, gestural, and orofacial modalities are considered, rather than focusing on individual signalling streams.

This thesis focuses primarily on video footage from a troop of chacma baboons (*Papio ursinus griseipes*) residing in Gorongosa National Park, Mozambique, with data from a smaller footage archive of olive baboons (*Papio anubis*) from Gombe National Park, Tanzania incorporated into Chapter 5 and Chapter 6. Both field sites have not been used in the study of approach behaviour or male greeting behaviour and additional male greeting data on chacma baboons is particularly critical as they are an outlier among savannah baboons when it comes to cooperative behaviour (Bulger, 1993) and are understudied (see Chapter 2).

The thesis addresses the following series of hypotheses and research questions across Chapters 4 - 6. The first empirical study (Chapter 4) focuses on male greeting behaviour within chacma baboons of Gorongosa National Park. It discusses the issues and limitations with existing approaches to male greeting in baboons and compares greetings by male chacma baboons in Gorongosa National Park to male greetings at other baboon sites, considering how this fits within the larger social complexity hypothesis for communicative complexity.

- ***Chapter 4 - Hypothesis***: Male greetings in chacma baboons are expected to show reduced contact behaviour and less elaborate greeting behaviour compared to other baboon species, as interactions between males in chacma baboons are higher risk with less socially tolerant relationships.

The second empirical study examines how signals are combined and how these combinations differ by the sex of the greeter and of the recipient and by infant

presence. A network analysis approach is used, which identifies clusters of signals that are often used together. Signal use is expected to have overlap between sex combinations of approacher and recipient, but to show clear patterns reflective of differences in the risk to the signaller associated with different sex combinations. Where risk is higher (i.e., male-male interactions), behaviour may be ritualised. After identifying signalling clusters, we then formulated hypotheses for the second stage of analysis based on the existing literature on these signals.

- ***Chapter 5; stage 2 - Hypothesis***: Identified signal combinations are associated with differences in interaction outcomes, specifically contact.

Finally, the third empirical chapter considers how contact behaviour, entropy, and event size may differ in high risk versus low risk interactions. Presence of the approacher's infant and the sex of the recipient are used as proxies for risk.

- ***Chapter 6 - Hypothesis***: Signal use by the approacher will be less complex and more predictable in higher risk interactions and will also involve less contact behaviour.

Complexity is measured by the number of the signals used in approaches, and predictability is measured using entropy (Mielke et al., 2021).

Together, these studies provide a more encompassing view of signal use during approach in chacma and olive baboons and of how patterns in signalling vary within and between sexes and species. This in turn gives us further insight into how risk may contribute to the social complexity hypothesis for communicative complexity.

1.4.1 Novelty

This project is novel both in methods, namely its use of video footage, a more inclusive definition of approach behaviour, and application of a network-based approach, and in its direct cross-sex comparison across signal modalities.

Usage of video footage

Most studies on greeting and approach behaviours in non-human primates have been completed using live field observation. This is at odds with human ethology research, which has espoused the benefits of video-based analysis for over 50 years. Using video allows for the capture of minutiae not visible or recordable during live observation (Eibl-Eibesfeldt, 1989; Eibl-Eibesfeldt & Hass, 1967; Gilmore & Adolph, 2017). It also provides the benefit of being able to rewind, move frame by frame, and record fine-scaled timing of events (Friard & Gamba, 2016). Use of video footage can help ensure high quality data collection and lets one return to previously coded events to confirm that a newly identified behaviour was not present and missed. It facilitates inter-observer reliability checks and allows for full reproducibility of findings (Eibl-Eibesfeldt, 1989; Gilmore & Adolph, 2017). This will be the first study of baboon greetings or approach behaviour to primarily rely on video recordings rather than focal follows, allowing, for the first time, more detailed analysis of fine-scale form, timing, and combining of behaviours. This also follows the example of Baehren, who used video-based methods to study leave-taking behaviour in the same population of chacma baboons (Baehren & Carvalho, 2022).

More encompassing definition

Many past studies on male greeting only collect data when there is an approach and then an interaction (Colmenares, 1991b; Dal Pesco & Fischer, 2018; Smuts & Watanabe, 1990; but see Kalbitzer et al., 2015), which is contrary to the criteria applied in most wider approach literature (e.g., Silk et al., 2018). Without looking at the cases in which there is an approach without interaction, we limit our understanding of why greeting behaviours are displayed or what circumstances do not require greeting. Following Chapter 4, which applies a more traditional male-greeting framework, the remaining studies in this DPhil use the criteria of a proximity event, here defined as any instance in which an individual comes within two meters of a conspecific after having previously been more than five meters away.

This allows for more objective decision-making regarding when data should be collected and avoids the circular definition of a "greeting" being any time "greeting behaviours" are exhibited. It also prevents the accidental exclusion of subtle behaviours which may be missed upon first – or live – viewing. This makes the study more comparable to *in situ* (rather than playback) grunting studies, where similar proximity-based data collection criteria have often been used (Silk et al., 2018).

Network analysis

Chapter 5 and Chapter 6 take a network-based approach, which allows for the study of how signals are combined in different types of interactions, rather than requiring a focus on individual signals. Signals may be changed by their combination with secondary signals and these effects may be entirely lost without a network-based approach (Mielke et al., 2021). Using a network-based approach allows for an improved understanding of how the different signal modalities combine and interact in an approach context.

Cross-sex comparison

The "greeting" literature on baboons is dominated by studies on male-male interactions. Meanwhile, female-female and male-female interactions have been studied through other lenses (e.g., grunting during approach Rendall et al., 1999) (see Chapter 2 for a full review of baboon approach behaviour) and female-female greetings are frequently mentioned *in passing* as an "affiliative behaviour" (Anthoney, 1968; Silk et al., 2010a, 2017). However, there do not appear to be any studies that dissect the physicality of female-female and female-male approaches as thoroughly as we see in the male-male literature. This thesis aims to fill this gap, providing a more comprehensive perspective on how signals are combined during approaches between all sex combinations.

Novel Populations

Finally, this study collects data on two sites which have not been used in greeting or approach behaviour studies previously. Gorongosa National Park is in its first years of primatological research (Baehren & Carvalho, 2022; Bobe et al., 2023; Hammond et al., 2022; Martinez et al., 2019, 2019; Santander et al., 2022; Stalmans et al., 2019, 2020), with the Chitengo Troop having been fully identified in 2019. Currently, only one other greeting-focused study has been completed in chacma baboons (Moremi Game Reserve, Botswana), making the addition of new sites very valuable (Kalbitzer et al., 2015). While olive baboons in Gombe National Park have been studied over decades, their approach behaviour has not been addressed yet (see Chapter 3 for field site descriptions). Adding new field sites, in particular a chacma baboon field site, to the literature will allow for more thorough testing of existing hypotheses on the function and evolution of approach and "greeting" behaviours in baboons, which relies on comparisons across species (Dal Pesco & Fischer, 2020).

2

Approach behaviour in baboons

Baboons have come in and out of fashion throughout the last century as models for various aspects of hominin evolution (Cheney & Seyfarth, 2007; Dunbar, 1976, 1983; Elton, 2006; Elton & Dunn, 2020; Fischer et al., 2019, 2019; C. J. Jolly, 2020, 1970, 2001; King, 2022; Meguerditchian et al., 2021; Rose, 1976; Strum, 2001, 2012; Strum & Mitchell, 1987; Swedell et al., 2012; Swedell & Plummer, 2019; Washburn & Devore, 1961; Wrangham, 1980). More recently, they have been proposed as a useful model genus for the study of communication and the evolution of human language (Fagot et al., 2019), where they had previously been outshone by species with more impressive vocal (Dunn & Smaers, 2018; McComb & Semple, 2005), gestural (Tomasello & Call, 2019), or facial signal repertoires (Waller et al., 2020). Fagot et al. review previous cognitive, vocal, gestural, and cultural research on baboons, emphasising that baboons share many of the same underlying cognitive mechanisms central to language evolution (2019). Beyond this narrow focus on the evolution of human language, however, baboons can provide insight into the selective pressures, such as perceived risk, that shape communication and signalling more generally. Baboons exhibit diversity in several key characteristics that make them useful models when studying the impact of risk on communication both within and between species. Social organisation and philopatry vary across the

species (C. J. Jolly, 2020). This is accompanied by differences in the level of sexual dimorphism and the quality of male-male relationships, ranging from competitive and hostile to cooperative and affiliative. The six baboon species furthermore show differing levels of ritualisation of and frequency of male greeting behaviour (Dal Pesco & Fischer, 2020). This chapter provides a general overview of baboon socioecology and reviews the existing literature on signalling during approaches in baboons to provide additional context for the following empirical chapters. In particular, this chapter focuses on male greeting behaviour and male and female grunting behaviour, outlining findings and differences in methodology. The baboon signalling literature generally suffers from a lack of integration with little discussion of how signals are used together, an issue which this thesis aims to help address.

2.1 Baboon phylogeny

Six species of the genus *Papio* currently range through Africa and the Arabian Peninsula (*Papio hamadryas, Papio papio, Papio anubis, Papio cynocephalus, Papio ursinus*, and *Papio kindae*); these can be considered allotaxa as they are separate species following the phylogenetic definition, but subspecies following the biological definition, and overlap in several key contact zones (Alberts & Altmann, 2001; Chiou et al., 2021; C. J. Jolly, 2001; C. J. Jolly et al., 2011; Martinez et al., 2019; Phillips-Conroy & Jolly, 1986; Samuels & Altmann, 1986). *Papio* experienced high levels of clade divergence between 1.3 and 1.5 million years ago, likely due to climatic changes (Roos et al., 2021). This distribution and differentiation of *Papio* species can be considered analogous to several periods within hominin evolution where multiple hominin species or subspecies coexisted temporally and geographically, with strong potential for hybridisation (Elton, 2006; C. J. Jolly, 2001; Roos et al., 2021). Studying behavioural and phenotypic diversity across modern sympatric allotaxa may give insight into the types of variation that could be expected during these periods of hominin evolution (Elton, 2006). *Papio* has a complicated evolutionary history, with the first sets of larger splits within the genus happening between 2 and 2.5 million years ago (Roos et al., 2021).

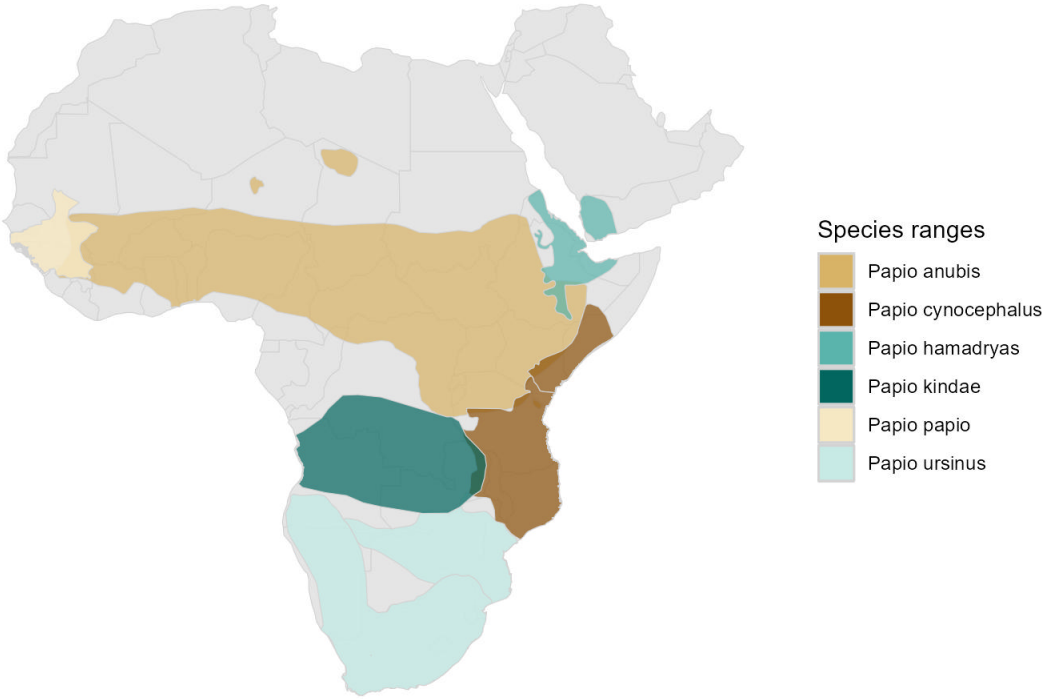

Figure 2.1: Baboon species distributions, made using IUCN species distribution data (IUCN, 2019, 2020a, 2020b, 2022; Wallis & IUCN, 2020, 2022) and Natural Earth.

Depending on geographic sampling, reconstructed phylogenies can vary and lead to different conclusions regarding the order in which clades diverged (Roos et al., 2021; Zinner et al., 2009, 2013). Generally, it appears that there was a larger southern *Papio* versus northern *Papio* split between around 2.3 million years ago and a split between northwestern and northeastern *Papio* between 1.5 and 2 million years ago, with clear poly- and paraphyletic relationships suggesting possible nuclear swamping and introgression (Roos et al., 2021).

2.2 Social organisation, structure, and philopatry

The chacma, olive, Kinda, and yellow baboon have similar social structure and organisation, living in uni-level multi-male multi-female polygynandrous groups. They are female philopatric with male dispersal from the natal group (Fischer et

al., 2019). Group size typically ranges from several dozen to a maximum of 100, but group size in Kinda baboons can range to above 200 (Fischer et al., 2019; Petersdorf et al., 2019; Stoltz & Saayman, 1970). In the olive, chacma, and yellow baboon, female-female relationships and matrilines create a solid social structure within the troop (Fischer et al., 2019; C. J. Jolly, 2020). Strong female-female relationships increase reproductive success and are biased towards maternal kin, especially in higher-ranking matrilines (Silk et al., 1999; Silk, Alberts, et al., 2006). In the Kinda baboon, however, male-female relationships are very important, with males being the most frequent grooming partner for most females, more often initiated by the male than by the female, and with male-female proximity more common than female-female proximity (Petersdorf et al., 2019). Chacma, olive, and yellow baboons also exhibit male-female friendships but proximity in these relationships is primarily maintained by females (Palombit et al., 2001). Male-female friendships are a form of joint parental care and protective against infanticide or harassment (Lemasson et al., 2008; Moscovice et al., 2010; Nguyen et al., 2009; Palombit et al., 2001; Smuts, 1985).

Hamadryas and Guinea baboons both exhibit multi-level social structures, with group sizes up to several hundreds at the highest level of organisation (Fischer et al., 2019; Patzelt et al., 2011; Schreier & Swedell, 2009). In hamadryas baboons, one-male units are the basic building block, which come together to form clans, and then bands (Henzi & Barrett, 2003; Kummer, 1984; Schreier & Swedell, 2009). One-male units typically consist of one leader male, a variable number of females, and a follower male who is often maternally related to the leader male (Romero & Castellanos, 2010; Städele et al., 2016). Bands merge at sleeping sights to form troops, though troop composition is variable. A leader male is typically dominant over the follower male in his unit, but across units within a band or troop dominance hierarchies can be difficult to identify, suggesting there is not a rigid hierarchy (Romero & Castellanos, 2010). Males close in rank are more likely to greet each other (Romero & Castellanos, 2010).

Guinea baboon males also have units which consist of a male, associating females, immature baboons, and secondary males, with higher-level organisation into parties and then gangs (Dunbar & Nathan, 1972; Fischer, Kopp, et al., 2017). Gangs with overlapping home ranges are referred to as communities (Patzelt et al., 2014). While the social organisation is similar to hamadryas baboons, the social relationships exhibited are very different (Fischer, Kopp, et al., 2017). Guinea baboons exhibit very low levels of male-male aggression, high spatial tolerance, and strong relationships between males. These relationships occur even between unrelated males (Patzelt et al., 2014). Unlike hamadryas baboon males, male Guinea baboons do not herd females, allowing more freedom of movement (Fischer et al., 2019). Dispersal in both hamadryas and Guinea baboons is predominantly female, though in hamadryas baboons this is largely a result of male takeovers rather than voluntary transfer (Fischer et al., 2019; Swedell et al., 2011).

2.2.1 Coalition behaviour and male-male relationships

During their oestrous cycle, females of all *Papio* species exhibit sexual swellings of different sizes and shapes (Fischer et al., 2019; Petersdorf et al., 2019). In most species, males exhibit strong competition over consortship and mating opportunities with receptive females, who typically mate with multiple partners each cycle. The Kinda baboon is the exception to this rule, generally employing queue-based rather than contest-based competition, with more stability in male hierarchies and longer tenure of alpha males (Petersdorf et al., 2019). In the yellow, olive, and chacma baboons, paternity is skewed towards higher ranking individuals, but especially so in chacma baboons (Alberts et al., 2003; Bulger, 1993; Fischer et al., 2019; Henzi & Barrett, 2003; Städele et al., 2019a). This difference in skew may be partially due to demographic differences, partly due to differences in coalitionary behaviour, and partly due to the higher rates of reported infanticide (Henzi & Barrett, 2003; Palombit, 2015; Palombit, 2000; Palombit, 2003). One of the major drivers of coalitionary behaviour is competition over access to receptive females (Noë & Sluijter, 1990; Noë & Sluijter, 1995). While

coalitionary behaviour has been documented in yellow, olive, and Guinea baboons, there has been little to no coalitionary behaviour reported in chacma baboons (Henzi et al., 1999; Henzi & Barrett, 2003; Henzi & Barrett, 2005; but see an early account by Saayman, 1971). Evidence regarding coalitionary behaviour in Kinda baboons is still lacking due to relatively limited study of their behaviour (Petersdorf et al., 2019). Henzi, Weingrill, and Barrett (1999) initially suggested that the lack of coalitionary behaviour in chacma baboons may be due to a reduced average number of males per troop as a result of the harsher environmental conditions chacma baboons tend to range in. However, even when environmental conditions and demographics are more similar to those of olive and yellow baboons, no male-male coalitionary behaviour is typically observed (Henzi & Barrett, 2005). Fischer et al. suggest that the lack of coalition formation may also relate to the emigration timeline of males – chacma baboons often emigrate from their natal group one to two years later than yellow and olive baboons (Alberts & Altmann, 1995; Beehner et al., 2009; Fischer et al., 2019; Packer et al., 1995). Female-female coalitionary behaviour has been observed across multiple baboon species including chacma baboons (Henzi & Barrett, 2005; Silk et al., 2004).

2.2.2 Sexual dimorphism

Papio is a highly sexually dimorphic genus (Plavcan, 2001). While highly sexually dimorphic primate species can typically be assumed to be polygynous and characterised by intense male-male competition, the complimentary assumptions cannot be made for monomorphic or minimally dimorphic species (Clutton-Brock et al., 1977; Lawler, 2009; Mitani et al., 1996; Plavcan, 2001). Factors affecting sexual dimorphism include mate competition and sexual selection, operational sex ratio, coalitionary behaviour, female competition, and predation defence (Plavcan, 2001; Plavcan, 2012). Species are often sexually dimorphic in body mass, canine tooth size, skeletal morphology, and pelage (Plavcan, 2001). Among baboons, Kinda are among the least dimorphic, while chacmas are amongst the most dimorphic in comparison to the other *Papio* species (see table 2.1). Together these differences

in social organisation, male-male relationships, and sexual dimorphism across *Papio* provide a valuable opportunity for studying how these factors are related to communication across and within species.

Table 2.1: Sexual dimorphism in body mass and canine height across *Papio*

Species	**Male mass (kg)**	**Female mass (kg)**	**Body mass ratio (M:F)**	**Canine height ratio (M:F)**
P. ursinus [1,3]	29.80	14.8	2	3.84
P. ursinus [5]	28.10	15.9	1.77	n.a.
P. papio [2,5]	20.20	11.8	1.71	n.a.
P. papio [4]	23.51	n.a.	n.a.	n.a.
P. hamadryas [1]	18.95	10.65	1.78	2.74*
P. hamadryas [3]	21.00	11.4	1.84	2.74*
P. hamadryas [4]	20.83	n.a.	n.a.	n.a.
P. hamadryas [5]	20.90	12	1.74	n.a.
P. cynocephalus [1]	17.20	9.75	1.76	2.8
P. cynocephalus[4]	22.76	n.a.	n.a.	n.a.
P. cynocephalus [5]	22.50	12.4	1.81	n.a.
P. anubis [1]	23.15	12.5	1.85	2.22*
P. anubis [3]	24.19	15.81	1.53	2.22*
P. anubis [4]	22.72	n.a.	n.a.	n.a.
P. anubis [5]	22.80	12.5	1.82	n.a.
P. kindae [3]	17.24	9.75	1.77	3
P. kindae [5,6]	16.00	10.3	1.55	n.a.

Sources: [1] Thoren et al., 2006; [2] Fischer et al., 2017; [3] Plavcan & Ruff, 2008; [4] Jolly & Phillips-Conroy, 2006; [5] Rogers et al., 2019; [6] Petersdorf et al., 2019; n.a. - Not available; * - sample reported across two publications

2.3 Signalling research in baboons

Communication in primate species is often split into three main streams: (1) vocalisations, (2) orofacial signals, and (3) gestures. Across primate research, these streams are frequently studied in isolation, with multimodal approaches limited (Aychet et al., 2021; Molesti et al., 2020; Pika, 2017; Slocombe et al., 2011; Waller et al., 2013). This greatly limits our understanding of how signals are combined and how they contribute to overall communicative complexity. The studies in this dissertation take a more integrated approach, considering how signals across modalities are used together, which has not yet been done in a comprehensive fashion for baboons.

The vocal repertoire of baboons includes contact calls (Rendall et al., 2000), barks (Fischer et al., 2001), multiple grunt variants (Owren et al., 1997; Rendall et al., 1999), copulation calls (Bouquet et al., 2018), screams (Hammerschmidt & Fischer, 2019), and several types of loud calls including wahoos (Fischer et al., 2002). Research on vocalisations across baboon species have indicated that the vocal repertoire is generally consistent among baboons (specifically chacma, olive, and Guinea baboons), with only subtle acoustic differences within call types (Hammerschmidt & Fischer, 2019). Within call-type acoustic variation was not associated with differences in social system, and was correlated with geographic distance only for male loud calls, but not for grunts or female loud calls (Hammerschmidt & Fischer, 2019). Hammerschmidt et al. argue that vocalisations are largely conserved across *Papio*, though the intensity and rate of signal occurrence may vary by species. This may be a sign that selection pressures were not strong enough to change neural pattern generation and that the vocalisations might serve similar functions across the species (Hammerschmidt & Fischer, 2019). Baboons have also been used as a model species for the evolution of human language, in particular regarding the formation (Boeè et al., 2017) and discrimination (Hienz et al., 2004) of vowel sounds. Similarly, baboons have been relevant to evolutionary questions on the adaptation of vocalisations to environmental conditions (Brown

et al., 1995; Ey et al., 2009; Ey & Fischer, 2011). Studying vocal communication within species on an individual level has also given insight into social behaviour such as reconciliation (Cheney & Seyfarth, 1997), recognition of social relationships between third parties (Cheney & Seyfarth, 1999), and affiliative interactions (Faraut et al., 2019). Much of the research on the perception and use of vocalisations in baboons has focused on grunting, discussed in more detail below (see Section 2.3.2).

While baboon orofacial and gestural repertoires may be smaller than those of other primates and particularly apes, they have been a topic of research since the early days of baboon observational research (Anthoney, 1968; Bolwig, 1959; Hall, 1962; Hall & DeVore, 1965; Pellatt, 1980; Washburn & Devore, 1961; Young, 1978). The most frequently mentioned signals are lip-smacking, ear-flattening, embracing, presenting, inspecting, soliciting grooming, mounting, various types of visual threats such as head-bobbing, and a variety of contact behaviours such as hind-quarter touching and genital touching, along with the aforementioned vocalisations. Larger behavioural contexts such as "social approaches" and "male greetings" (discussed in more detail below) are also frequently referenced (Coelho & Bramblett, 1984; Dal Pesco & Fischer, 2018; Smuts & Watanabe, 1990). Several studies have addressed the development of social behaviour in baboons, for example Anthoney's observations on the ontogeny of lip-smacking, grooming, and embracing (1968) or captive studies comparing between individuals in peer-peer and mother-infant raising contexts (Bramblett & Coelho JR., 1985; Coelho & Bramblett, 1984; Young, 1978). Other studies have focused on differences in signalling by social factors such as rank or relationship. For example, Easley and Coelho investigated the relationship between rank and lip-smacking in yellow baboons, finding that there was an association between the use of lip-smacking and affiliative interactions, but not with rank (1991). This is contrary to findings indicating that lip-smacking is more commonly directed by the more dominant individual towards the subordinate individual in olive baboons (Rowell, 1966). Of the aforementioned studies, research on male-male greetings has taken the most integrated approach towards signalling, considering how signals are used together within the specific context of male-male

greetings (Dal Pesco & Fischer, 2020). However, our understanding of how signals are combined more generally is still lacking.

More recently, the baboon signalling repertoire has been reconsidered from a gestural perspective, which considers the intentionality and flexibility of signal use (Graham et al., 2019; Leavens, 2018; Townsend et al., 2017). There are various definitions of "gesture", with some referring to any "communication by means of hands, feet, or limbs" (Pollick & De Waal, 2007, p. 8184) as gestures, while others define gesture through some combination of body parts involved, modality, social expression, and intentional and communicative properties (Rodrigues et al., 2021). Intentionality is often assessed by actions of the signaller that account for the attentional state of the recipient, for example using more visual gestures when the recipient is watching compared to tactile or audible gestures when they are not, or by the signaller waiting for a desired response from the recipient and repeating or elaborating the gesture when it is not received (Townsend et al., 2017). Gestures are used flexibly when they are observed across a number of social contexts, rather than being constrained to a single context (Pollick & De Waal, 2007). A study of gestures in captive olive baboons identified 67 visual, audible, and tactile gestures (Molesti et al., 2020). Repertoire size was variable across age classes, with repertoire size decreasing with age. Individuals showed intentionality by taking into account the recipient's attentional state, waiting for responses, and repeating or elaborating gestures when the desired response was not given (Molesti et al., 2020). Molesti et al. also noted that many of these gestures were used flexibly across contexts, indicating means-ends dissociation. The study of primate gestures has been of particular relevance in the last decade due to increased interest in the gestural hypothesis for the origin of language (Arbib et al., 2008; Armstrong, 2008; Corballis, 2017; Hewes et al., 1973; Meguerditchian, 2022; Pollick & De Waal, 2007). This hypothesis is based on the role gesture plays in human language, highlighting that many of the underlying cognitive processes necessary for language production are also involved in gestural communication, which was likely to have predated language.

Though it would be a useful future direction for the work resulting from this thesis, I do not take a gestural approach here. This is because signals transmit information even when not intentional on behalf of the signaller and as such are under selection during social interactions regardless of their status as gestures. As this thesis centres on the relationship between risk and signalling, I consider signalling more broadly, rather than focusing on gestures. When it comes to signalling during approaches between conspecifics, research in baboons has focused on two main contexts: first, male-male greetings (Dal Pesco & Fischer, 2020), and second, grunting during approaches towards females with infants (Silk et al., 2018). As these two areas are particularly relevant to the following empirical chapters which focus on signalling during approaches bestween individuals, I review both in more detail below.

2.3.1 Male greetings across *Papio*

In the baboon literature, "greeting" refers to a ritualised set of non-aggressive signals between adult males and is not limited to arrivals and departures (Dal Pesco & Fischer, 2020). Male greeting is also reported in a number of other nonhuman primate species (see the introduction of Chapter 4 and Table H.1), and may relate to the strength of male bonds and the level of social tolerance exhibited in the species (Dal Pesco & Fischer, 2020). While there are strong similarities in male greeting across *Papio*, species specific differences exist in signals, frequency, and intensity, along with potentially differing or flexible functions within and across species (Dal Pesco & Fischer, 2020). Greeting in male baboons often begins with approach by the initiator in a swaggering gait, accompanied by lip-smacking, ear-flattening, scalp-retraction, and occasionally grunting. This is often followed by presentation of the hindquarters, which the other individual may respond to with physical contact such as brief touches, mounting, penis-diddling, or embracing (see Figure 2.2) (Colmenares, 1991b, 1991a; Dal Pesco & Fischer, 2018, 2020; Smuts & Watanabe, 1990). Assessing relationship strength, maintaining social bonds, assessing cooperative potential, reducing tension, and signalling social status

Figure 2.2: Examples of male-male baboon greeting behaviours. From top left to bottom right: Examples of ear-flattening, hind-quarter touch, mounting, penis-diddling, embracing with mutual penis-diddling, and hip-grasping in response to presentation. (Photos and video stills: Jana Muschinski and Lucy Baehren; Gorongosa National Park, Mozambique).

have been proposed as functions of greeting in male baboons, with support for individual hypotheses varying by species (Dal Pesco & Fischer, 2020). Greeting has been studied to different extents across the species, with little systematised research on chacma baboons, and no research yet on greeting in Kinda baboons, though this is understandable given how recent the first studies of this species are (Petersdorf et al., 2019).

Hamadryas baboon

Hamadryas baboons have been one of the most popular baboon greeting study species, with early studies using the word "notification" (Colmenares, 1990, 1991b, 1991a; Fraser & Plowman, 2007; Kummer, 1968; Pelaez, 1982). This earlier term originated because the behaviour was often observed as individuals left the sleeping cliffs in the morning, suggesting it may be used to initiate travel or indicate group travel direction (Fraser & Plowman, 2007). Further study, however, indicates other functions are more likely (Fraser & Plowman, 2007). Unlike in

most other species, most research on hamadryas greetings has been completed in captive rather than wild settings, some in a mixed group of hamadryas and yellow baboons (Colmenares, 1990, 1991b; Fraser & Plowman, 2007; Pelaez, 1982). Hamadryas greetings typically begin with a circular approach in a swaggering gait, followed by the aforementioned signals and contact behaviours, and finally a quick separation that slows the more distance is gained (Colmenares, 1990; Pelaez, 1982). Vocalisations often include geckers or kecks while grimacing and grunting (Colmenares, 1990). In a captive mixed group, the hamadryas baboons exhibited a greater diversity of movements and more "refined" movements compared to the yellow baboons (Pelaez, 1982).

Greetings in hamadryas baboons may function to test the competitive potential of a partner and thereby act as a form of negotiation, but more recent work indicates that the function may be more flexible and could also be a form of tension reduction or may signal submission or alliance (Fraser & Plowman, 2007). Greetings are often used in tense circumstances, for example during competition over a female, to prevent attack or flight of the recipient (Colmenares, 1990; Colmenares et al., 2000; Dal Pesco & Fischer, 2020; Fraser & Plowman, 2007). New leader males were the most likely to exhibit aggressive behaviour in response to a greeting and as an initiator (Colmenares, 1990). Nonprime (older and past their physical prime) males were more likely to initiate greetings and greetings were more likely to be directed at prime rather than nonprime males (Fraser & Plowman, 2007). However, greetings happen most frequently between individuals with undecided or close ranking (Fraser & Plowman, 2007; Romero & Castellanos, 2010). These characteristics together suggest that greetings may function to reduce tension in insecure or undecided relationships.

Guinea baboon

Guinea baboons stand out amongst *Papio* for their intense level of male-male spatial tolerance and strong affiliative relationships between males (Patzelt et al., 2014). Their greetings have been studied both in the wild (Dal Pesco & Fischer,

2018) and in captivity (Whitham & Maestripieri, 2003). Greetings between males are an important part of the behavioural repertoire, happening ten times more frequently than aggression and twice as frequently as affiliative behaviours (Dal Pesco & Fischer, 2018). In comparison to other baboons, they exhibit more physically intense and ritualised greetings. Greetings are physically "intense" (incorporating close contact such as embracing, mounting, or genital touching) in over 40% of all occurrences (Whitham & Maestripieri, 2003). Their greetings also include a more diverse range of contact behaviours, including the polonaise, for example, not reported in other species (Dal Pesco & Fischer, 2018).

Greeting does not appear to be tied to specific contexts and has no correlation with aggression or tension (Dal Pesco & Fischer, 2018). As such, greetings are unlikely to be a form of reconciliation or tension reduction (Whitham & Maestripieri, 2003). Instead, they likely serve to "strengthen in-group affiliation and promote cooperation" (Dal Pesco & Fischer, 2018, p. 87). Spatial tolerance in dyads is positively related to their greeting frequency, and pairs with strong bonds greet more frequently and more intensely (Dal Pesco & Fischer, 2018; Whitham & Maestripieri, 2003). Greetings are also more common when partners were previously more than 5 meters apart (Dal Pesco & Fischer, 2018). There is no correlation between rank and low intensity greetings, but lower ranking males are more likely to be the recipients of high intensity greetings (Whitham & Maestripieri, 2003). There is no correlation between the rank difference in a dyad and greeting intensity (Whitham & Maestripieri, 2003). In sum, these results suggest that greeting is more tied to measures of relationship quality, rather than to dominance relationships or context, with little support for the social buffering hypothesis or for the use of greeting as a negotiation mechanism, as suggested for hamadryas baboons.

Olive baboon

In most cases, male-male interactions in olive baboons are tense, with a high potential for agonistic behaviour. An approach is usually followed by threat or avoidance behaviour, but the display of a "greeting" can circumvent these options,

being the only instance in which males come into close contact without aggression (Smuts, 2002; Smuts & Watanabe, 1990). Greeting in olive baboons has been studied primarily in wild populations (Smuts & Watanabe, 1990). Similar to other *Papio* species, their greetings typically begin with approach in a swaggering gait, incorporate a variety of the signals mentioned previously, and may include contact behaviours (Smuts, 2002; Smuts & Watanabe, 1990; Watanabe & Smuts, 2004). Mounting or attempting mounting and hip grasping are the most common contact behaviours (Smuts & Watanabe, 1990). Greetings are often asymmetrical, with one individual presenting and the other performing a contact behaviour, resulting in individuals sometimes "jockeying" for roles (Smuts & Watanabe, 1990). Greetings between young adults are more likely to be "uncompleted" where one individual interrupts or resists the greeting, while in dyads of older males with established relationships greetings are typically completed (Smuts & Watanabe, 1990).

Lower ranking males are more likely to present, while higher ranking males are more likely to perform the responding contact behaviour, but greeting roles are variable across the age and residence classes (Smuts & Watanabe, 1990). Dominant males are more likely to approach and perform gestures compared to lower ranking males (Smuts & Watanabe, 1990). Greetings are more likely to be incomplete or interrupted when individuals are close in rank or both participants are younger males (Smuts, 2002; Smuts & Watanabe, 1990). A marked difference exists between the tenor and potential function of greetings in old and young dyads. Younger individuals may use greetings to test dominance relationships in a safe context, while older dyads' greetings appear to reflect their coalitionary behaviour (Watanabe & Smuts, 2004). Greetings between older males are more likely to be completed and are more balanced, occasionally even with "courteous" alternation of greeting roles in succession (Smuts & Watanabe, 1990). Frequent coalition partners tend to have more symmetrical, egalitarian greetings. Greeting between older olive baboon males is thought to reinforce relationships and reduce tension (Smuts & Watanabe, 1990). Overall, greetings in olive baboons tend to be less physical than in Guinea baboons, with more negotiation of role and variability in function.

Yellow baboon

Research on greeting in yellow baboons is more limited than in the hamadryas, Guinea, and olive baboons, with one study addressing presentation behaviour in wild yellow baboons in Amboseli National Park (Kenya) and further studies recording greeting behaviour of captive yellow and hamadryas baboon hybrids (Hausfater & Takacs, 1987; Pelaez, 1982). Yellow baboon male greetings differ slightly from those previously reviewed. While approaches are similar to those described above, responses to presentation may include grabbing, slapping, and holding or pressing down the approacher in addition to the non-agonistic behaviours seen in the other species (Hausfater & Takacs, 1987). Compared to other sex-age classes, presentations between adult males involve the most intense reactions, both aggressive and submissive (Hausfater & Takacs, 1987). These greetings also often involve submissive vocalisations and other submissive signals. Lower ranking males typically present towards the dominant individual, with responses often including physical contact (Hausfater & Takacs, 1987). Presentations are also seen across all other age-sex classes, with female-female approaches at times including inspection, hindquarter touching, in a manner similar to, but less intense than male-male interactions (Hausfater & Takacs, 1987). Greeting in yellow baboons has been less studied than in other baboons, can include more forceful motions such as grabbing, slapping, and pinning to the ground, and may signal submission of the approacher.

Chacma baboon

Research on greeting in chacma baboons is similarly limited, with authors generally claiming the chacma baboon exhibits *limited to no greeting behaviour* (Dal Pesco & Fischer, 2020). As coalitionary behaviour has also not yet been reported in chacmas, this has led to a connection being drawn between coalition formation and male-male greeting behaviour (Dal Pesco & Fischer, 2020). While systematic study is limited, greeting between males has been mentioned in the literature since the 1960s (Hall, 1962; Saayman, 1971). Greeting behaviour between adult/subadult males was observed in the early 1960s in Cape of Good Hope Nature

Reserve in South Africa, but only three adult or subadult males resided in the study troop, and two of these were not completely mature (Hall, 1962). These greetings were typically initiated by the smaller male and involved "embracing or 'kissing' the genital or lower abdomen area" along with lip-smacking and 'kissing' on the head or face (Hall, 1962, p. 305). Further greetings were observed when a previously captive 4.5-year-old male was released near the troop and began integrating. Similar greeting behaviour was frequently displayed between him and troop members across all types of sex/age classes, though rarely with the dominant male. These interactions involved presenting, mounting, lip-smacking, ear-flattening, embracing, genital touching, nuzzling, and grunting (Hall, 1962). Saayman also reported presenting and hindquarter touching between adult males and subadult or juvenile males (1971). They observed no such behaviour between adult males at Honnet Nature Reserve (only 3 adult males in the troop) but did in chacma baboons at Kruger National Park (Saayman, 1971). It is unclear if the limited reporting of greeting between adult males in these studies was simply due to lack of opportunity in troops with one or very few mature adult males. A more recent study compared chacma baboon approaches with Guinea baboon approaches across both sexes (Kalbitzer et al., 2015). Male chacma baboon approaches are less likely to occur with greeting behaviours than without. Fewer greetings are exhibited in comparison to male Guinea baboon approaches (Kalbitzer et al., 2015). Kalbitzer et al. propose that smaller group size in chacma baboons during their evolution may have resulted in easier monopolisation of reproductive opportunities by one or a few males, leading to fewer coalition opportunities, higher paternity certainty, and higher infanticide risks (2015). The limited data on chacma baboon greetings means that our understanding of function, form, and context are very limited, making it difficult to compare to other *Papio* species.

Species comparison of male greeting

While significant variation does exist in frequency, intensity, and elaborateness of greetings across *Papio*, overall greetings seem to facilitate non-aggressive inter-

action and elicit non-agonistic responses (Colmenares et al., 2000; Dal Pesco & Fischer, 2020). Functions and contexts of male-male greeting vary across *Papio*, often aligning with differences in coalitionary behaviour, social organisation, and social structure (Dal Pesco & Fischer, 2020). Of all baboon species, the Guinea baboon performs the most elaborate and most frequent greeting (Whitham & Maestripieri, 2003). Chacma and yellow baboon have the lowest rate of hourly greeting at 0.088/hour and 0.08/hour respectively. Hamadrayas and olive baboons follow with 0.57/hour and 1.20/hour respectively. Guinea baboon greeting is far more frequent, at 2.06 adult male greetings per hour (Dal Pesco & Fischer, 2020). Physical contact and reciprocity of greetings has not been studied in chacma, Kinda, or yellow baboons, but has been recorded in olive, hamadryas, and Guinea baboons. While physical and intense physical contact is rare in olive and hamadryas baboons, over 90% of greetings in Guinea baboons include physical contact, and nearly 60% include intense physical contact (Dal Pesco & Fischer, 2020). Reciprocity of greetings in yellow baboons is unrecorded, but 71% of olive hamadryas baboons are reciprocated, and nearly 82% of Guinea baboon greetings (Dal Pesco & Fischer, 2020).

Table 2.2: Modified reproduction of a table from Dal Pesco & Fischer (2020) - "Features of male-male ritualised greeting behaviour in the genus *Papio*"

Species	**Main male initiator**	**General tenor**	**Context/function**
Chacma	n.a. (possibly subordinate - see Saayman, 1971)	n.a.	n.a.
Kinda	n.a.	n.a.	n.a.
Yellow	Subordinate	Tense, tentative	Submissive/signal status
Olive	Dominant	Tense, tentative	Neutral/negotiation and confirmation of social relationships
Hamadryas	Leader	Tense	Competitive/tension buffering

Table 2.2: Modified reproduction of a table from Dal Pesco & Fischer (2020) - "Features of male-male ritualised greeting behaviour in the genus *Papio*"

Species	Main male initiator	General tenor	Context/function
Guinea	No rank effect	Positive, relaxed	Neutral/signal party membership, assess relationship quality

However, as highlighted in Table 2.2, knowledge on both chacma and Kinda baboon male-male greeting behaviour is extremely limited, leaving important gaps in the literature due to their unique characteristics – lack of coalitionary behaviour in the chacma baboon and limited contest competition in the Kinda baboon. The unequal level of investigation across species, mix of captive and wild study populations, and unstandardised methods of study across the decades make it difficult to determine whether some of these findings, particularly the lack of greeting behaviour in chacma baboons, are reflections of real cross-species differences. Captive studies are particularly problematic due to the artificial concentration of individuals, potentially changing dynamics around sharing of space, and may be better viewed as a form of experimental study than a reflection of what could be expected in wild populations. Furthermore, focus on solely male-male encounters limits our understanding of signal function, with many of the same signals and signal combinations exhibited in approaches across other sex combinations. Additional systematised and replicable study on wild populations, particularly in the under-studied *Papio* species, will add to our knowledge on inter- and intra-species behavioural variation, what variables may explain variation across species, and what steps need to be taken to effectively compare and understand approach behaviour across the genus.

2.3.2 Grunting in baboons

Grunts are harmonically rich, low amplitude vocalisations and are one of the most frequently observed approach signals in baboons (Meise et al., 2011; Seyfarth & Cheney, 2003). Grunting is exhibited by both male and female baboons across

scenarios including initiating group movement (the "move" grunt), reconciliation, and approaches, particularly towards females with infants (Cheney & Seyfarth, 1997; Meise et al., 2011; Owren et al., 1997; Rendall et al., 1999; Seyfarth & Cheney, 2003). While call-types are acoustically distinct, production specificity is relatively low once arousal level has been accounted for in comparison to other call types such as alarm calls (Meise et al., 2011; Owren et al., 1997). Female-female interactions have been the primary focus of grunting research, but function in males appears similar. Male grunts have a lower frequency than female grunts and baboons can discriminate between sexes when listening (Rendall et al., 2004). Baboons can recognise caller identity and may change their reaction to calls based on the caller's social and familial relationships (Cheney & Seyfarth, 1999; Wittig et al., 2007). Vocal interactions between others affect a listener's behaviour (Cheney & Seyfarth, 1999). Baboons are also able to recognise when expected social relationships are not followed in vocal exchanges and make assumptions regarding the intended target of vocalisations based on their recent interaction history with that individual (Cheney et al., 1995; Engh et al., 2006).

Subtle acoustic differences in grunting do exist across species, but generally these are minor, and vocalisations are highly conserved. There is no correlation between social system or geographic distance and vocal structure in grunts across *Papio* (Hammerschmidt & Fischer, 2019). However, grunt rate and length does vary across populations and species and is situationally affected by environment. Grunt duration tends to be longer in closed habitats and grunting rate is at times adjusted based on visibility (Ey et al., 2009; Ey & Fischer, 2011). However, these effects are stronger for non-interactive contexts, and seem to be overridden by other social drivers in interactive contexts (Ey et al., 2009). Most variation in acoustic qualities of grunting is due to inter-individual rather than contextual differences, but structural differences do exist in grunts directed towards infants versus those used when participating in group movement (Owren et al., 1997; Rendall et al., 2004; Rendall, 2003). The different calls result in different responses from listeners,

but these responses are also mediated by context and relative rank differences between caller and receiver (Rendall et al., 1999).

The effects of grunting

Interaction rates between females increase in the minutes following an altercation between them, with grunting calls being the most frequent interaction, suggesting that grunting may have a reconciliatory function (Silk et al., 1996). Reconciliation is more likely if the partner is high ranking, with females with young infants, or with related mothers of older infants (Silk et al., 1996). Dominant chacma baboon females grunt at subordinate females following approximately 13% of instances (Cheney & Seyfarth, 1997). Grunting after an altercation affects recipient behaviour and gives an indication of the caller's intended actions. Victims are more likely to approach and tolerate approach by the aggressor, less likely to allow themselves to be supplanted, and less reactive to unclearly directed threat screams by the aggressor when aggressors grunted following the preceding altercation (Cheney et al., 1995; Cheney & Seyfarth, 1997). Aggressors are less likely to supplant recipients and more likely to perform affiliative behaviour when grunting during the approach (Cheney & Seyfarth, 1997). There are similar reconciliatory effects on receiver's behaviour when they hear a grunt from close kin of the aggressor, rather than the aggressor themselves (Wittig et al., 2007). While studied quite extensively, much of our understanding of reconciliatory grunting behaviour comes from playback studies which test the function of grunting in isolation and do not allow for study of how different modalities are integrated.

Grunting occurs in over 25% of all female-female approaches and its most frequent use is when approaching females with infants (Silk et al., 2016). The effects of grunting suggest that it is a signal of "benign intent," particularly in relationships which are less secure or predictable (Silk et al., 2016, 2018). Grunting approachers are 48 times more likely to handle a recipient's infant in chacma baboons (Silk et al., 2016) and seven times more likely in olive baboons (Silk et al., 2018). They are also more likely to perform affiliative behaviours upon arrival and both the

approacher and recipient are less likely to act aggressively (Silk et al., 2016, 2018). Grunting usually results in a longer time spent in proximity (Silk et al., 2018). However, these effects are weak or non-existent when the approacher and recipient are mother-daughter pairs, suggesting grunting plays a particularly important role in weak relationships (Silk et al., 2016).

While most grunting research focuses on female-female reactions, males also use grunts when approaching females whom they do not wish to displace and with whom interacting would be beneficial. Grunting affects whether the approaching male and recipient female have an affiliative interaction but does not affect the likelihood of the female moving away (Palombit et al., 1999). Instead, female reproductive status and friendship with the approaching male affects both whether the male will call and the female's response (Palombit et al., 1999). Higher ranking males are more likely to grunt when approaching females than lower ranking males are. Grunting in males is dependent on the female's reproductive status, with males rarely grunting when approaching pregnant females and are more likely to grunt towards females with infants (Palombit et al., 1999).

Predictors of grunting

In female-female approaches, the likelihood of the approacher grunting is affected by relatedness, rank, and infant presence. In chacma baboons, only 5% of grunts are directed towards females without infants, and 60% towards females with infants younger than three months of age (Cheney et al., 1995; Silk et al., 2003). However, even controlling for infant presence, grunting has an effect on social interaction (Cheney et al., 1995). A mother/daughter relationship between approacher and recipient decreases the likelihood of grunting, but other types of familial relationships (e.g., sisters) do not have the same effect (Silk et al., 2016). Grunting occurs in between 40% and 60% of approaches towards non-kin with an infant, with females more likely to grunt when approaching lower ranking females (Silk et al., 2016). As such, grunting does not appear to reinforce social bonds, instead being used in less secure relationships.

Species comparison of grunting

The grunting literature is heavily weighted towards chacma and olive baboons, with relatively little research on the other species. Overall, the structure and use of grunts is similar across Guinea, chacma, and olive baboons – yellow, hamadryas, and kinda baboons were not included (Faraut et al., 2019; Fedurek et al., 2019; Hammerschmidt & Fischer, 2019; Silk et al., 2016, 2018). Guinea baboon grunting behaviour and perception of grunts does differ slightly from that of olive and chacma baboons, explained by differences in their social structure and organisation (Faraut et al., 2019). Grunting occurs in 20% of female-female Guinea baboon approaches, comparable to the rate observed in chacma and olive baboons (Faraut et al., 2019; Silk et al., 2016, 2018). Like in the other baboons, grunting in female Guinea baboons is more likely when infants are present and less likely in strong relationship. In contrast to other species, rank has no effect on the likelihood of grunting during approach, but females are more likely to grunt when approaching females from another unit, rather than their resident-unit (Faraut et al., 2019).

Grunting is also seen in Guinea baboons across other sex combinations, with grunting occurring in 18% of male approaches towards females, over 7% of male-male approaches, and approximately 2% of female approaches towards males (Faraut et al., 2019). Like females, males are more likely to grunt if infants are present. There is no effect of relationship strength on grunting in male-male, male-female, or female-male approaches (Faraut et al., 2019). Compared to other species, male Guinea baboons use a relatively high amount of grunting in their approaches (Fischer, Kopp, et al., 2017). Attention to and perception of grunting also differs in Guinea baboons, with males paying more attention to grunting between females and leader males that are paired as expected (from the same unit) rather than unexpected (indicating the female may be changing units) (Faraut & Fischer, 2019). This is opposite of what is seen in chacma baboons, who pay more attention to calls that break social expectations (Cheney et al., 1995). Across species, grunting serves as a signal of benign intent on approach and provides social information to listeners.

2.4 A lack of integration

What we see in much of the literature on signalling during baboon approaches is a focus on either individual signals (e.g., grunting) or sets of signals used in a ritualised manner in specific contexts (i.e., male greeting). In general, there is little consideration of how signals are combined and how this may vary across context or by characteristics (e.g., sex) of the signaller or receiver. Signalling in primates is complex and studies in other primates demonstrate that information is carried in how signals are combined (Mielke et al., 2021; Waller et al., 2013). As detailed in the introduction, this thesis aims to help fill this gap by studying how signals are used and combined during approaches between individuals. Approaches are the opening point of most interactions and set the stage for the interactions that do (or in some cases do not) follow. This thesis grew first from an interest in how male greetings in chacma baboons compare to those of other *Papio* species and how these differences relate to variation in social organisation and the quality of male relationships. Similarities between the social complexity for communicative complexity hypothesis and discussions on male greeting in baboons, which both focus on communicative repertoires at a species level, caused me to consider how interpersonal relationships and risk may shape signalling at an interaction level as well. The thesis itself follows this same progression, beginning with a species level approach by comparing male greetings in chacma baboons to those in other baboons in Chapter 4. The process of developing data collection methods for Chapter 4 led me to consider approach behaviour more broadly, in particular how signals are used in combination and how signal use may differ between sex combinations. Chapter 5 and Chapter 6 address how signals are combined and how differing levels of risk and complexity may shape complexity of signalling within species as well.

3
Methods

This thesis incorporates data from two field sites: Gorongosa National Park, Mozambique, and Gombe National Park, Tanzania (see Figure 3.1). Gorongosa National Park and Gombe National Park lie at the northern and southern limits, respectively, of their species' distributions. Gorongosa is a novel site for the study of chacma baboons (*Papio ursinus griseipes*) and is currently in its early years of primatological research. As such, it provides a new look at behavioural diversity within the species. We additionally developed a collaboration with Dr Anthony Collins and researchers at Gombe National Park to include a further baboon species, the olive baboon (*Papio anubis*). The Gombe baboons have been studied for half a century and their social relationships are well characterised. At the outset of data collection, the intention was to complete a cross-species comparison. Unfortunately, data collection at Gombe National Park proved more difficult than expected due to the dense vegetation, which limited the amount of collected data and precluded direct cross-species comparisons. This chapter provides field site overviews and describes the general methodology that pertains to all empirical chapters. Following the integrated thesis format, each empirical chapter is presented as a standalone study, with further methodological details presented in the methods sections of the individual chapters.

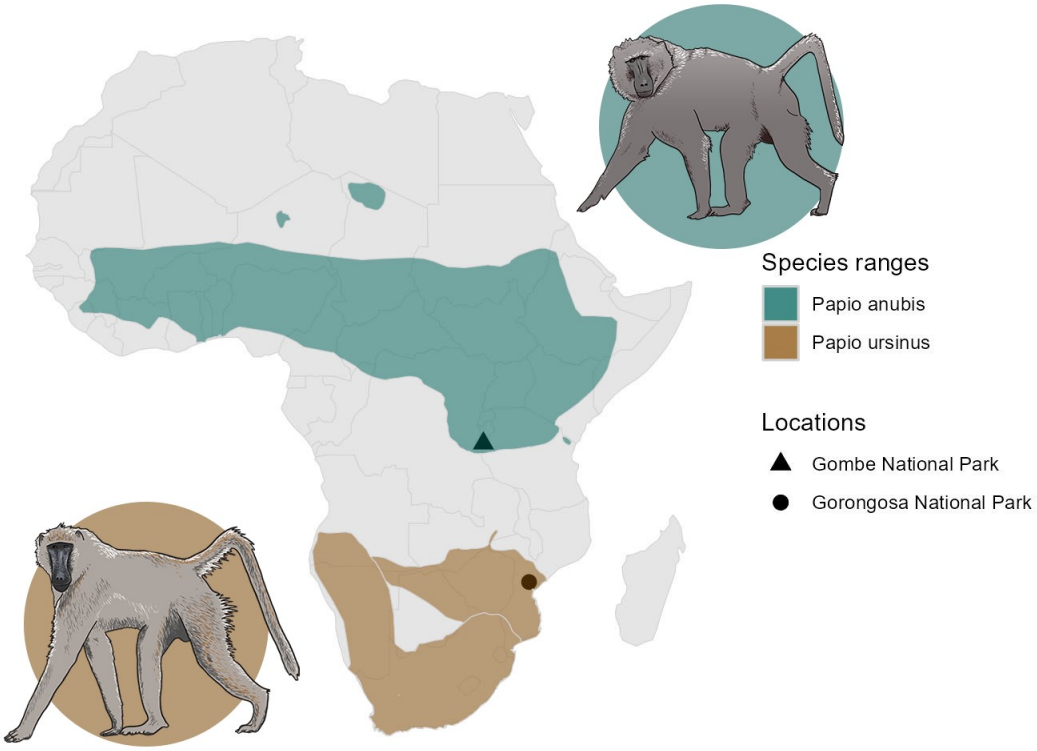

Figure 3.1: Map of *Papio ursinus* (IUCN, 2022) and *Papio anubis* (Wallis & IUCN, 2022) ranges according to IUCN data, with Gorongosa National Park and Gombe National Park marked. Baboon drawings by Lisa Muschinski; base map made with Natural Earth.

3.1 Gorongosa National Park, Mozambique

3.1.1 Site description and ecology

Gorongosa National Park was first established as a game reserve in 1921, before being named a Mozambican national park in 1960 (Daskin et al., 2016; Tinley, 1977). The park is situated in central Mozambique in the southern end of the East African Rift System (EARS), with the most biodiverse part of the park situated in the Rift Valley trough (Bobe et al., 2023; Macgregor, 2015; Martinez et al., 2019; Tinley, 1977). The park's 3770 km^2 cover a significant part of the Urema drainage basin with the Pungue and Nhandue Rivers on the south and north, the Cheringoma Plateau in the east, and the Báruè Midlands in the west (Bobe et al., 2023; Martinez et al., 2019; Tinley, 1977). Gorongosa Mountain is located on the

Midlands and its forests play a key role in the surrounding region's water supply as the mountain receives over 2000 mm of rain per annum (Tinley, 1977). The park experiences a dry season from May through October and a wet season between November and April where up to 40% of the park floods each year (Daskin et al., 2016). Precipitation in the Rift Valley trough is more variable, totalling on average 840 mm of rain per annum (Tinley, 1977). This is the region of the park with the highest level of biodiversity and concentration of wildlife (Tinley, 1977). During the Mozambican civil war (1977 – 1992), much of the wildlife, particularly the mega-herbivore and carnivore populations, was decimated, resulting in a significant increase in tree cover in most of the park's major habitat zones (Daskin et al., 2016). The Gorongosa Restoration Project has been working for over a decade to successfully restore the park's ecosystems while supporting the local community through sustainable tourism and local initiatives (Correia et al., 2017; GNP, 2019).

According to Stalmans and Beilfuss (2008), there are 15 broad landscapes throughout the park, which Daskin et al. group into five major types: "(i) Midlands miombo woodland (Brachystegia and Julbernardia spp.) on the western rim of the Rift Valley (331 km^2); (ii) alluvial fan acacia, combretum and palm savannas (1265 km^2); (iii) floodplain grasslands (759 km^2) around Lake Urema; (iv) colluvial fan savannas (326 km^2) within the Rift Valley; and (v) Cheringoma Plateau miombo woodlands and forested limestone gorges on the eastern rim of the Rift Valley (938 km^2)" (Daskin et al., 2016, p. 81). This mosaic ecosystem hosts a high level of biodiversity and makes the park a unique and valuable analogue model for the environmental conditions of the EARS during important periods of human evolution (Bobe et al., 2023; Habermann et al., 2018; Woldegabriel et al., 2009).

3.1.2 Study population

A 2022 aerial wildlife survey identified 231 baboon troops (see Figure 3.2), highlighting the unprecedented number of troops available for study spread across a variety of ecosystems (Stalmans et al., 2022). The park lies near a potential hybridisation zone between northern chacma baboons and southern yellow baboons (Martinez

et al., 2019). Existing hybridisation zones between the various *Papio* species have been identified in the Awash River, Ethiopia; Amboseli, Kenya; and the Kafue River Valley, Zambia (Chiou et al., 2021; C. J. Jolly et al., 2011; Martinez et al., 2019; Phillips-Conroy & Jolly, 1986; Samuels & Altmann, 1986; Zinner et al., 2009). Gorongosa National Park sits south of the recognised hybridisation zone between northern chacma baboons and southern yellow baboons, but phenotypic features of Gorongosa's baboons indicate potential past or present parapatric gene flow between the two species in the region of the park (Martinez et al., 2019). A survey of 14 phenotypic features and geometric morphometric analysis using 43 cranial landmarks indicate that Gorongosa National Park baboons are likely the result of hybridisation between the grayfooted chacma baboon (*Papio ursinus griseipes*) and yellow baboon (*Papio cynocephalus*) (Martinez et al., 2019). High and low coverage whole genome sequencing of Gorongosa baboon samples have helped clarify this relationship (Santander et al., 2022). This analysis confirms that Gorongosa baboons are most closely related with *Papio ursinus*, with past, but not recent, gene flow with *Papio cynocephalus* which was possibly male-biased (Santander et al., 2022).

The primary troop studied here lived in and around the Chitengo base camp during the study period, which houses both the tourist and staff/researcher facilities. This troop (the Chitengo Troop) was in regular, close proximity to humans and as a result was well habituated. During 2019, the troop included 11 adult females, one subadult/large juvenile female, eight resident adult males, three peripheral adult males, one large juvenile male, approximately 15 small/medium juveniles, and three to six infants (see Appendix A). A small number of likely familial relationships (mother and juvenile/subadult daughter pairings) were identified based on field observations and association data. A second troop occasionally features in the video footage used for this thesis and is referred to as the Montebelo Troop. This troop ranged in the woodland surrounding the southern half of the Chitengo base camp, often visiting the areas surrounding the tourist cabins and other guest amenities. During the 2019 field season, this troop was larger than the Chitengo Troop,

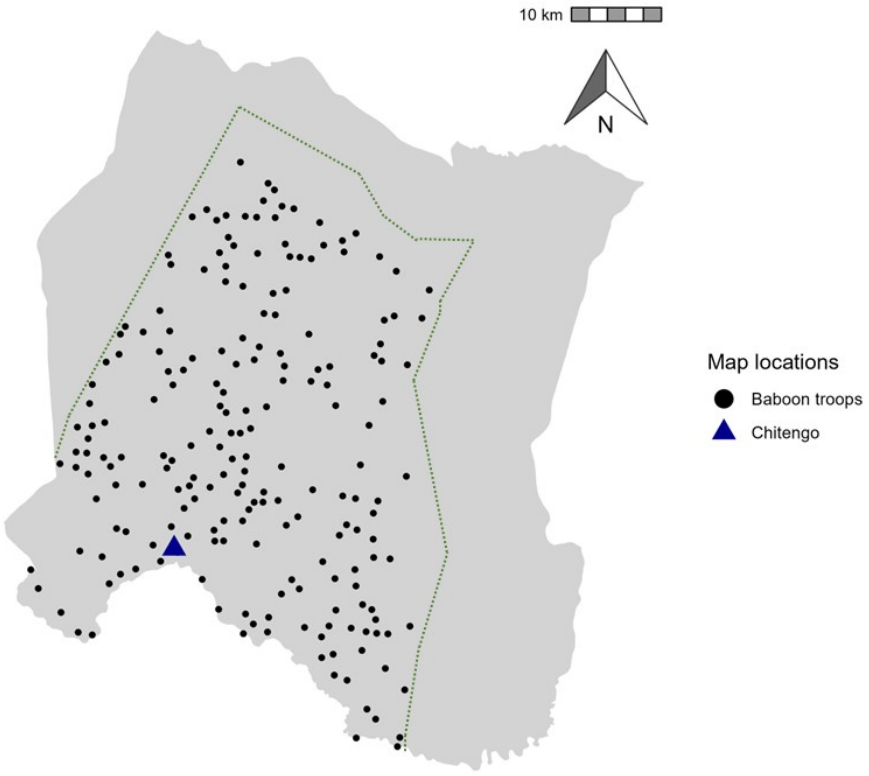

Figure 3.2: Map of Chitengo base camp within Gorongosa National Park, with black dots representing locations of baboon troops observed during the 2022 aerial survey (Stalmans et al., 2022). Note that the aerial survey was not conducted across the entire park, primarily focused on a count block in the centre of the park outlined in a dotted green line.

estimated at 40 to 50 individuals and was less habituated to the presence of people, often avoiding approaches closer than 15 to 20 meters. Both troops were first studied in 2018 by Lucy Baehren (Baehren & Carvalho, 2022), during which time she recorded much of the video analysed in the subsequent chapters. During 2018, few individuals had been identified and no individual-specific rank or behavioural data were collected. I conducted fieldwork between July and November 2019 and worked to identify all members of the Chitengo Troop, compiling photographic identification guides that highlighted identifying features (e.g., scars, facial or tail characteristics) for all adults and subadults. I collected further video data and preliminary dyadic interaction data. I also began building an identification catalogue for the Montebelo Troop, identifying 14 adult females and 12 adult males

before the end of the field season. The 2019 field season was intended to be my pilot season, laying the foundation for further data collection in 2020. However, the second field season was cancelled as a result of the Covid-19 pandemic, preventing me from collecting further *in situ* behavioural data.

3.1.3 Field-based data collection methods

Lucy Baehren and I filmed 65 hours of footage in Gorongosa National Park during October and November 2018 and between July and November 2019. Filming was opportunistic as members of both troops had not been identified yet during most of the filming period and the two troops could not always be differentiated, but an effort was made to rotate through subgroups of individuals who were sat near each other. As I identified troop members in 2019, I narrated while recording to facilitate identification from video footage. A Nikon P900 video camera was used both years. Individuals in 2018 and 2019 footage were identified *post hoc* when possible while I reviewed footage in 2020 and 2021. In addition to videography, I spent a substantial amount of time during the first half of the 2019 field season identifying individuals and creating a photographic portfolio of individuals to assist future students and field researchers with identifying individuals. This portfolio was also helpful during *post hoc* identification from video footage.

As more individuals were identified during fieldwork, I began collecting *ad libitum* dyadic interaction data in the field to gain familiarity with the data collection application and calculate rank indices. Observations were logged using CyberTracker, which is a free software program through which users develop their own data collection application for use on mobile devices (see http://cybertracker.org). For all observed dyadic interactions, the identities of the initiator and the recipient were recorded, along with the type of interaction. Recorded interactions included: aggression (bite), aggression (tackle), threaten (approach), threaten (chase), threaten (headbob and brow raise), threaten (swat), grimace (mouth retracted, teeth exposed - submissive), solicit grooming, present, play, mount, inspect (sexual), inspect (infant), ignore threat, handle infant, groom, flee

from, embrace, displace, and copulate. Data on a total of 374 dyadic interactions were collected between 7 October 2019 and 10 November 2019 during live observation in the field.

The purpose of collecting dyadic interaction during the pilot season was to familiarise myself with the individuals and *in situ* data collection techniques, and to start collecting displacement data that would supplement data from the next field season and allow for calculation of rank indices. Unfortunately, cancellation of the 2020 field season due to the Covid-19 pandemic eliminated the opportunity for any further data collection. This meant that calculated rank indices were unstable (see Processing of rank data below) and could not be used in further analyses.

3.2 Gombe National Park, Tanzania

3.2.1 Site description and ecology

Gombe National Park is located approximately 16 km north of Kigoma on the western border of Tanzania. It is approximately 52 km^2 in area and runs along the eastern shore of Lake Tanganyika (Müller-Graf et al., 1996). The eastern boundary of the park is a steep rise to an escarpment ridge of the Rift Valley. The park contains mixed savannah woodland, dense gallery forests, open deciduous woodland, and fishing beaches (Nash, 1976; Ransom, 1981; Van Lawick-Goodall, 1968). The park is about 16 km in length north to south, with ten major valleys crossing through east to west (Ransom, 1981). Similarly to Gorongosa, Gombe experiences a wet season October through May and a dry season June through September (Ransom, 1981). The baboons in the park have been studied since the 1970s, alongside the Jane Goodall Institute's work on Gombe's chimpanzees, which has been ongoing since the 1960s.

The basic needs of baboons (food, water, and sleeping sites) are easily met in Gombe, with high food availability and abundant sleeping site choices thanks to the tree canopy (Ransom, 1981). Calorie dense foods such as fruits are more readily available than in the savannah environment that many baboon populations

Figure 3.3: Map of Gombe National Park along the eastern shore of Lake Tanganyika. Made using Google Earth Pro. The white dotted line denotes the park boundary (Lonsdorf et al., 2022) and the white triangle the location of the Gombe Stream Research Centre.

inhabit. Ransom suggests that the relatively low ecological pressure is at least partly responsible for the large troop size and small home ranges of Gombe baboons (Ransom, 1981). Primates are the most common fauna present, unlike at many other baboon study sites, including Gorongosa, where ungulates are more prevalent (Stalmans et al., 2019). Multiple primate species range in the park including baboons, chimpanzees, vervets, red colobus monkeys, red-tailed monkeys, and blue monkeys. There is generally little predation pressure on the baboons, with civets, genets, servals, and the very occasional leopard being the only carnivores ranging locally (Ransom, 1981; Williams et al., 2008; Wilson et al., 2004).

3.2.2 Study population

The baboons ranging in Gombe National Park are classified as olive baboons (*Papio anubis*) and reside along the southeastern boundary of the species' geographic range.

Analysis of a Gombe baboon's mitochondrial genome indicates that there may be a level of polyphyly within the olive baboons, and that the Gombe baboons, along with baboons sampled in the Democratic Republic of Congo (DRC), are a sister clade of populations of northeastern olive baboons, yellow baboons, and hamadryas baboons (Roos et al., 2018, 2021). The central olive baboons (Gombe and DRC) are estimated to have diverged from the eastern olive baboons, hamadryas baboons, and northern yellow baboons 0.61 to 0.92 million years ago (Roos et al., 2021). Previous work on male greeting behaviour in olive baboons was conducted in Kibale National Park, Uganda (Fedurek et al., 2019) and Gilgil, Kenya (Smuts, 2002; Smuts & Watanabe, 1990), which fall in the northeastern olive baboon clade.

During the study period (January - September 2021), there were six troops in the park under observation (personal communication, A. Collins). Several of these were infected with *Treponema pallidum*, a bacterium causing severe genital lesions (Harper et al., 2012). However, this does not include the troop studied here, which is referred to as the AC Troop. The AC Troop was well habituated and resided in convenient proximity to the Gombe Stream Research Centre (personal communication, A. Collins). AC Troop and Chitengo Troop demographics are comparable and all AC Troop members were identified previously. During the study period, the troop consisted of a total of 36 individuals, four being adult males, nine adult females, three subadult females, four subadult/large juvenile males, one large juvenile female, and 15 small/medium juveniles (personal communication, A. Collins). Being a long-term study site, familial relationships and rank were well recorded in comparison to the Gorongosa data set (see Appendix A).

3.2.3 Field-based data collection methods

Dr Anthony Collins and research technician Nuhu Buke coordinated and collected data on site including videography. Filming in Gombe took place in two sets, first between January and May 2021 and again between August and September 2021 using a Panasonic Lumix FZ82 Bridge Camera. Collaborators attempted to complete 15-minute focal follows of all adult and subadult troop members, following

a randomised list. However, it quickly became apparent that the dense vegetation in Gombe would make this very difficult. We modified the data collection protocol, with a goal of capturing as many approaches between individuals as possible across as wide a selection of adult troop members as possible. The research technician, Nuhu Buke, completed partial or full day follows of the AC Troop across a total of 47 days. He was instructed to follow subgroups of individuals and to begin filming any time an individual stood up to move or began to approach the group. He filmed adult proximity events within the subgroup using all occurrence sampling and narrated individual identity while filming. A total of 18 hours of footage were recorded.

3.3 Video coding

Video coding was completed using different methods for Chapter 4 versus Chapters 5 and 6. Chapter 4 followed data collection protocols previously used in the baboon male greeting literature, which define "greetings" based on the presence of "greeting behaviours." To allow for comparability with the existing literature, the chapter on male greetings in Gorongosa chacma baboons followed this approach (more details available within the methods section of the relevant chapter). In that chapter, the individual who is approaching and initiating the interaction is referred to as the "greeter" and the approached individual the "greetee", to align with past work (Dal Pesco & Fischer, 2018; Smuts & Watanabe, 1990; Whitham & Maestripieri, 2003) and in reference to the requirement for "greeting behaviours" to be exhibited. However, following review of the male greeting literature, I found it problematic to ignore instances in which males came into physical proximity but did not perform "greeting behaviours". A lack of signalling is often meaningful in itself, potentially providing insight into the relationships between individuals (e.g., grunting and familial relationships (Silk et al., 2018)).

I developed a different data collection framework for Chapters 5 and 6, which used a distance-based definition to study approach behaviours. I collected be-

havioural data on all approaches between adults and/or subadults that met the criteria of a "proximity event". A proximity event was here defined as occurring when an individual (*the approacher*), moves continuously from outside of a five meter radius of a conspecific (*the recipient*) to within a two meter radius (see Table 3.1). Physical contact, eye contact, or any form of signalling from either is not required. This definition is based on other areas of approach literature (i.e., grunting), which use cut-offs between one meter (Faraut et al., 2019; Silk et al., 2018) and two meter proximity (Cheney et al., 1995; Cheney & Seyfarth, 1997; Palombit et al., 1999; Silk et al., 2016; Silk et al., 1996). I applied a minimum starting distance of five meters to increase independence between observations, as it was not uncommon for individuals to approach a conspecific to within two meters, then forage or interact with a third individual seated within two to three meters, and then again come within two meters of the original recipient, often within a very short time frame.

Table 3.1: Event criteria definitions

Term	**Definition**
Proximity event	When an approacher reduces the distance between themselves and the recipient from over five meters to less than two meters
Approacher	Individual moving towards the second participant
Recipient	Individual being approached. Often seated

Data collection began when the approacher visibly began approaching and all interactions, glances, facial expressions, vocalisations, and identifiable movements were recorded for both individuals (see Ethogram in Appendix B). Quality of footage measures, e.g., audibility and visibility of both individuals, were recorded for each observation to ensure observations were only included in analyses when appropriate. Other information such as individuals' primary activities (e.g., grooming, foraging, resting) prior to the event, high value resources that may have caused competition, and instances of aggression that happened prior to the event were recorded whenever possible (see Appendix C).

I recorded behavioural data from video footage using Behavioral Observation Research Interactive Software (BORIS) (Friard & Gamba, 2016). I developed an in-depth ethogram, independent variables list, and sampling procedures in BORIS (see Appendix B and Appendix C). I then completed a short pilot study, coding approximately three hours of footage, allowing me to test my protocols and develop clear criteria for what would be considered a proximity event prior to beginning final data collection. During final data collection, the order of all Gorongosa videos was randomised prior to coding, to ensure that the effect of coding experience would be randomised across dates, rather than chronological. Gombe video data were not available for coding until after I had completed coding the Gorongosa dataset, but I reviewed ten Gorongosa observations in detail prior to commencing with the Gombe coding and reviewed all footage a second time following coding to check for mistakes and ensure consistent coding.

Inter-observer reliability checks were completed and included in the supplementary materials of Chapter 5. This involved a research assistant, blind to all study hypotheses, coding 13% of observations recorded for Chapter 5. I then calculated Gwet's AC1 values in addition to Cohen's Kappa to assess agreement (Gamer et al., 2019; Gwet, 2019). Inter-observer reliability checks are not described further here as they are detailed in the supplementary materials of Chapter 5, submitted for publication.

3.4 Processing of rank data

I originally aimed to account for both individual identity and rank in analyses, and as such analysed the dyadic interaction data collected at Gorongosa National Park with the Chitengo troop to assess whether rank data from the limited field season was robust enough to use. I resampled the dataset of displacements (n = 87) with replacement 200 times and created a ranking for each bootstrapped sample using the Elo sequencing function from the *EloRating* package (Neumann & Kulik, 2020). This function calculated Elo ratings from an ordered list of directional interactions

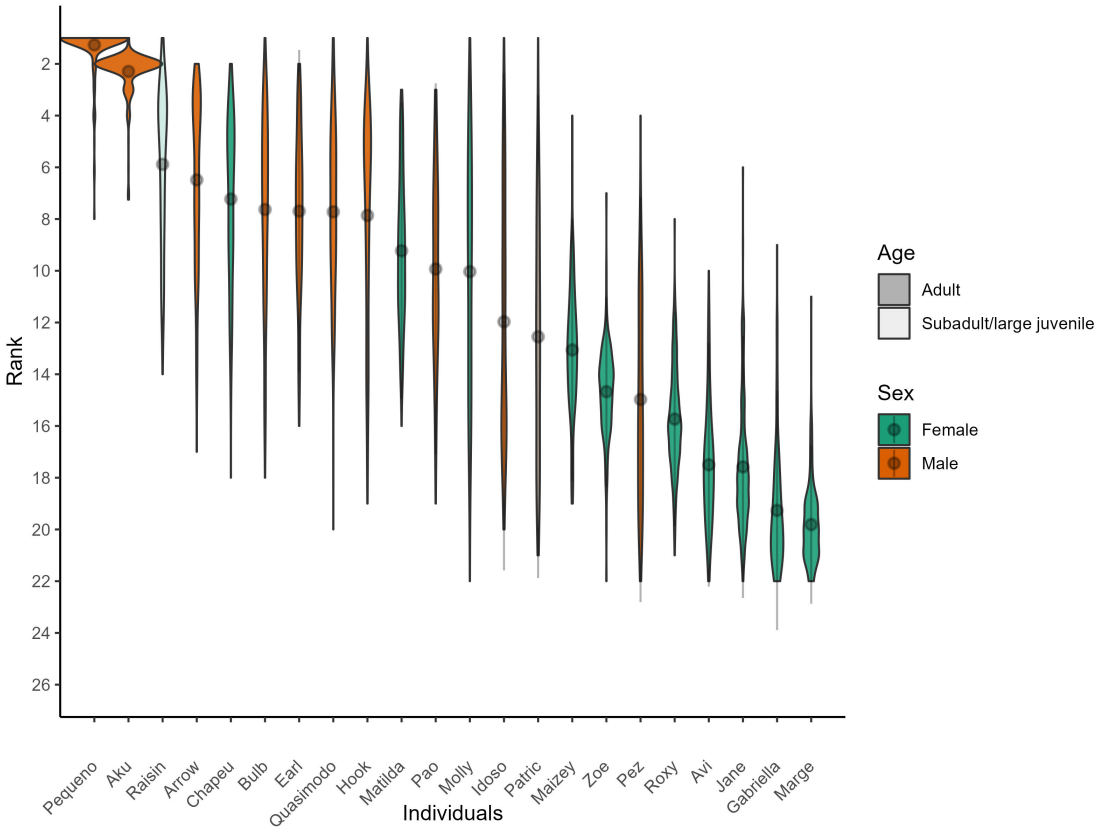

Figure 3.4: Distribution of estimated Elo ratings for each Chitengo troop member using 200 resamples of the displacement dataset (n = 87) from the 2019 field season.

(Neumann et al., 2011). Visualisation of calculated ratings by individual showed high levels of uncertainty about individuals' ranks (see Figure 3.4). The lack of robust rank data from 2019, combined with the likely changes in male hierarchy between 2018 when the majority of filming occurred and 2019 led to the exclusion of rank in further analyses.

3.5 Data availability and reproducibility

Data cleaning and analysis were completed in Python (version 3.8.5) and R (version 4.3.0). Statistical analysis methods are discussed in the individual chapters. Data for all chapters and the developed ethogram have been or will be made publicly available on the Zenodo repository (Muschinski & Carvalho, 2023a, 2023b). Analysis code is also being made publicly available as supplemental material in any publications and preprints. This thesis was written using RMarkdown and bookdown

(Xie, 2016) following Dr Ulrik Lyngs' OxfordDown template (Lyngs et al., 2022).

4

Male-male greeting behaviour observed in chacma baboons (*Papio ursinus*) in Gorongosa National Park, Mozambique

Author Contributions: I completed data collection, data analysis, and writing for this chapter. Lucy Baehren (acknowledgements) permitted data collection from videos she filmed in Gorongosa National Park in 2018, prior to the start of my PhD. Susana Carvalho (acknowledgements) reviewed the paper and provided feedback prior to submission.

Abstract:

Greetings in primates fulfil important functions including navigation of rank, maintenance of social relationships, and potentially establishing coalition partnerships. *Papio* makes a particularly valuable study genus as baboons show variation in greeting, male-male cooperation, philopatry, and social systems. It has previously been suggested that ritualised behaviour such as stereotyped male-male greetings in *Papio* may strengthen social cohesion by facilitating cooperative behaviour, with chacma baboons being the non-coalition forming outlier. Accordingly, we hypothesised that chacma baboons observed in Gorongosa National Park, Mozambique (*Papio ursinus griseipes*) should not exhibit the same male-male

greeting behaviour observed in other baboon species. We collected behavioural data from video footage recorded in 2018 and 2019, comparing identified male greetings with those of other baboon species. We found strong similarities in signal use between the sample of chacma baboon greetings and published accounts of olive, hamadryas, and yellow baboon greetings. Rates of physical contact, intense physical contact, and visual reciprocity were similar to those of the other *Papio* species, excluding the Guinea baboon which exhibit more stereotyped and highly physical greetings. The proportion of observed chacma baboon greetings which were considered "incomplete" (i.e., exhibiting only facial signals, with no presenting or contact) however, was greater than in the other baboon species, highlighting a key difference that may reflect the lower level of male tolerance and weaker male relationships in chacma baboons compared to other baboon species.

4.1 Introduction

Understanding how males navigate interpersonal relationships, particularly in species with intense competition, is critical for studying relationships between behaviour, male competition, social structure, and the evolution of sexual dimorphism. Non-aggressive, ritualised interactions between males have been identified across a number of primate species and are typically referred to as "male greetings" (Corewyn & Setchell, 2019; De Marco, 2017; Dias & Rangel-Negrín, 2017), though similar interactions are at times also seen involving females (e.g., chimpanzees: de Waal & Roosmalen, 1979; black-and-white colobus monkeys: Kutsukake et al., 2006). Male greeting interactions are of particular interest because they often involve high-risk physical contact such as genital touching (De Marco, 2017). Across primates, brief touches appear to serve a different purpose than extended touching (i.e., grooming) and are often used in post-conflict contexts, to signal benign intent, or to assess social relationships (Aureli & Schino, 2022). The functions of male greetings may differ by species, population density, and even individual or dyad (Corewyn & Setchell, 2019). Across species, conflict management, tension reduction, social

bonding, confirming or signalling of rank, and coordinating action have been suggested as functional explanations of male greeting behaviour (Corewyn & Setchell, 2019; De Marco, 2017; Mercier et al., 2017). These interactions are often referred to as "stereotyped" or "ritualised", defined as "stylized, attention-getting, invariantly sequenced, [and] often repetitious" behaviours (Rossano, 2015, p. 81). Ritualised behaviours are a forerunner of ritual, which differs in that it involves symbolism and ceremony (Bell, 1997). In humans, rituals may enhance social cohesion, reduce competition, and enforce adherence to normative values (Dal Pesco & Fischer, 2020; Rossano, 2012, 2015; H. Whitehouse & Lanman, 2014).

The form these male greetings take differs across species, though they generally involve brief physical touch. In mantled howler monkeys, for example, male greetings typically involve embraces, vocalisations, sniffing of armpits and genitals, and shoulder grasping (Corewyn & Setchell, 2019; Dias et al., 2008). Similarly, embraces feature in greetings in chimpanzees (de Waal & Roosmalen, 1979), black-and-white colobus monkeys (Kutsukake et al., 2006), spider monkeys (Schaffner & Aureli, 2005), black-horned capuchin monkeys (Alfaro, 2008), and bonnet macaques (Silk, 1994; Sugiyama, 1971). Mounting and genital touch or inspection is also a common form of brief contact in male-male greetings, exhibited by baboons (Dal Pesco & Fischer, 2020), mantled howler monkeys (Corewyn & Setchell, 2019; Dias et al., 2008), Tonkean macaques (De Marco et al., 2014), moor macaques (Riley et al., 2014), and bonnet macaques (Silk, 1994; Sugiyama, 1971). Other signals include facial expressions (Riley et al., 2014; Sugiyama, 1971) and vocalisations (Alfaro, 2008; Corewyn & Setchell, 2019; de Waal & Roosmalen, 1979; Dias et al., 2008; Sugiyama, 1971). Across these species, a variety of hypotheses regarding function and association with the steepness of dominance hierarchies have been tested, examining rates, directionality, and reciprocity of greetings (Corewyn & Setchell, 2019; De Marco, 2017; Mercier et al., 2017). Baboons are particularly relevant for this line of inquiry due to their variability in male relationships across species (Dal Pesco & Fischer, 2020).

4. Male-male greeting behaviour in chacma baboons

Baboon male greeting behaviour, studied extensively for over five decades, has recently received renewed interest due to the study of Guinea baboons, which exhibit highly physical and frequent male greetings compared to other baboon species (Dal Pesco & Fischer, 2018). Stereotyped greetings between adult male baboons, which are potentially high-risk due to close physical contact, may be related to the formation and testing of coalitions, and may have deeper implications for the evolution of ritualised behaviour and cooperation, male tolerance, and sexual dimorphism across *Papio* (Dal Pesco & Fischer, 2020). In baboons, "greeting" refers to approaches between males which involve some combination of a swaggering gait, ear-flattening, lip-smacking, presenting, and, depending upon species, physical contact behaviours including mounting, hip grasping, and genital touching (Colmenares, 1990; Dal Pesco & Fischer, 2018, 2020; Mondada & Meguerditchian, 2022). Baboon species with higher rates of physical greeting tend to also exhibit higher degrees of spatial tolerance and increased male coalitionary behaviour (Dal Pesco & Fischer, 2018, 2020). It has been suggested that baboon greeting may be an example of ritualised behaviour and that there is a link between presence and intensity of male greetings and social system, degree of sexual dimorphism, and male competition (Dal Pesco & Fischer, 2020; De Marco et al., 2014; Kavanagh et al., 2021; Maestripieri, 2005; Whitham & Maestripieri, 2003).

The high level of variation in social structure, male relationships, cooperation, and sexual dimorphism in the *Papio* genus provides an ideal natural experiment to study relationships between these factors. The environments *Papio* ranges in vary, which may also influence signalling repertoire and frequency (Ey et al., 2009; Graham et al., 2022). Six species of baboon currently range through a variety of environments across Africa and the Arabian Peninsula (*Papio hamadryas, P. papio, P. anubis, P. cynocephalus, P. ursinus, P. kindae*), with several hybridisation zones (Roos et al., 2021; Zinner et al., 2013). The four "COKY" baboons (chacma, olive, Kinda, and yellow baboons) all exhibit multi-male, multi-female groups with polygynandrous mating systems, female philopatry, and male dispersal (Henzi & Barrett, 2003). Unlike the COKY baboons, Guinea and hamadryas baboons exhibit

multi-level hierarchical social structures. In both species, males are philopatric, remaining in their natal clan/party, while females disperse from their natal groups (Fischer, Kopp, et al., 2017; Kummer, 1984). Unlike hamadryas baboons, male Guinea baboons demonstrate strong bonds with other males, with high levels of male – male tolerance and affiliative behaviours such as grooming, even between less closely related males (Patzelt et al., 2014).

Male coalitions have been reported consistently across olive and yellow baboons (Henzi & Barrett, 2003; Henzi & Barrett, 2005). Kinda baboons have only been studied as of relatively recently, with coalitionary behaviour not yet reported, but chacma baboons have been studied for many decades, with minimal reports of male coalitions (Henzi & Barrett, 2003; Henzi & Barrett, 2005; but see Saayman, 1971). While sexual dimorphism across *Papio* is relatively high in comparison to other genera, chacma baboons in particular exhibit high sexual dimorphism (Table 4.1) (C. J. Jolly & Phillips-Conroy, 2006; Plavcan & Ruff, 2008; Thorén et al., 2006).

Table 4.1: Greeting behaviour, philopatry type, and sexual dimorphism (ratios of male versus female canine height and body size) across *Papio*.

Species	**Greeting exhibited**	**Physical contact**	**Philopatry Type**	**M-M Coalitions**	**Canine Height Ratio (M:F) [3]**	**Body Size Ratio (M:F) [3]**
chacma baboon	Contested [1]	Unknown	Female [2]	No [2]	3.84	2.01
yellow baboon	Yes [4]	Unknown	Female [2]	Yes [2]	2.80	1.76
Kinda baboon	Unknown	Unknown	Female [5]	No [5]	3.00	1.77
olive baboon	Yes [6]	Rare [6]	Female [2]	Yes [2]	2.22	1.53; 1.85; 1.81; 1.89
hamadryas baboon	Yes [7]	Rare	Male [8]	Yes [2]	2.74	1.84; 1.78; 1.71

[1] Saayman 1971; Hall 1962; Kalbitzer et al. 2015, [2] Henzi and Barrett 2003; Henzi and Barrett 2005; Henzi, Weingrill, et al. 1999; but see Saayman 1971; [3] Thorén et al. 2006; Fischer et al. 2017; Plavcan & Ruff 2008; Jolly and Phillips-Conroy 2006; Rogers et al. 2019; and Petersdorf et al. 2019; [4] Hausfater and Takacs 1987; Pelaez 1982; [5] Petersdorf et al. 2019; [6] Smuts and Watanabe 1990; [7] Colmenares 1990; Fraser and Plowman 2007; Pelaez 1982; [8] Swedell et al. 2011; [9] Dal Pesco and Fischer 2018; Whitham amd Maestripieri 2003; [10] Fischer et al. 2019

Table 4.1: Greeting behaviour, philopatry type, and sexual dimorphism (ratios of male versus female canine height and body size) across *Papio*.

Species	Greeting exhibited	Physical contact	Philopatry Type	M-M Coalitions	Canine Height Ratio (M:F) [3]	Body Size Ratio (M:F) [3]
Guinea baboon	Yes [9]	93.40%	Male [10]	Yes [2]	3.14	1.7

[1] Saayman 1971; Hall 1962; Kalbitzer et al. 2015, [2] Henzi and Barrett 2003; Henzi and Barrett 2005; Henzi, Weingrill, et al. 1999; but see Saayman 1971; [3] Thorén et al. 2006; Fischer et al. 2017; Plavcan & Ruff 2008; Jolly and Phillips-Conroy 2006; Rogers et al. 2019; and Petersdorf et al. 2019; [4] Hausfater and Takacs 1987; Pelaez 1982; [5] Petersdorf et al. 2019; [6] Smuts and Watanabe 1990; [7] Colmenares 1990; Fraser and Plowman 2007; Pelaez 1982; [8] Swedell et al. 2011; [9] Dal Pesco and Fischer 2018; Whitham amd Maestripieri 2003; [10] Fischer et al. 2019

Stereotyped male greetings occur in hamadryas and Guinea baboons, and at a lesser rate, yellow and olive baboons (Dal Pesco & Fischer, 2018; Fraser & Plowman, 2007; Hausfater & Takacs, 1987; Smuts & Watanabe, 1990). The most ritualised and physical of greetings are exhibited by Guinea baboons; more varieties of physical contact are exhibited and physical contact is generally more frequent, intense, and risky than in the other species (Dal Pesco & Fischer, 2018, 2020; Whitham & Maestripieri, 2003). Greetings take on a variety of functions in male baboons, and may assist with in-group identification, bond testing, and relationship reinforcement (Guinea baboons) (Dal Pesco & Fischer, 2018; Whitham & Maestripieri, 2003), test potential for coalitions (olive baboons) (Smuts & Watanabe, 1990), or ease tension and avoid confrontation through signalling of competitive power (hamadryas baboons) (Colmenares, 1990, 1991a; Fraser & Plowman, 2007).

Systematic study of greeting in chacma baboons is limited (Tables 4.1 and 4.5), despite the importance of chacma baboons when studying relationships between greeting behaviour, coalitionary behaviour, and sexual dimorphism (Henzi & Barrett, 2005; Kalbitzer et al., 2015). They are generally reported as exhibiting limited

greeting behaviour, with little to no physical or high-risk (i.e., genital) contact (Dal Pesco & Fischer, 2020; Henzi et al., 2008; Kalbitzer et al., 2015). While chacma baboons do exhibit some of the less intense greeting behaviours reported in other species, close proximity approaches by male chacma baboons, whether towards a recipient adult male or adult female, are more likely to happen without contact greeting behaviours than with and physical contact in general is rare (Hall, 1962; Kalbitzer et al., 2015; Saayman, 1971). It is suggested that this may be due to the weak social bonds (i.e., no coalition formation) and high rates of aggression between male chacma baboons (Dal Pesco & Fischer, 2020; Kalbitzer et al., 2015). Given their status as a potential outlier among *Papio* species and the limited relevant published data, further systematic research on chacma greeting behaviour would be a valuable addition to the literature.

We provide here a further account of male approach behaviour in chacma baboons and situate this within the existing greeting literature. We hypothesised, based on past work, that male greetings are tied to coalition formation and male tolerance, particularly in female-philopatric species where adult males are unlikely to be related to each other. While ear-flattening and lip-smacking are low-cost signals that do not put the signaller at risk, contact and intense contact pose a higher risk and could result in severe physical injury, therefore requiring higher amounts of trust (Smuts & Watanabe, 1990; Watanabe & Smuts, 2004). It is not uncommon for interactions between male baboons to lead to fights and injuries, with injury also contributing to overall mortality (Drews, 1996; Taniguchi & Matsumoto-Oda, 2018). As such, we predicted that chacma baboons, who generally exhibit little to no coalitionary behaviour, high levels of male competition, and high levels of sexual dimorphism, would show less contact behaviour, particularly intense contact, in male-male approaches when compared to other baboon species.

4.2 Methods

4.2.1 Study site and population

Fieldwork was conducted in Gorongosa National Park, Mozambique, located in the southern end of the East African Rift System (Bobe et al., 2023; Macgregor, 2015; Martinez et al., 2019; Tinley, 1977). The park covers 3770 km^2 and has a mosaic ecosystem with high biodiversity and recovering megafauna and carnivore populations (Correia et al., 2017; Stalmans et al., 2019, 2020). There are over 230 baboon troops ranging throughout the park, with genetic work indicating they are chacma baboons (*Papio ursinus griseipes)* (Ferreira da Silva et al., Preprint; Hammond et al., 2022; Martinez et al., 2019; Santander et al., 2022; Stalmans et al., 2022). Gorongosa National Park is situated 100 km south of the suggested hybridisation zone between southern yellow baboons and northern chacma baboons (Ferreira da Silva et al., Preprint; Martinez et al., 2019; Santander et al., 2022). This study involved collection of behavioural data from video footage of two troops, the Chitengo Troop and the Montebelo Troop, both of which range around the tourist lodge and research centre of the national park. The Chitengo Troop is highly habituated to the presence of humans and can be approached to within 5 meters, while the Montebelo troop is less habituated, avoiding human approach within 15-20 meters. The environment is heavily developed and adjoins to surrounding savannah woodland. During the 2019 field season, the Chitengo troop had 11 adult females, one subadult/large juvenile female, eight resident adult males, three peripheral adult males, one large juvenile male, approximately 15 further juveniles, and an indeterminate number of infants (five births recorded between July - November 2019). The Montebelo troop had an estimated troop size of 40 to 50 individuals during 2019, with 14 identified adult females and 12 identified adult males. Jana Muschinski identified all Chitengo troop adults, subadults, and large juveniles during the 2019 field season, but the Montebelo troop remained largely unidentified at the time. Filming of both troops was completed between October and November 2018 by Lucy Baehren (Baehren & Carvalho, 2022) and in July through November

2019 by Jana Muschinski, amounting to a total of 65 hours of footage. All filming was done opportunistically, with the camera centred on groups of baboons seated near each other, rotated throughout the day. Recording could not be randomised or completed during focal follows as individuals were not identified until towards the end of the 2019 field season. Field work was conducted under permit number PNG/DSCi/C145/2019 (J. Muschinski) and PNG/DSCi/C110/2018 (L. Baehren) and was approved by the University of Oxford Animal Welfare and Ethical Review Board (APA/1/5/ACER/10Dec2018).

4.2.2 Data collection procedure

We reviewed all video footage and identified instances of male greeting, defined in line with Smuts and Watanabe (1990). An interaction was considered a greeting when at least one of the following signals was observed: ear-flattening, lip-smacking, hind-quarter touching, presenting, hip-grasping, mounting, or penis diddling (genital touch) (Colmenares, 1991a; Smuts & Watanabe, 1990). As in previous work on male greetings, the approaching individual was considered the initiator or "greeter", and the other individual the recipient or "greetee" (Dal Pesco & Fischer, 2018; Smuts & Watanabe, 1990; Whitham & Maestripieri, 2003). Similar to work by Smuts and Watanabe (1990), we used *ad libitum* sampling, as we were not calculating hourly rates of greeting and instead were focused on the behavioural components of the greetings.

We coded all greetings between male adults, subadults, and medium to large juveniles, with at least one participant being an adult or subadult. Birth years were unknown, so ages were estimated using physical characteristics. Medium to large juveniles were defined as those who had reached or were approaching the height of adult females but had not developed secondary sex characteristics, subadult males as those who had increased testicular size, were of adult male height, but appeared lanky and less well muscled (Alberts & Altmann, 1995; J. Altmann et al., 1981; J. Altmann & Alberts, 1987; J. Altmann & Alberts, 2005; C. J. Jolly & Phillips-Conroy, 2003; Packer, 1979). Adults were considered "old adults" rather

than "prime adults" when they were visibly aged, with poor body condition and thinning/dull coats (Fraser & Plowman, 2007; Smuts & Watanabe, 1990). We fully coded all greeting events using an ethogram (available publicly: Muschinski & Carvalho, 2023a) developed based on those of Colmenares (1991b), Silk (2013), and Dal Pesco & Fischer (2018). Greeter and greetee identities were recorded when known. When the two minutes prior to the greeting were filmed, the context of each interaction was recorded. The context was classified as "neutral" where individuals were foraging, resting, grooming, or travelling and neither involved in aggressive interactions prior to the greeting (Smuts & Watanabe, 1990). The context was labelled as "food present" where a high-value, monopolisable resource was present within one meter of one of the individuals (e.g., one of the males sat along the edge of the firepit where refuse and food scraps are burnt) but the greeting was not preceded by active contesting of the resource. Greeting context was classified as involving "explicit conflict" where one of the two individuals had been involved in a chase or aggressive interaction in the two minutes prior to the greeting, or as "startled" where at least one of the individuals was vigilant towards a human or other potential threat (e.g., construction noise) prior to the greeting. Coding was completed using Behavioral Observation Research Interactive Software (BORIS) version 7.10.2 (Friard & Gamba, 2016). Data were cleaned using Python version 3.8.5 and R version 4.3.1.

4.2.3 Data analysis

Signal use across greeter ages was calculated for ear-flattening, lip-smacking, presenting, embracing, mounting, penis diddling, hind-quarter touching, and hip-grasping. These accounted for instances of poor visibility, and a table with sample sizes accounting for facial visibility can be found in the supplementary material (Table D.1). The total count of interactions for each age group can be seen in Table 4.2.

Table 4.2: Number of greetings observed for greeters and greetees of each age class

	Greetee age					
Greeter age	**Medium juvenile**	**Large juvenile**	**Subadult**	**Prime adult**	**Old adult**	**Total**
Medium juvenile	0	0	0	6	2	**8**
Large juvenile	0	0	0	1	0	**1**
Subadult	1	0	2	2	1	**6**
Prime adult	0	0	2	26	2	**30**
Old adult	0	1	0	2	3	**6**
Total	**1**	**1**	**4**	**37**	**8**	**51**

For greeting involving only adults or subadults (n = 40), we calculated the proportions of greetings that included physical contact and intense contact, were complete versus incomplete, and were reciprocal to compare to the existing baboon greeting literature. Previous studies have defined intense physical contact as genital touching, embracing, or mounting (Dal Pesco & Fischer, 2018; Whitham & Maestripieri, 2003). Approaches that involved facial signals but did not include presentation or physical contact from either individual were considered "incomplete", in line with the terminology of Smuts and Watanabe (1990), while those that did were considered "complete". We did not include a "partially complete" category, contrary to work by Smuts and Watanabe (1990), due to difficulty in defining the term. Greetings were scored as "visually reciprocal" when the approacher and recipient both performed at least one greeting behaviour, which could include ear-flattening or lip-smacking (Colmenares, 1991a). The proportion of visually reciprocal greetings was calculated in relation to all greeting events (i.e., complete and incomplete). Greetings were considered "physically reciprocal" where both individuals performed some type of physical motion, i.e., either presenting or a contact behaviour, following Dal Pesco & Fischer (2018). Physical reciprocity was calculated only in relation to complete greetings, to align with work by Dal Pesco

and Fischer, who did not consider incomplete greetings as greetings (Dal Pesco & Fischer, 2018). We calculated bootstrapped 95% confidence intervals using the boot R package, version 1.3-28.1 (Canty & Ripley, 2022; Davison & Hinkley, 1997).

For each of these descriptive summaries, the datasets were screened based on visibility, to avoid biasing estimates (sample sizes presented in Table 4.4 alongside results). Contact and intense contact percentages were estimated from observations where either the face of both individuals was fully visible, or where at least one individual was seen to ear-flatten or lip-smack. This was to avoid including approaches in the estimate with no facial visibility, that were only classed as greetings due to presence of contact behaviours that are more easily identifiable. This would have otherwise artificially inflated the estimated percentage of greetings that involved physical contact. Reciprocity was assessed in three variations of the dataset. Physical reciprocity was limited to greetings that could be considered "complete". Visually reciprocity was estimated twice, once only including observations where the full face was visible for both greeter and greetee (referred to as the strict estimate), and once where there was at minimum ear visibility for both individuals (the loose estimate).

The total number of male-male greetings reported across the 65 hours of video footage cannot be directly compared to hourly rates reported elsewhere due to differences in methodology (opportunistic videography vs. focal follows), so we will not discuss hourly rates of greeting. Further analysis, for example comparing likelihood of contact between age-group pairings or by rank differences to test hypotheses regarding greeting function, was not possible due to the small sample size, limited information on individual identity, and lack of rank data. Thus, the primary purpose of this paper is to describe the form of male greeting behaviour within chacma baboons, providing a point of comparison with the existing *Papio* literature.

4.3 Results

Ear-flattening and lip-smacking were the most common signals used by greeters in approaches between adults and/or subadults. Greetings by juvenile approachers most often involved presenting, with little use of facial expressions (see Table 4.3). Of the nine greetings involving a medium juvenile, three involved physical contact. The two interactions involving a large juvenile were both with the same large juvenile, but different adult males, and involved physical contact.

Table 4.3: Proportion of greetings by each age category of greeter incorporating each signal of interest. Number of observations for each greeter age can be seen in Table 4.2. Further sample sizes based on facial visibility limitations can be found in Table D.1.

Greeter age	**Ear-flattening**	**Lip-smacking**	**Present**	**Embrace**
Medium juvenile	0.25	0	1	0
Large juvenile	0	0	1	0
Subadult	0.5	0.5	0.17	0.33
Prime adult	0.89	0.42	0.03	0
Old adult	1	0.75	0.33	0
Greeter age	**Mount**	**Penis diddle**	**Hind-quarter touch**	**Hip-grasp**
Medium juvenile	0	0	0	0
Large juvenile	0	0	0	0
Subadult	0.17	0.33	0.33	0
Prime adult	0.03	0.07	0.13	0.03
Old adult	0.17	0	0	0

Of the adult greetings where context was known, 21 occurred in neutral contexts, nine in close proximity to a monopolisable high-value resource, and only one in a tense context followed an aggressive interaction. In addition to the signals reported in Table 4.3, grunting and grimacing, which have also been reported in other studies, were seen in some greetings.

Figure 4.1: An example of the phases of an intense male greeting observed in chacma baboons at Gorongosa National Park. From top left to bottom right: Approach with mutual gaze, lip-smacking, and ear-flattening; presentation and hip-grasp; hip-grasp extended with the addition of a hind foot; genital touching; genital inspection; distancing and ending of mutual observation

4.3.1 Adult and subadult greetings

We found that over 30% of greetings between adults and/or subadults involved physical contact, with 13% involving intense physical contact (see Figure 4.1 for an intense greeting example). When greetings were considered to be reciprocal if both individuals performed any partner-directed greeting behaviours (i.e., not limited to gestures or contact), over 70% of greetings qualified. The majority of greetings were considered incomplete, i.e., involved only facial signals without further physical or tactile signals (see Table 4.4).

Table 4.4: Bootstrapped confidence intervals for the percentage of adult/subadult greetings which met the criteria for contact, intense contact, completeness, physical reciprocity, or general reciprocity

Criteria	Mean	Lower bound	Upper bound	Sample size
Physical contact	31%	16%	45%	39
Intense contact	13%	2%	24%	39

Sample sizes that each bootstrap is based on are provided and differ due to differences in visibility criteria (see methods). Physical reciprocity is presented as a percentage of greetings that involved presenting or physical contact by at least one participant. 'Loose' and 'strict' refer to inclusion of any greetings where at least ears were visible for both individuals or where the full face had to be visible for both individuals, respectively.

Table 4.4: Bootstrapped confidence intervals for the percentage of adult/subadult greetings which met the criteria for contact, intense contact, completeness, physical reciprocity, or general reciprocity

Criteria	Mean	Lower bound	Upper bound	Sample size
Incomplete	65%	50%	80%	40
Physically reciprocal	50%	24%	76%	14
Generally reciprocal (loose)	71%	56%	86%	35
Generally reciprocal (strict)	73%	54%	92%	22

Sample sizes that each bootstrap is based on are provided and differ due to differences in visibility criteria (see methods). Physical reciprocity is presented as a percentage of greetings that involved presenting or physical contact by at least one participant. 'Loose' and 'strict' refer to inclusion of any greetings where at least ears were visible for both individuals or where the full face had to be visible for both individuals, respectively.

4.3.2 Chacma baboons within *Papio*

While Guinea baboons are certainly exceptional in terms of physical and intense physical contact, it does not appear that chacma baboons are an outlier when compared to the other COKY baboons in regards to likelihood of physical contact or intense physical contact (see Table 4.5). Visual reciprocity was also similar in the chacma baboon sample and previously reported hamadryas studies (see Table 4.5). Unfortunately, most published work on greeting in other baboons, with the exception of Guinea baboons, does not provide estimates and confidence intervals, making more in depth comparison difficult. Estimates for Guinea baboons presented in the table below are from Dal Pesco & Fischer (2018) and the estimate for percentage of greetings that are visually reciprocal for hamadryas baboons was calculated from Table 4 of Colmenares (1991a). A minimum percent of all greeting attempts exhibiting contact and intense contact in olive baboons was estimated

from Tables 2 and 3 in Smuts & Watanabe (1990). We could only calculate a minimum percentage as percentages were only listed by behaviour, with no overall category for contact. Where percentage estimates were not available, descriptors such as "present" or "often" are used based on descriptions within the literature.

Table 4.5: Comparison of male greetings across baboon species

Species	Contact	Intense	Incomplete	Visually reciprocal	Physically reciprocal
chacma (Gorongosa)	**31%**	**13%**	**65%**	**73%**	**50%**
yellow[a]	present	present	N.A.	N.A.	N.A.
kinda[b]	N.A.	N.A.	N.A.	N.A.	N.A.
olive[c]	> 32%	> 12%	24%	often	N.A.
hamadryas[d]	rare	rare	N.A.	77%	N.A.
Guinea[e]	93.4%	59.2%	0.3%	N.A.	81.9%

[a]low rate of greeting observed - Hausfater and Takacs, 1987; [b]no available data; [c]Smuts and Watanabe 1990; [d]Colmenares 1990; Colmenares 1991; Fraser and Plowman 2007; [e]Dal Pesco and Fischer 2018; Dal Pesco and Fischer 2020; Whitham and Maestripieri 2003;

4.4 Discussion

It has been suggested that there is little to no male-male greeting in chacma baboons and that their greetings are far less elaborate than those of other COKY baboons (Kalbitzer et al., 2015), but this impression may stem partly from a lack of research on greeting in the species. Across only 65 hours of footage, we identified 40 adult male "greetings," with about one third of these involving physical contact. While we cannot compare the rate of greeting per hour, we found that 31% of greetings involved contact and 13% intense contact, that over 70% of greetings were visually reciprocal, and that 50% of greetings that were complete were physically reciprocal. These align well with proportions seen in yellow, olive, and hamadryas baboons (see Table 4.5). The most noticeable difference, we found,

was the percentage of greetings which were considered incomplete, i.e., where only lip-smacking and/or ear-flattening occurred, with no presenting or contact behaviours. A markedly higher percentage of greetings were incomplete when compared to olive baboons and Guinea baboons (see Table 4.5). However, the term "incomplete" in itself is potentially misleading, as it suggests that such greetings are in some way interrupted or missing components, when they may simply be a simplified variant of greeting.

Dal Pesco & Fischer suggested that male-male greeting behaviour in baboons follows a geographic cline in elaboration and ritualisation, with a large phylogenetic split between the southern (chacma, yellow, and kinda baboon) versus northern (olive, hamadryas, Guinea baboon) clades (2020). In future it would be beneficial to sample populations located in hybridisation zones, to see how behavioural differences between hybridising species are reflected. Dal Pesco & Fischer point out that species where males are more spatially tolerant and affiliative also have the highest rates of greeting and most ritualised greeting behaviour, supporting suggested connections between human prosociality, larger group living, and the evolution of ritual. Guinea baboons are the noticeable outlier when it comes to male-male greetings, with a particularly high hourly rate, 93.4% of all greetings involving contact, and 59.2% involving intense physical contact; they also demonstrate high levels of male-male spatial tolerance, affiliative behaviour, and the lowest, though comparable, level of sexual dimorphism in *Papio* (Dal Pesco & Fischer, 2018).

Existing research on greeting in chacma baboons is limited, with early studies by Saayman and Hall reporting limited presenting and contact behaviour between males (Hall, 1962; Saayman, 1971). At odds with the remaining chacma literature, Saayman does report limited male-male coalitionary behaviour, suggesting there may be within-species variation in male cooperative behaviour (1971). Kalbitzer et al. studied approach behaviour in chacma and Guinea baboons, recording all approaches within one meter, and reported limited physical greeting among chacma baboons in the Moremi Game Reserve, Botswana (2015). They recorded interactions as greetings only when non-agonistic contact and non-affiliative contact

occurred (i.e., an approach in swaggering gate with lip-smacking and ear-flattening would not be considered a greeting, unlike in other greeting studies), finding that greetings occurred in about 7% of close proximity approaches (calculated from supplementary material Kalbitzer et al., 2015). Given the differences in definition and data collection, it is difficult to determine how the Gorongosa chacma baboons compare to those studied in the Moremi Game Reserve, though within-species variation is not unlikely and would be a valuable direction for future research. Substantial behavioural variation can exist within species, reinforcing the need for additional in-depth cross-population studies with standardised methodology.

Importantly, Gorongosa chacma baboon male greeting behaviour appears to align broadly with that of the yellow, olive, and hamadryas baboons. Signals used are similar (see Table 4.3), with ear-flattening, lip-smacking, presenting, and various types of physical contact observed. It appears that overall, chacma greetings are more likely to involve only ear-flattening and lip-smacking, with no attempt of contact, compared to the other baboon species. The presence of physical greeting, however, contradicts expectations if greeting is only expected in baboon species with high male-male tolerance or with male coalitionary behaviour. Given the presence of similar types of male greetings in *Macaca* (De Marco et al., 2014; Riley et al., 2014; Silk, 1994; Sugiyama, 1971), having diverged from *Papio/Theropithecus* between 10.30-11.10 million years ago (Roos et al., 2019), we expect that a base level of ritualised greeting is present across the genus and is likely ancestral, but that the function of greeting behaviour has diverged across the *Papio* genus. Our study's sample size prevents further in-depth comparison with other *Papio* species but does suggest that further research on greeting in southern clade baboons, and particularly in chacma baboons, is warranted.

4.4.1 Greeting behaviour across age groups

While most of the greetings in the sample were between various classes of adults and/or subadults, we did observe nine greetings directed by medium or large juveniles towards adults, one greeting by a subadult towards a medium juvenile and

one by an old adult towards a large juvenile. Unlike adult greeters, juvenile greeters were unlikely to use ear-flattening and lip-smacking, but all involved presentations (see Table 4.3). Lip-smacking, while exhibited by baboons from an early age (Anthoney, 1968; Chevalier-Skolnikoff, 1973), has been shown in cercopithecines to change throughout development as infants and juveniles mature, going through a development phase similar to human speech rhythm (Morrill et al., 2012). There are a wide variety of potential causes for the lack of lip-smacking and ear-flattening in juvenile-led greetings, one being that the components of greeting are not added together until later during the development of this "ritualised" behaviour. It is also possible that ear-flattening and lip-smacking are less likely to occur in greetings by juveniles towards adults simply because they are not needed since the interaction is very unlikely to be tense. Further research into the ontogeny of male greeting behaviour would provide valuable insight into how use of these signals develop, how they differ from other interactions, and how rank and perception of risk influence the greeter's signal use.

While formal comparison was not possible due to limited sample sizes, presenting appears more common by old male greeters compared with prime males. Old adult males also lip-smacked in more of their interactions as both greeters and greetees than prime males did (see Table D.2 in supplementary materials). These differences could be an indication of where we may expect to find differences due to rank, as old males are often lower ranking in comparison to prime males. This aligns with findings by Colmenares that prime leader males in groups of hamadryas baboons were less likely to present and more likely to be the interaction partner making physical contact (Colmenares, 1990). However, our limited sample sizes and the small number of individuals involved means this could easily be a product of individual differences or sample size, rather than a consistent difference. Across both prime and old adults, ear-flattening was more common than lip-smacking for both greeters and greetees. Ear-flattening and lip-smacking are generally considered affiliative signals (Easley & Coelho, 1991; Silk et al., 2018; Smuts, 1985), suggesting that the combination of both may be used in

particularly tense situations, but that ear-flattening may be the "default" in male greetings. Alternatively, lip-smacking may be an invitation for further progression of the greeting. Colmenares similarly noted that ear-flattening could occur with or without other signals, often happening at a greater distance and that "within a short-range, ear-flattening is usually accompanied by lip-smacking or grimacing depending on the level of fear of the displaying animal" (Colmenares, 1990, p. 87).

4.4.2 Consistent definitions and cross-site comparisons

While developing criteria for the concepts of "completion", "reciprocity", and "greeting" itself for this study, it became evident that there is a lack of consistency across the baboon greeting literature that makes cross-site and cross-species comparison difficult. As demonstrated in Table 4.5, many of these characteristics have not been systematically collected across species. The largest lack of agreement lays in the definition of greeting itself, with some using looser definitions where approaches with lip-smacking and/or ear-flattening count (Colmenares, 1990; Smuts & Watanabe, 1990), while others require a "gestural" component or "behavioural element" such as presenting or physical contact occurred (Dal Pesco & Fischer, 2018; Whitham & Maestripieri, 2003), and others are even stricter, requiring physical contact (Kalbitzer et al., 2015). Varying definitions of other terms such as reciprocity, symmetry, and completion complicate the matter further. We recommend that the study of greeting shift focus away from defining a "greeting" as a time when a "greeting behaviour" occurred, and instead use a distance based-criteria, similar to Kalbitzer et al. (2015) and studies on grunting in baboons (Silk et al., 2018). Using a distance-based cut-off for data collection, for example any approaches within 2-meters as used in many grunting studies (Cheney et al., 1995; Palombit et al., 1999; Silk et al., 2016), would allow for a more direct comparison between species, especially where approaches per focal hour can be recorded. This would also allow for more robust testing of hypotheses regarding function, because recording the circumstances of close proximity approaches between males without greeting provides valuable information about when greeting is and is not necessary.

Following identification of such "proximity events", signal use patterns across events can then be described more consistently, while also allowing authors to classify sets of approaches with terms such as "visually reciprocal", "physically reciprocal", "complete", and "symmetrical" if desired. Open access publishing of produced datasets will also contribute greatly to cross-site comparisons and meta-analyses.

4.4.3 Limitations and future directions

While our results have interesting implications regarding chacma baboons' male greeting behaviour within the context of the *Papio* genus, there are several points on which direct comparison cannot be made to existing literature. Our small sample size of male greetings means that our degree of uncertainty regarding our reciprocity and contact/intense contact estimates are higher, which should be considered when comparing to estimates from other species. Furthermore, we did not calculate a per hour rate of greeting, as several other studies have done, because our video data were not collected using randomised focal follows. The small sample size of this study in addition to lack of rank data does not allow for testing of hypotheses on the function of greeting within chacma baboons.

4.4.4 Conclusions

Even with the limited sample size, the data presented here provide valuable insight into male greeting behaviour in chacma baboons, which has a history of being poorly described in the literature and understudied. We provide estimates regarding contact behaviours, reciprocity, and completion that allow for a basic comparison with the existing literature. Our results suggest that chacma baboon greeting behaviour generally aligns with that of yellow, olive, and hamadryas baboons, with the largest noticeable difference being the proportion of greetings which can be considered "incomplete" versus "complete". Male chacma baboons in Gorongosa exhibit the same behaviours as described in other baboon species excluding the Guinea baboon, who have a more varied and ritualised greeting repertoire. The relatively common presence of physical contact in the studied population of chacma

baboons indicates that high male-male social tolerance or coalitionary behaviour is not a pre-requisite for high-risk greeting behaviour, though the high rate of incomplete greetings does align with previously suggested connections between quality of male relationships and greeting behaviour (Dal Pesco & Fischer, 2020). We furthermore highlight inconsistencies in previously used greeting definitions, suggesting use of a distance-based criteria for data collection in the future to allow for greater standardisation and easier cross-species and cross-site comparison.

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5

Signal combinations during approach interactions in chacma and olive baboons

Author Contributions: I completed video coding, data analysis, and writing for this chapter. Alexander Mielke and Susana Carvalho provided project design, statistical, and editorial advice. Lucy Baehren permitted data collection from videos she filmed in Gorongosa National Park, Mozambique in 2018, prior to the start of my PhD. Nuhu Buke filmed olive baboon interactions in Gombe National Park, Tanzania for use in this project. Anthony Collins assisted with designing the data collection protocol, coordinated filming in Gombe, and provided editorial input.

Abstract:

Signals used during approaches between conspecifics shape the interactions that follow; previous research has often focused on the use of individual signals rather than signal combinations. A network-based approach was used to study how signals co-occur in approaches between conspecifics in two baboon species (*Papio ursinus griseipes*; *Papio anubis*). We compared signal clusters dependent on sex combinations and infant presence. Results indicate that signals were used flexibly across approach type, but that differences existed by approacher-recipient sex combination and infant presence. We then tested hypotheses regarding signal

use and interaction outcomes, specifically recipient contact and infant contact. The approacher observing the recipient or recipient's infant during the approach was associated with an increased likelihood of recipient contact and infant contact respectively. Contrary to expectation, grunting was not associated with an increased likelihood of infant contact. Ear-flattening with lip-smacking in the same approach was associated with a sharp decrease in the likelihood of recipient contact, but separately they were associated with an increase or no change in the likelihood of contact. Our results significantly expand on what we know about signal use during approach interactions, and highlights the need to investigate signal combinations to better understand the functions and variability of signal use in *Papio*.

5.1 Introduction

Primates generally live in complex social environments requiring constant navigation of relationships with conspecifics, involving many daily interactions and negotiations of access to space, resources, and cooperative commitment (e.g., grooming). Entering spatial proximity and initiating interactions is managed through signalling (e.g., grunting (Silk et al., 2016)). These signals help maintain group cohesion, establish social hierarchies, facilitate cooperation, and avoid conflict, ultimately contributing to the functioning of social groups (Dal Pesco & Fischer, 2020). In primate communication, signals are often combined, used simultaneously or sequentially, to form multi-modal signals or signal bouts (Hebets & Papaj, 2005; Rodrigues et al., 2021; Rowe, 1999). Signal combinations can modulate the otherwise expected response of the recipient or result in an entirely new response (Higham & Hebets, 2013). Understanding how signals are used and combined, and how combining signals may modify the expression of intent is also highly relevant to studying the evolution of human language (Meguerditchian, 2022), providing insight into more complex linguistic features such as compositionality (Zuberbühler, 2018, 2019).

Signalling during approaches towards conspecifics is particularly important as it sets the tone for the following interaction and has been studied in many primate

species (Corewyn & Setchell, 2019; Dias et al., 2008; Fedurek et al., 2019; Heesen et al., 2021; Kutsukake et al., 2006; Laporte & Zuberbühler, 2010; Luef & Pika, 2017, 2019; Nakamura, 2022; Rodrigues et al., 2022; Scheumann et al., 2017; Silk, 1994). An approaching individual may have a variety of underlying goals including affiliation, infant access, prevention of aggression, or reconciliation (de Waal & Roosmalen, 1979; Kutsukake et al., 2006; Luef & Pika, 2019; Schaffner & Aureli, 2005; Scheumann et al., 2017). Certain signals or signal combinations can be associated with changes in interaction outcomes; for example, in chimpanzees signalling modality was found to influence the likelihood of reciprocation by the receiver (Luef & Pika, 2017). Similarly, grunts during approaches between baboons have been found to increase the likelihood of subsequent affiliative interactions and decrease the likelihood of a recipient leaving (Cheney et al., 1995; Palombit et al., 1999; Silk et al., 2018).

Baboons have for decades been a popular study species on topics related to social behaviour and communication (Elton, 2006; Meguerditchian, 2022; Strum, 2012). Baboons have complex societies that show variation across species, in particular between the hamadryas and Guinea baboon and the remaining "COKY" baboons (chacma, olive, Kinda, yellow) (Fischer et al., 2019; C. J. Jolly, 2020). COKY baboons live in hierarchical, multi-male multi-female groups with female philopatry, and social interactions affected by rank, kinship, friendship, infant presence, and other factors. While adult males generally outrank females, the two sexes have dominance hierarchies established through different means, with female rank tied to matrilines and male rank determined through competitive power in the chacma, yellow, and olive baboons (Alberts & Altmann, 2012; Beehner et al., 2009; Hausfater et al., 1982; Kappeler et al., 2022). The potential competitive implications and associated risk should differ in approaches between two males versus between two females or between a male and female. Risk and the diversity of potential interactions between a dyad influence signalling (Clark et al., 2022), as seen when comparing macaque species that differ in their level of despotism or egalitarianism (Rebout et al., 2020).

5. Signal combinations during approach interactions

The social complexity hypothesis for communicative complexity posits that increased social complexity requires more complex communication (Freeberg et al., 2012; Peckre et al., 2019). However communication studies often focus on single information streams, e.g., facial expressions, vocalisations, or manual visual signals (Waller et al., 2013), and definitions of complexity are variable and at times contradictory (Peckre et al., 2019). For example, some argue that linear dominance hierarchies are more complex than egalitarian societies (MacLean et al., 2008), while others argue the opposite (Taborsky & Oliveira, 2012). Peckre et al. contend that the more mechanism-based question of how signalling is directly impacted by social factors is still critically understudied (2019). Here, we study species with linear dominance hierarchies that are strongly dominated by a single sex, with the goal of comparing signal combinations across sex combinations and infant presence/absence. Interactions and access to space are both resources in themselves, strengthening social bonds or providing opportunities for social learning (Carter et al., 2016; Palombit et al., 1997; Silk et al., 2010b); interactions which may have a greater potential for conflict (i.e., same-sex interactions) may see signals combined in more predictable ways, as may those where the risk of a recipient disengaging is high (i.e., infant presence).

Studies of approach behaviour in baboons are currently limited to two main avenues - (1) stereotyped male-male greeting behaviour (for review see Dal Pesco & Fischer, 2020), and (2) grunting in approaches towards females (Palombit et al., 1999; Rendall et al., 1999; Silk et al., 2018). Baboon approaches involve a balance between conflict resolution/avoidance and cooperation. Across *Papio*, higher rates of physical male-male stereotyped greeting, particularly high-risk physical greetings, are correlated with increased male coalitions and spatial tolerance, with chacma baboons reportedly being the non-coalition forming outlier (Dal Pesco & Fischer, 2020). These types of approaches often include a swaggering gait, lip-smacking, ear-flattening, direct gaze, and a variety of hind-quarter contact (Colmenares, 1990; Dal Pesco & Fischer, 2018; Mondada & Meguerditchian, 2022; Pelaez, 1982; Smuts & Watanabe, 1990; Whitham & Maestripieri, 2003). The other well-studied area

is grunting during approaches towards females and its relevance for friendships, reconciliation, and infant contact (Cheney et al., 1995; Rendall et al., 1999; Silk et al., 2016; Smuts, 1985). Across baboon species, grunting increases when infants are present and may depend on social bonds and kinship (Faraut et al., 2019). Grunts may be used in a reconciliatory context and interactions following grunting are more likely to be affiliative and involve infant contact (Cheney et al., 1995; Cheney & Seyfarth, 1997; Palombit et al., 1999; Silk et al., 2018). Other studies of baboon approach behaviour have focused on single behaviours such as hind-quarter presentations (Hausfater & Takacs, 1987) or vocalisations (Fedurek et al., 2019).

Much of the existing approach literature in baboons focuses on individual signals rather than signal combinations. This is common in animal communication research and impedes our understanding of how multiple signalling and differences in composition modify meaning and potentially affect outcomes (Micheletta et al., 2013; Rodrigues et al., 2022). Here, we study approach behaviour in male and female chacma baboons (*P. ursinus griseipes*) and olive baboons (*P. anubis*) using video footage from Gorongosa National Park, Mozambique and Gombe National Park, Tanzania. The study has two main objectives – to test how signals are used in combination and to identify links between signal combinations and interaction outcomes. Using a network approach allowed us to study the relationships between signals themselves and between signals and specific sex combinations and infant presence, providing a greater degree of insight into the structure of approaches (Mielke et al., 2021). Following these analyses, we tested whether certain identified signals, i.e., ear-flattening, lip-smacking, grunting, and observing, were associated with an increased likelihood of contact with the recipient and, where relevant, the recipient's infant, after approach.

5.2 Methods

This study used video-based data collection to study approach behaviour between individuals, which is common in the study of facial and gestural signalling in

primate species (Aychet et al., 2021; Cartmill & Byrne, 2010; Clark et al., 2022; Micheletta et al., 2013; Molesti et al., 2020). Use of video footage allows observers to re-watch interactions and complete detailed coding, making it easier to record less salient signals or review observations, decreasing the likelihood of human error (Eibl-Eibesfeldt & Hass, 1967; Friard & Gamba, 2016; Gilmore & Adolph, 2017; Grund et al., 2023).

5.2.1 Study sites and populations

Videos were recorded of chacma baboons in Gorongosa National Park, Mozambique and of olive baboons in Gombe National Park, Tanzania. These datasets were combined due to sample size limitations and due to the many social and communicative similarities between olive baboons and chacma baboons. Social structure and organisation are similar across the two species (Fischer et al., 2019), with relationships also strongly affected by kinship and friendships in both (Silk et al., 2017; Silk et al., 2009). Previous studies have shown strong similarities in the use of grunting in the two species (Silk et al., 2016, 2018; but see Fedurek et al., 2019) and baboon vocal repertoires are highly conserved across *Papio* species (Hammerschmidt & Fischer, 2019). While it has been suggested that chacma baboon male-male greetings differ from those of other *Papio* species (Dal Pesco & Fischer, 2020), relevant published data on chacma baboons is limited and we have found the use of signals in male-male greetings recorded in Gorongosa National Park to be comparable to those of olive and yellow baboons (unpublished data, in preparation). While we acknowledge that some differences in signalling likely do exist between olive baboons and chacma baboons (e.g., minor differences within call types: Hammerschmidt & Fischer, 2019), we argue that existing literature on signalling repertoires across the female-philopatric baboons is sufficiently similar to justify combining these data sources in this instance.

Gorongosa: Gorongosa National Park covers 3770 km^2 of the Urema drainage basin in the southern end of the East African Rift System (EARS) (Macgregor, 2015; Tinley, 1977). A mosaic ecosystem resulting in high biodiversity makes the

park a unique and valuable analogue model for the environmental conditions of the EARS during important periods of past human evolution (Bobe et al., 2023). Recent genetic and genomic work clusters the baboons in the park with the chacma baboons (*P. ursinus griseipes*), but the park is located 100km south of the proposed hybridisation zone between northern chacma baboons and southern yellow baboons (Ferreira da Silva et al., Preprint; Hammond et al., 2022; Martinez et al., 2019; Santander et al., 2022). Our study group, the Chitengo Troop, resides in the open woodland area surrounding the research centre, located in the Riftvalley Alluvial Fan (Stalmans & Beilfuss, 2008), and is well habituated to humans. As of November 2019, the troop consisted of eight resident adult males, three peripheral adult males, one large juvenile male, 11 adult females, one subadult/large juvenile female, approximately 15 small/medium juveniles, and an indeterminate number of infants. All adult, subadult, and large juvenile baboons were identified and named by JM in 2019 and could successfully be identified *in situ* and from video footage. Sixty-five hours of footage were recorded opportunistically during October and November 2018 and between July and November 2019 by colleague Lucy Baehren and JM (Baehren & Carvalho, 2022). Recording focused on subgroups of baboons sitting near each other, with the target subgroup within the troop rotated throughout the day, but was not randomised as individuals had not been identified at the time of recording. Video recording in Gorongosa National Park was completed under research permit number PNG/DSCi/C145/2019 (J. Muschinski) and PNG/DSCi/C110/2018 (L. Baehren) and was cleared by the University of Oxford Animal Welfare and Ethical Review Board (APA/1/5/ACER/10Dec2018).

Gombe: Gombe National Park sits on the western border of Tanzania along the eastern shore of Lake Tanganyika, covering approximately 52 km^2 (Ransom, 1981). The mix of habitats including dense gallery forests, open deciduous woodland, mixed savannah woodland, and beaches is home to multiple primate species including olive baboons and chimpanzees, with little predation pressure (Ransom, 1981; Williams et al., 2008; Wilson et al., 2004). The park's olive baboons (*P. anubis*) are at the southeastern edge of the species' geographic range and are split into

six troops. The AC troop, studied here, ranges near the research camp and is well habituated. The troop consisted of 36 members at time of filming in 2021 including four adult males, nine adult females, three subadult females, four subadult/large juvenile males, one large juvenile female, and 15 small/medium juveniles (personal communication, A. Collins). All adult, subadult, and large juvenile troop members were well known to staff and their identity narrated during videography. Video footage of the AC troop was recorded between January and May 2021 and between August and September 2021 as part of long-term data collection in the park under research permit numbers 2020-287-NA-1990-170, and 2021-447-NA-1990-170 (Anthony Collins). The adult and subadult/large juvenile members of the troop were followed in randomised order, with videos taken opportunistically of any approach interactions amongst nearby individuals. This was due to the limitations posed by the dense vegetation in the troop's home range.

5.2.2 Video coding procedure

All proximity events were identified from video, defined as *any instance in which one individual, the approacher, decreased the distance between themselves and the recipient from over approximately five meters to less than two meters (two meters estimated as three body-lengths between individuals' centre points* (J. Altmann et al., 1993; Leigh, 2009; Levy et al., 2023; Rutenberg et al., 1987)). Male-male greeting studies in baboons have not typically used definitions based on distance, instead defining male-male greetings based on the behaviours exhibited (Colmenares, 1991a; Pelaez, 1982; Smuts & Watanabe, 1990; Whitham & Maestripieri, 2003; but see Kalbitzer et al., 2015 who use a one meter distance cut-off). Grunting studies, however, do use distance-based measures, with cut-offs typically at one meter (Faraut et al., 2019; Silk et al., 2018) or two meters (Cheney et al., 1995; Cheney & Seyfarth, 1997; Palombit et al., 1999; Silk et al., 2016; Silk et al., 1996). We opted for a length of approximately two meters as we observed *in situ* that this was the radius within which reactions from the recipient were more likely. We required

a starting distance of approximately five meters to ensure that approaches were independent of each other and that "access" had not already been negotiated.

The proximity event began once the approacher entered a five-meter radius of the recipient and we considered the initial interaction to have concluded once the approacher had either diverted, passed-by, or had stopped within two meters of the recipient and then sat, began walking away, foraging, grooming, resting, or being groomed. We opted for this cut-off as we were interested in signals used specifically during the reduction of interpersonal space. In most cases, the approacher could be easily identified, with one individual approaching and the other remaining stationary. If both approached each other, the individual who began approaching first was considered the approacher. We excluded any triadic interactions, events with unclear recipients, or events where the approacher had signalled towards more than one recipient. Interactions where a third individual was present within a two-meter radius were included only where they did not interact with, signal towards, or interfere with the interaction between recipient and approacher.

We included adults, subadults, and large juveniles in the analyses, with cut-off ages of four for females and five for males. Where ages were not known, age was estimated from body characteristics, specifically height in comparison to adult females for large juveniles (J. Altmann et al., 1981), rapid increase in body mass, testicular size, and canine length for subadult males (Alberts & Altmann, 1995; J. Altmann & Alberts, 1987; C. J. Jolly & Phillips-Conroy, 2003; Packer, 1979), onset of menarche in subadult females (J. Altmann et al., 1981; J. Altmann & Alberts, 2005; Charpentier et al., 2008), and achieving adult rank and onset of reproduction for adulthood (J. Altmann et al., 1981; Charpentier et al., 2008). Males start to rank higher than adult females once they reach the late juvenile period, gaining rank among adult males about two years following puberty, while females begin to acquire their adult rank, independent of direct maternal assistance, during the late juvenile and subadult period (Cheney, 1977; Hamilton & Bulger, 1990; Holekamp & Smale, 1991; Johnson, 1987; Walters, 1980). Given their maturing social relationships (Cheney, 1977; Hamilton & Bulger, 1990; Holekamp

& Smale, 1991; Johnson, 1987; Walters, 1980) and evidence suggesting exclusion of juveniles can lead to biased results when studying social behaviour (Fedurek & Lehmann, 2017), we opted to include interactions which involved large juveniles and subadults.

Events were only included in analysis if over 50% of the entire sequence could be seen and if visibility allowed for identification of the approacher's facial signals (e.g., lip-smacking). The ethogram used to collect behavioural data was modelled primarily after Dal Pesco & Fischer (2018), Colmenares (1991b), and Silk (2013) (for full ethogram see Muschinski & Carvalho, 2023a). The cleaned dataset is publicly available (Muschinski & Carvalho, 2023b). Inter-observer reliability methods and results can be seen in the supplementary materials. Behavioural data were collected using BORIS version 7.10.2 (Friard & Gamba, 2016) and data cleaning and analysis performed using Python version 3.8.5, R version 4.3.0 (2023-04-21 ucrt), NetFACS version 0.5.0, and stats version 4.3.1. The following analyses focus on actions performed by the approacher during the approach and initial interaction. NetFACS, used for network analysis, requires presence/absence data for each signal of interest for each event and does not account for signal order, intensity, count, or duration (Mielke et al., 2021). We excluded any signals which occurred in fewer than 1% of events from analysis because it is difficult to reliably detect signal combinations involving them (Levshina, 2015; Mielke et al., 2021; Silge & Robinson, 2017).

5.2.3 Identification of signal combinations - community detection

Our analysis consisted of two main steps: (1) identifying signal combinations using network analysis and (2) assessing whether the likelihood of certain interaction outcomes differed with identified signal combinations (see "Testing outcome-related hypotheses" below). We used network analysis to study co-occurrence of signals using NetFACS (Mielke et al., 2021), originally designed for the study of complex facial signals. Network analysis represents systems as a combination of nodes (in our case, the different approach behaviours) that are connected through edges

(in our case, the co-occurrence probability of these behaviours), allowing more intuitive visualisation and inference that accounts for the structural properties of the graph (Newman, 2018). It is well-established across disciplines (Baronchelli et al., 2013), but has recently been applied to animal signal combinations as it allows for the detection of higher-order patterns (Allen et al., 2019; Aychet et al., 2021; Weiss et al., 2014).

To identify differences in approach signals by sex combination and infant presence, we created a network of behaviour co-occurrences for each of the sex combinations and conducted analyses separately for each of them. Importantly, while the randomisation procedures underlying NetFACS account for signal combination complexity and element probability, they do not account for individual identities, so analyses are to a degree pseudoreplicated because of the over-representation of some individuals over others (J. Whitehouse et al., 2023). Edges represent the conditional probability that two behaviours occur in the same approach, and significance is established by comparing this probability with a null model that shuffles behaviours across approaches while keeping the number of behaviours per approach and the behaviour probability the same. Thus, a 'significant' link is one that is more likely than would be expected if approach behaviours were combined randomly (Mielke et al., 2021). We applied community detection with a modularity threshold of > 0.3 (Mielke et al., 2021; Newman, 2004). NetFACS community detection uses the "fast greedy" modularity optimisation algorithm to determine which groups of elements co-occur more than expected (Mielke et al., 2021).

Effects of field sites and inclusion of subadults and large juveniles

We completed the following checks to ensure that inclusion of large juveniles and subadults, as well as combining data from two field sites did not substantially affect overall results. We completed community detection once with only observations from Gorongosa (n = 298) and compared this to results when including only observations from Gombe (n = 73). Each was run with 2000 randomisations, a significance level of 0.05, minimum count of 5% of the total number of events, and

minimum probability of 0.05. We also compared community detection including all observations (n = 371) to community detection excluding observations involving subadults or large juveniles (n = 310). Graphical results for these analyses are included in the supplementary materials (see Appendix F). Once these checks were completed, the main analyses followed, comparing signal use across sex combinations and infant presence.

Sex combinations and infant presence

To identify overall patterns of signal combinations across all observations and sex combinations, we ran community detection once with all observations. Then, to identify whether the identified signal combinations were associated with specific sex combinations or whether combining all sex combinations into one analysis hid sex-specific patterns, we split the dataset into the four sex combination categories (male-male, female-female, female-male, and male-female) and completed community detection for each subset (for sample sizes see Table 5.3). Any interactions where the recipient's natal or transitional coat infant was present within the five meter radius were excluded from these analyses. All were run including interactions which involved subadults and large juveniles. Each of these analyses was run with 2000 randomisations, a minimum probability of 0.05, a minimum count of 5% of the number of observations, and a significance level of 0.05.

Finally, we ran three community detection analyses focused on interactions where recipients' natal or transitional coat infants were present within five meters of the recipient. The analyses were (1) all approaches towards females with infants, (2) male approaches towards females with infants, and (3) female approaches towards females with infants (for sample sizes see Table 5.4). This was to allow us to identify how signalling in approaches towards females differed with infant presence. Again, all analyses included observations involving subadults/large juveniles, used 2000 randomisations, a minimum probability of 0.05, significance level of 0.05 and minimum count equivalent to 5% of events.

5.2.4 Testing outcome-related hypotheses

Through community detection, we identified several clusters which may be linked to two main outcomes of interest for approaches: (1) physical contact with the recipient and (2) physical contact with the recipient's infant, where an infant was present. Social touch has been shown to promote social bonding and also plays an important role in emotional development of maturing primates, so we expect touch to be a desirable outcome for an individual initiating an interaction in most cases (Dunbar, 2010; Jablonski, 2021). Infants are very attractive to troop members, with troop members often attempting contact (Silk et al., 2003), therefore we assume that infant contact is a desired outcome for the approacher. It is also a risky outcome for the infant's mother, given the potential for negative effects on the infant, depending on the circumstance (Kleindorfer & Wasser, 2004; Palombit, 2003). We tested whether use of signals identified during community detection was associated with increases in the respective outcomes of interest (see Table 5.1). Many of the identified signals (i.e., ear-flattening, lip-smacking and grunting) have been identified elsewhere as affiliative signals or signals of benign intent (Easley & Coelho, 1991; Silk et al., 2018; Smuts, 1985), which is why we predicted they would be associated with increased likelihoods of physical contact. Grunting here refers to what has elsewhere been called basic grunting or social approach/infant grunting (Rendall et al., 1999). Where community detection identified clusters, we hypothesised that combined use of signals (i.e., interaction effects) may be meaningful. The datasets for these analyses were prepared differently than above. Observations were assigned the presence or absence of the outcome of interest. Where the outcome of interest occurred, we checked whether the signals of interest occurred prior to this outcome. Where the outcome of interest had not occurred, we checked whether the signals of interest occurred prior to the end of the initial interaction between approacher and recipient. We used these criteria to ensure that the signals relevant to our hypotheses occurred prior to, rather than following, the outcomes of interest.

We initially attempted to run all models with random effects of approacher identity and recipient identity. While this did work for both recipient-contact models, it resulted in convergence issues for all three infant-contact models due to the large number of random effect levels and limited sample sizes. As a result, we removed random effects to allow for reproducibility. This may introduce issues with pseudoreplication due to unaccounted for repeated measures. All models were run using the *stats* package with a logit link function and fit using maximum likelihood with iteratively reweighted least squares estimation (R Core Team, 2021). All hypothesis models were compared using likelihood ratio tests to null models which excluded the term of interest (Lewis et al., 2011). Multicollinearity was checked using the generalised variance inflation factor where appropriate (Fox et al., 2023).

Table 5.1: Outcome-related hypotheses

Outcome	Signal	Hypothesis
Physical contact with recipient	Ear-flattening and lip-smacking	Ear-flattening and lip-smacking performed in the same approach increases the likelihood of contact more than the sum of the individual signals
	Observing during the approach	Observing the recipient during the approach increases the likelihood of physical contact with the recipient
Infant contact	Grunting and ear-flattening	Grunting and ear-flattening in the same approach increases the likelihood of infant contact
	Observing the infant or recipient during the approach	Observing the infant or the recipient increases the likelihood of infant contact
	Ear-flattening and lip-smacking	Ear-flattening and lip-smacking in the same approach increases the likelihood of infant contact

Physical contact with recipient

We used two models with an outcome of the presence or absence of physical contact between recipient and approacher to test whether the approacher observing during the approach or ear flattening together with lip-smacking was linked to an increased likelihood of physical contact with the recipient later in the interaction. All

interactions where the recipient did not have an infant (n = 215) were included in these analyses. The first model, investigating the use of lip-smacking combined with ear-flattening, included predictors of approacher sex, recipient sex, ear-flattening, lip-smacking, and an interaction between lip-smacking and ear-flattening. We compared this to a null model excluding the interaction term. We also compared models including approacher sex, recipient sex and the signals individually to null models excluding the respective signals to compare direction of the effect of the joint use of the two signals to individual use of signals.

The second set of models for recipient contact were focused on observing during the approach. The hypothesis model included predictors of approacher sex, recipient sex, and observing the recipient during the approach, while the null model excluded the observing term.

Contact with recipient's infant

Analyses of infant contact were limited to observations where recipients were female and the recipient's natal or partially transitional coat infant was present within arm's reach of the mother (n = 137). The outcome was defined as whether or not the approacher made physical contact with the recipient's infant during the interaction. Signals of interest identified through community detection were observing of the recipient and/or infant during approach, ear-flattening combined with grunting, and ear-flattening combined with lip-smacking.

Grunting and ear-flattening: The first hypothesis model included predictors of approacher sex, recipient sex, grunting, ear-flattening, and an interaction of grunting and ear-flattening. This was compared to a null model excluding the interaction term. We also compared a model including approacher sex, recipient sex, and grunting to a null model excluding grunting, due to the literature indicating grunting is a sign of benign intent during approaches (Palombit et al., 1999; Silk et al., 2016, 2018). During these analyses, any observations where audibility was low due to environmental noise (e.g., a nearby river) were removed (remaining n = 121). As the original dataset included only grunts where the vocalizer could

be identified, these two analyses were run again with a dataset where grunts that were recorded but could not be confidently assigned to either the approacher or recipient were included.

Observing infant and observing recipient: We again completed two sets of model comparisons, one focused on observing the recipient's infant and one on observing the recipient. The first hypothesis model included predictors of approacher sex and observing the recipient's infant during the approach, with an outcome of infant contact. The model was compared to a null model including only approacher sex using a likelihood ratio test. The same process was followed with the infant-observing term replaced by observing the recipient (mother).

Ear-flattening and lip-smacking: Our final model for infant contact included predictors of approacher sex, lip-smacking, ear-flattening, and an interaction between lip-smacking and ear-flattening. This was compared to a null model excluding the interaction term.

5.3 Results

A total of 379 interactions were identified from 55 hours of video footage in Gorongosa National Park and 133 from 18 hours of footage from Gombe National Park. Of these 512 total observations, 371 (see Table 5.2) met all approacher visibility and inclusion criteria (see section 5.2.2). The approacher was identifiable in all but 30 of the qualifying interactions and the recipient in all but 26 (in 10 interactions neither approacher nor recipient could be identified confidently). Of the interactions meeting inclusion criteria, 62 involved a large juvenile or subadult.

Table 5.2: Counts of interactions by sex combination

	Approacher sex	
Recipient	**Female**	**Male**
Female	181	72
Male	84	35

5.3.1 Community detection: Identification of signal combinations

Following removal of signals which occurred in fewer than 1% of all events, 42 signals of the original 68 remained. The mean numbers of unique signals included per approach were 2.37 (SD = 1.57) for male-male approaches, 3.67 (SD = 2.42) for female-female approaches, 2.42 (SD = 1.63) for male-female approaches, and 2.11 (SD = 1.28) for female-male approaches. Community detection identified four clusters (modularity = 0.61). The first cluster included passing without contact and glancing toward the recipient; the second cluster contained observing the recipient, arriving (an approach that ends in the individual stopping at and/or interacting with the recipient rather than diverting, stopping short, or passing without contact), presenting, and grabbing at the recipient's infant (touching and attempting to pull the infant from the mother); the third consisted of observing the recipient's infant and grunting; the fourth cluster consisted of lip-smacking and ear-flattening (Figure 5.1).

These clusters remained largely consistent whether juveniles and subadults were excluded (see Figure F.1 in the supplementary materials), and when Gorongosa and Gombe data were analysed separately (see Figures F.2 and F.3 in the supplementary materials). Fewer clusters were identified in the Gombe dataset, but this is unsurprising given the smaller dataset.

Sex combination (no recipient infant present)

When the dataset was split into subsets by sex combination and observations where recipients' infants were present were excluded, clusters could be identified at a modularity above 0.3 in male-female and male-male approaches (see Table 5.3). Analyses for male-male encounters detected clusters of (1) ear-flattening, lip-smacking, and observing, (2) interacting upon arrival together with making hind-quarter contact, and (3) presenting to the recipient, grimacing, and dodging or flinching. Interacting upon arrival clustered with observing the recipient in male-female approaches. This pair of signals was also present in the female-female

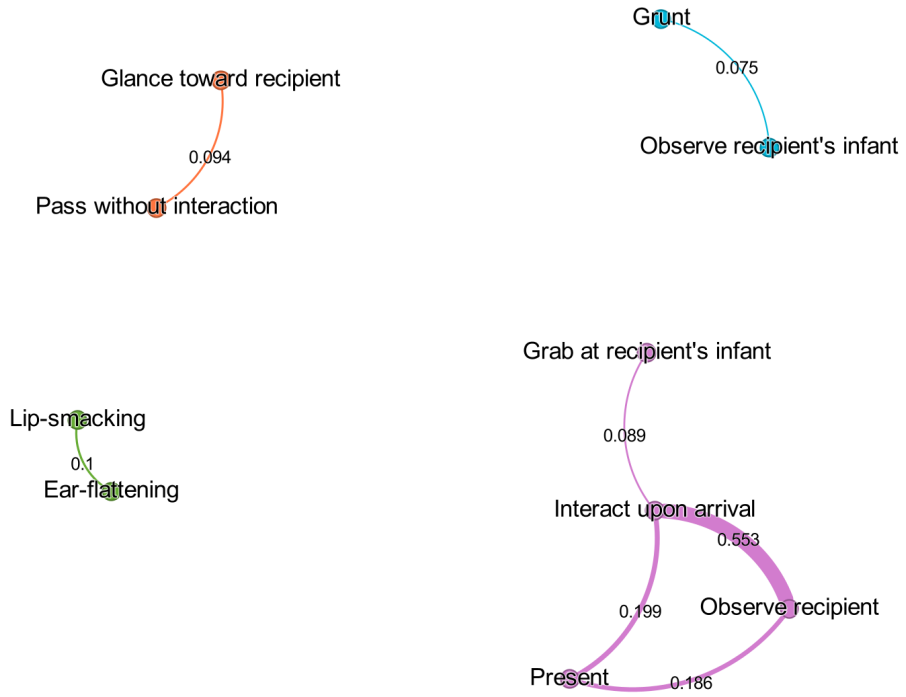

Figure 5.1: Community detection across all approaches. Linked and coloured behaviours are detected clusters, with edges labelled with the combination's observed probability. Figure created using Gephi.

(modularity = 0.21) and female-male (modularity = 0.28) analyses, though the modularity of clusters in these analyses did not meet the required threshold of 0.3. Ear-flattening and lip-smacking did not cluster together in cross-sex interactions, but did in same-sex interactions.

Table 5.3: Community detection results for sex combination subsets with no recipient infant present

Sex Combination	Other Criteria	Modularity	Clusters
Female-female (n = 47)	No recipient infant (all individuals)	0.21	Ear-flattening, lip-smacking, and hind-quarter contact
			Observing recipient, presenting to recipient, and interacting upon arrival
			Passing without contact and glancing toward recipient
			Ear-flattening, lip-smacking, and observing the recipient

Table 5.3: Community detection results for sex combination subsets with no recipient infant present

Sex Combination	Other Criteria	Modularity	Clusters
Male-male (n = 35)	All individuals	0.38	Hind-quarter contact and interacting upon arrival
			Presenting to the recipient, grimacing, and dodging or flinching
Female-male (n = 84)	All individuals	0.28	Passing without contact and glancing toward recipient
			Observing recipient, presenting to recipient, interacting upon arrival, and reaching towards the recipient
Male-female (n = 50)	No recipient infant (all individuals)	0.44	Observing recipient, interacting upon arrival, and soliciting grooming
			Inspecting and hind-quarter contact

Infant presence

Differences in signalling involving infants were highlighted by comparing community detection results where infants were present and absent (see Table 5.4). When all approaches towards females with infants were considered, community detection identified four clusters (modularity = 0.67): (1) grabbing at the infant together with interaction upon arrival, (2) ear-flattening together with grunting, (3) glancing toward the recipient during the approach together with passing without contact, and (4) picking the infant up, carrying the infant, and releasing the infant following carrying. The fourth cluster is of little relevance here because these three actions are all part of the same larger action chain of carrying an infant after picking it up from the ground.

Table 5.4: Community detection results with and without recipient infant presence

Sex Combination	Recipient Infant Presence	Modularity	Clusters
All (n = 215)	Absent	0.38	Ear-flattening and lip-smacking
			Observing recipient, interacting upon arrival, presenting, and hind-quarter contact
			Passing without contact and glancing toward recipient
All (n = 156)	Present	0.67	Ear-flattening and grunting
			Grabbing at the infant and interacting upon arrival
			Infant pickup, infant carry, infant release
			Passing without contact and glancing toward recipient
Male-female (n = 50)	Absent	0.44	Observing recipient, interacting upon arrival, and soliciting grooming
			Inspecting and hind-quarter contact
Male-female (n = 22)	Present	0.56	Ear-flattening, grunting, observing recipient, and interacting upon arrival
			Recipient avoiding and approacher following
			Soliciting grooming and self-scratching
Female-female (n = 47)	Absent	0.21	Ear-flattening, lip-smacking, and hind-quarter contact
			Observing recipient, presenting to recipient, and interacting upon arrival
			Passing without contact and glancing toward recipient
Female-female (n = 133)	Present	0.56	Ear-flattening and lip-smacking
			Grabbing at the infant and interacting upon arrival
			Infant pickup, infant carry, infant release

5.3.2 Outcome models

Model comparisons are detailed below with results summarised in Table 5.5.

Table 5.5: Outcome model results compared to hypotheses; asterisk indicates hypothesis model is a significantly better fit than null model according to a likelihood ratio test

Outcome	Signal	Hypothesis	Results
Recipient Contact	Ear-flattening with lip-smacking	Increase	**Decrease compared to individual use***
	Ear-flattening	Increase	**Increase***
	Lip-smacking	Increase	**Increase***
	Observing recipient	Increase	**Increase***
Infant Contact	Ear-flattening with lip-smacking	Increase	No change
	Ear-flattening	Increase	No change
	Lip-smacking	Increase	No change
	Grunting with ear-flattening	Increase	No change
	Grunting	Increase	No change
	Observing recipient	Increase	**Decrease***
	Observing infant	Increase	**Increase***

Contact with recipient

Ear-flattening with lip-smacking: We compared a model with predictors of approacher sex, recipient sex, lip-smacking, ear-flattening, and an interaction between lip-smacking and ear-flattening to a reduced model without the interaction term. The full model performed better than the reduced model according to a likelihood ratio test ($\chi^2(1) = 6.99, p < 0.01$). The interaction term indicates a large reduction in the likelihood of contact when both signals are combined (Table 5.6), compared to when one or the other signal is used individually. For example, in a female-female interaction, the probability of contact in an approach with neither

ear-flattening nor lip-smacking is 0.35, in one with ear-flattening it is 0.61, with lip-smacking it is 0.89, while with both lip-smacking and ear-flattening it is only 0.48. A model including only ear-flattening, approacher sex, and recipient sex performed better than a null excluding ear-flattening ($\chi^2(1) = 4.10, p < 0.05$), while a model including only lip-smacking, approacher sex, and recipient sex, did not perform significantly better than a null model excluding lip-smacking ($\chi^2(1) = 3.21, p = 0.07$). The odds ratios for both terms in their respective models were positive (ear-flattening: 2.18, lip-smacking: 2.53), indicating that while the individual signals were associated with increased likelihood of contact, the combination of both in the same approach was associated with a significant decrease in the likelihood of contact.

Table 5.6: Log odds ratios, standard error, z-value, and p-values for model coefficients. The interaction term related to the hypothesis is highlighted.

Term	Log-odds ratio	Std. error	Z-value	p-value
Intercept	-0.617	0.270		
Lip-smacking	2.676	1.130		
Ear-flattening	1.058	0.437		
Approacher sex (male)	-0.504	0.357		
Recipient sex (male)	-0.290	0.308		
Lip-smacking * ear-flattening	-3.186	1.351	-2.358	**0.018**

Observing: The model including a predictor of observing the recipient during the approach performed better than a reduced model which included only predictors of approacher sex and recipient sex ($\chi^2(1) = 20.45, p < 0.001$). Physical contact with the recipient was more likely when the approacher observed them during the approach (odds ratio = 4.77).

Contact with recipient's infant

Grunting with ear-flattening: The model including an interaction between ear-flattening and grunting did not perform better than one excluding the interaction term ($\chi^2(1) = 0.63, p > 0.05$). We then compared a simplified model including only predictors of grunting and approacher sex to a null model excluding grunting, finding again that grunting was not associated with a change in the likelihood of infant contact ($\chi^2(1) = 1.14, p > 0.05$). This was the case even when interactions between an assumed mother-daughter pair were excluded.

When grunts were included in analysis even if the approacher could not be confidently assigned as the vocalizer, results did not change. The model including an interaction between ear-flattening and grunting did not perform better than the associated null model ($\chi^2(1) = 2.01, p > 0.05$). A model including only grunting and approacher sex also did not perform better than a model including only approacher sex ($\chi^2(1) = 0.73, p > 0.05$).

Observing recipient: The model with an outcome of infant contact including predictors of observing the recipient and approacher sex was not a better fit compared to a model including solely approacher sex ($\chi^2(1) = 1.76, p > 0.05$).

Observing infant: The model including observing the infant and approacher sex performed better than the model without infant observing ($\chi^2(1) = 9.04, p < 0.01$). Infant contact was significantly more likely (odds ratio = 3.37) following an approacher observing the infant.

Ear-flattening with lip-smacking: A model including an interaction of ear-flattening and lip-smacking was not a better fit than one excluding the interaction term ($\chi^2(1) = 0.79, p > 0.05$). Ear-flattening and lip-smacking, were also not associated with a change in the likelihood of infant contact on their own (ear-flattening: $\chi^2(1) = 0.00, p > 0.05$; lip-smacking: $\chi^2(1) = 0.39, p > 0.05$). This indicates that ear-flattening, lip-smacking, and their combination were not associated with a change in the likelihood of infant contact.

5.4 Discussion

Our study addressed three research questions: first, whether signals in approaches by baboons are reliably combined; second, in what ways approach behaviour differs across sex combinations and infant presence; and third, how some of the identified signals or signal combinations may be related to interaction outcomes. We identified four clusters during community detection when including all observations, which were (1) glancing toward the recipient and passing without contact, (2) grunting and observing the recipient's infant, (3) lip-smacking and ear-flattening, and (4) presenting, observing the recipient during the approach, interacting with the recipient upon arrival, and grabbing at the recipient's infant. Further investigation highlighted how infant presence and sex combination played a role in these signal clusters. Themes relating to gaze direction and key facial signals (i.e., ear-flattening and lip-smacking) were present across many scenarios. Finally, binomial models provided insight into how gaze direction, lip-smacking, ear-flattening, and grunting related to the likelihood of contact with the recipient and contact with the recipient's infant (see Table 5.5).

Signal clusters identified in the male-male analysis align with the existing literature on stereotyped male-male greetings in baboons (Dal Pesco & Fischer, 2020). Published literature on these interactions in chacma baboons is limited, with much of the literature referring to chacmas as having little to none of the stereotyped male-male greeting behaviour seen in other baboon species (Dal Pesco & Fischer, 2020; Henzi et al., 2008; Kalbitzer et al., 2015). All but four of the male-male interactions included in the community detection analysis were from the Chitengo troop, suggesting that the types of greeting behaviours described in yellow, olive, and hamadryas baboons are also seen in chacma baboons, though intensity or frequency may differ (see Chapter 4).

There was substantial overlap in clusters across sex-combinations. Lip-smacking together with ear-flattening, identified in the overall community detection analysis, appears to have been driven primarily by same-sex combinations and is discussed

in more detail below. Hind-quarter contact appeared in clusters in both sets of approaches by males, and presenting appeared in clusters across multiple sex combinations. The presence, but relatively low observed frequency, of the signal combinations identified through community detection indicates there is significant flexibility in how signals are combined and that approach behaviour in chacma baboons likely cannot be considered "ritualised" (Rossano, 2012). However, it is possible that interactions may be "ritualised" around single signals, rather than around signal combinations. If signals were reliably combined following strict rules, we would expect to see detected clusters used more frequently and we may also expect to see a higher modularity. Lack thereof could indicate that combinations are flexible to allow for more information transmission, that few signals are generally used in a signalling bout and therefore there is little opportunity for signal combinations, or that signals are combined randomly. Modularity of both female-male and female-female interactions fell below the cut-off of 0.3, even though sample sizes were larger than for the respective male-approacher interactions (see Table 5.3). This indicates that clusters were more readily identified in male-approacher interactions, possibly reflecting lower flexibility in male signal use or more diversity in female-led interactions. However, this could also be a result of inter-individual variation, with observations included from fewer males (15 individuals) compared to females (25 individuals).

5.4.1 Gaze direction

The juxtaposition of the use of prolonged gaze during approaches that resulted in interaction (cluster 4) versus the use of short glances during approaches that resulted in passing by without interaction (cluster 1) emphasizes the importance of gaze. Continued observation of the recipient is a potential indicator of intention to interact or may be a by-product of the approacher spending time assessing the recipient and context. Cluster 1 (glance toward and pass without contact) was also detected in female-male approaches and female-female approaches without infants though the modularity for both analyses was below the cut-off of 0.3.

Interacting upon arrival with observing during approach was detected in male-female interactions both with and without an infant present (also detected in female-male interactions, but modularity < 0.3). Gaze direction is likely associated with the outcome of interactions to some degree across all sex combinations, though this relationship could be weaker in certain sex combinations where approaches either are very likely or very unlikely to result in interaction regardless of gaze direction, for example male-male approaches. Recipient contact was significantly more likely in approaches where the approacher observed the recipient, and infant contact was more likely where the approacher spent time observing the infant.

Many primate species follow the gaze of conspecifics (Tomasello et al., 1998) and also of human experimenters successfully (Parron & Meguerditchian, 2016). While the underlying cognitive mechanisms may differ by species, the ability to gaze follow is important to primates navigating complex social environments (Rosati & Hare, 2009). Baboons specifically have been shown to modify their manual signals (Bourjade et al., 2014; Meunier et al., 2013) and adjust their own gaze and body position (Parron & Meguerditchian, 2016) to account for the visual attention or gaze direction of human experimenters. Even if direct gaze here did not serve as an intentional signal, primates are generally adept at identifying when they are being looked at (Emery, 2000), suggesting that direct gaze of an approacher will always serve to transmit information, even if unintentionally (Bourjade et al., 2014; Harrod et al., 2020).

5.4.2 Ear-flattening and lip-smacking

The third cluster detected in general community detection – lip-smacking and ear-flattening – appeared to be driven by both female-female and male-male encounters, based on community detection within the sex combination subsets. The "come hither" or "NEEF" face, which consists of ear-flattening and scalp retraction, is frequently referred to as an affiliative signal in the baboon literature (Smuts, 1985, 2002; Smuts & Watanabe, 1990). Lip-smacking is exhibited by multiple primate species and has been found to be associated with affiliative behaviours

(Easley & Coelho, 1991; Fedurek et al., 2015; Micheletta et al., 2013). It is one of the most common signals observed in baboons and is used across a wide variety of contexts (Molesti et al., 2020). How lip-smacking is combined with other signals may influence interaction outcomes, for example the likelihood of physical contact in crested macaques (Micheletta et al., 2013). In chimpanzees, grooming solicitations accompanied by lip-smacking resulted in longer grooming bouts with higher probabilities of reciprocity (Fedurek et al., 2015).

Following community detection, which identified the combination of lip-smacking and ear-flattening together in male-male and female-female with infant approaches, we hypothesised the combination may be a particularly strong affiliative signal, used when a particular outcome, for example physical contact, is desired. We expected the combination of lip-smacking and ear-flattening to be associated with a higher likelihood of contact in observations where a recipient infant was not present and with a higher likelihood of infant contact when a recipient infant was present. Contrary to our expectations, while ear-flattening and lip-smacking individually were associated with an increase or no change in the likelihood of contact with the recipient, the use of both within the same interaction was associated with a sharp decrease in the likelihood of recipient contact compared to use of the signals individually, and no change in the likelihood of infant contact. This difference in outcomes when the two signals are combined could be an example of what Oña et al. refer to as componentiality, which they argue is a precursor to compositionality (Oña et al., 2019). Compositionality is a key characteristic of human language, enabling the generation of novel expressions by systematically combining and recombining linguistic components.

We suggest that the use of both signals together could be a particularly strong appeasement signal, but that in the types of interactions where such a strong composite signal is needed the likelihood of contact may be lower as the perceived risk to the approacher is particularly high. As these signals cluster together only in same-sex interactions, where both participants fall within the same dominance hierarchy, this signal combination may be used primarily in scenarios where rank

plays an important role. As we do not have reliable rank data available for the study period from the Chitengo troop this possibility cannot be explored further here, but is a promising direction for further research.

5.4.3 Grunting and infant presence

The second cluster from the main community detection analysis (grunting and infant observing) replicates findings of other baboon studies where grunting was found to be associated with approaches towards infants (Faraut et al., 2019; Rendall et al., 1999; Silk et al., 2016, 2018). When community detection was performed with only approaches where a recipient's infant was present, ear-flattening together with grunting was a cluster in the overall community detection and was also part of clusters identified in approaches by males. In male-female approaches there were three clusters identified: (1) ear-flattening, grunting, observing the recipient, and interacting upon arrival, (2) the recipient avoiding the approacher and the approacher following, and (3) soliciting grooming and self-scratching. In female-female approaches with a recipient's infant present, three clusters were identified: (1) ear-flattening and lip-smacking, (2) grabbing at the infant and interacting upon arrival, and (3) picking up the infant, carrying the infant, and releasing the infant.

Infants are highly attractive to other troop members, in particular other adult females (Frank & Silk, 2009; Silk et al., 2003), and a variety of hypotheses exist explaining the high prevalence of non-maternal infant handling (Kleindorfer & Wasser, 2004). Grunting in approaches towards females with infants is argued to be a sign of benign intent, reducing the recipient's uncertainty about the likely interaction outcome (Cheney et al., 1995; Cheney & Seyfarth, 1997; Faraut et al., 2019; Silk et al., 2016). Grunting in chacma, olive, and Guinea baboons has been associated with a higher likelihood of affiliative interaction, often including contact behaviour (Cheney et al., 1995; Faraut et al., 2019; Palombit et al., 1999; Silk et al., 2016, 2018). Based on this, we hypothesised that (a) grunting was associated with a higher likelihood of infant contact, and that (b) the interaction between use of grunting and of ear-flattening would be linked with an increased likelihood of infant

contact due to the clustering of the two signals in community detection. Contrary to expectation, both ear-flattening with grunting and grunting alone were associated with no change in the likelihood of infant contact. However, past research has also shown the likelihood of an approacher to grunt is influenced by their kinship (Silk et al., 2016) and rank differential (Cheney et al., 1995; Cheney & Seyfarth, 1997; Rendall et al., 1999; Silk et al., 2016, 2018) with the recipient. These variables could not be controlled for in our analyses due to lack of rank and kinship data, which may explain the lack of effect of grunting, as daughters/mothers may be less likely to grunt, but more likely to be allowed infant contact (Silk et al., 2016).

5.4.4 Limitations and future directions

Due to data collection limitations (no further data could be collected at the time due to the Covid-19 pandemic), it was not possible to further test hypotheses relating to the effects of rank, sexual status, and friendships. While we began to collect rank and association data in Chitengo during 2019 after individuals were identified, the bulk of video footage used here was recorded in 2018 and we did not feel it was appropriate to assume ranks, particularly for males, had remained constant. The study is also limited by the inability to account for repeated individual identities during community detection. While outcomes models were initially run with random effects of approacher and recipient identity, the models had to be simplified due to the small sample sizes, leading to possible issues due to pseudoreplication. However, this study demonstrates that this same methodological framework could in future be used successfully with larger datasets to investigate differences in signalling based on rank, kinship, friendships and other social relationships.

5.4.5 Conclusions

We used a two-step analysis pipeline, first identifying signals used together through community detection, and second testing whether those signal combinations were associated with differences in the likelihood of contact with the recipient or recipient's infant. Community detection identified several clusters of signals that tended

to co-occur and provided insight into which sex combination approaches drove the presence of each cluster within the main community detection analysis. Gaze direction, ear-flattening and lip-smacking, and grunting during infant presence were all identified as important signal use themes. There was substantial overlap in signal use and similarities in signal clusters between sex combinations, indicating that signals are not specific to sex and are used flexibly. We used binomial models to test hypotheses related to signal use and recipient and infant contact. Notably, while use of ear-flattening and lip-smacking independently were associated respectively with an increase or no change in the likelihood of contact with the recipient, the use of both together was linked with a sharp decrease in the likelihood of contact compared to when the signals were used individually. We suggest this may be because the use of both signals together may be a particularly strong signal of appeasement, used in circumstances where the approacher may already be less likely to attempt contact, particularly in same-sex interactions.

It is time for a widening of the study of baboon approach behaviour, expanding past the traditional focus on male-male encounters or single signals such as grunting, and considering approach behaviour more broadly. Using a network-based approach allows for a deeper understanding of the co-occurrence of signals, helping us to identify combinations used in specific contexts and providing further insight into how combining signals may modify meaning.

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6

Complexity, risk, and physical contact in chacma and olive baboon approaches

Author Contributions: I completed video coding, data analysis, and writing for this chapter. Susana Carvalho and Alexander Mielke provided project design, statistical, and editorial advice. Lucy Baehren permitted data collection from videos she filmed in Gorongosa National Park, Mozambique in 2018, prior to the start of my PhD. Nuhu Buke filmed olive baboon interactions in Gombe National Park, Tanzania for use in this project. Anthony Collins assisted with designing the data collection protocol, coordinated filming in Gombe, and provided editorial input.

Abstract:

Environmental and social selective pressures shape signalling, with evidence suggesting these selective pressures are particularly intense where both the risk and cost of miscommunicating are high. We hypothesised that in situations where personal risk posed to a signaller by a recipient is high, the signal bout should be clearer, more predictable, and exhibit less physical contact. Here we study signalling during approaches between conspecifics in video footage from two troops of baboons (*Papio anubis* and *Papio ursinus griseipes*) to test these hypotheses. We recorded contact and event size and calculated entropy, comparing these measures

across two sets of conditions. First, we compared approaches by females with infants to approaches by females without infants, with the expectation that risk to the approacher would be perceived as higher in females with infants, resulting in more clear, less variable signalling in their approaches. Second, we compared approaches towards males versus approaches towards females, expecting that approaches towards males would be perceived as higher risk, again resulting in less variable, clearer signalling by the approacher. We used hierarchical Bayesian regression models and bootstrapped entropy estimates to compare likelihood of physical contact, event size, and entropy across conditions in both of the two comparisons (1: approacher with infant versus without infant, 2: male versus female recipient). Hypotheses regarding likelihood of contact and event size were largely unsupported, though findings are difficult to interpret due to limited sample sizes. While entropy was not found to differ by recipient sex, it did differ significantly by approacher sex, with approaches by males showing higher variability, whether the recipient was male or female. It may be that the larger driver of complexity in approacher signalling may be the risk they pose to the recipient, with approachers using redundant benign intent signals when risk to the recipient is higher in order to facilitate an interaction.

6.1 Introduction

Living in social groups can come with many benefits, such as increased protection from predators, friendships and social support, and greater inter-group competitive power (Clutton-Brock & Janson, 2012). However, proximity to conspecifics may also result in increased competition over resources, such as foraging opportunities, mating opportunities, and sleeping sites, and may increase the risk of agonistic social interactions that could result in injury (Clutton-Brock & Janson, 2012). In chacma baboons in particular, there are frequently agonistic interactions between males, or from males directed towards females or their infants (Archie et al., 2014;

Drews, 1996; Kalbitzer et al., 2015; Kitchen et al., 2009; Taniguchi & Matsumoto-Oda, 2018). Group living requires the management of social relationships and of shared space through communication.

While all signals, by definition, undergo selective pressure related to communication (Higham & Hebets, 2013), these pressures may differ depending upon the social context, function, and environment a signal is used in. When the risk of miscommunication is high and the potential for negative repercussions strong, signals should be selected for decreased ambiguity (Clark et al., 2022). As such, signals used in higher risk contexts, more interfering environments, or between individuals with uncertain relationships (e.g., closer in rank) may be selected for increased specificity, stereotypy, and intensity to improve the clarity of signalling (Clark et al., 2022). Such selection can occur as a result of the natural environment (Pohl et al., 2009) or the social environment (Maestripieri, 2005).

Weather, habitat structure, and other environmental noise sources can cause signal degradation between point of issue and reception, leading to potential miscommunication (Brumm & Naguib, 2009; Gomes et al., 2022). Many species account for risk of miscommunication (Gomes et al., 2022; Uetz et al., 2013); baboons, for example, adapt grunting rate and duration based on environment and visibility conditions (Ey, 2008; Ey et al., 2009). The selective pressure resulting from a higher likelihood of miscommunication should also, however, change with the strength of the negative outcome that could result from miscommunication (Clark et al., 2022). Threats posed by predators are a prime example, with evidence of high specificity in alarm calls across a number of taxa, transmitting more specific information about the direction or type of threat (Crockford & Boesch, 2003; Digweed et al., 2005; Frederiksen & Slobodchikoff, 2007; Gill & Bierema, 2013; Manser, 2001; Price et al., 2015).

As Clark et al. (2022) point out, most research concerning risk of miscommunication in signalling has focused on vocalisations, with little research investigating how risk of miscommunication may affect other signalling modalities. However, particularly in socially cohesive species which spend less time far apart, we might

expect more of the signalling repertoire to be visual (e.g., orofacial signals or physical gestures) as compared to vocal, making it critical to consider signals beyond vocalisations. Furthermore, few studies have investigated the relationship between signalling and interpersonal risk posed by the recipient to the approacher, with most studies on risk and communication focused on environmental risk or environmental interference. Clark et al. studied the facial expressions of crested macaques, hypothesising that more intense, less variable facial expression would be used in higher risk interactions. They found that interactions in affiliative contexts had greater variability and lower intensity than those in aggressive contexts, and that facial expressions used in interactions between closely ranked individuals ("riskier" interactions) were more intense (Clark et al., 2022). They also observed greater variability in same-sex interactions than in different-sex interactions (Clark et al., 2022). A study of the use of the play face by adult bonobos found similar patterns relating to risk, with play face use changing with the level of risk in the interaction (Palagi, 2008). Play faces were used more in dyadic or polyadic play than in solitary play and when there were more frequent aggressive interactions during the play bout (Palagi, 2008).

Rincon et al. similarly found that at a species level, facial signal use in more tolerant macaque species was more flexible across submissive, aggressive, and affiliative encounters than that of more despotic macaque species (Rincon et al., 2023). The social complexity hypothesis for communicative complexity posits that the level of communicative complexity of a species is linked to its level of social complexity and social tolerance (Blumstein & Armitage, 1997; Freeberg et al., 2012; Maestripieri, 2005; Peckre et al., 2019; Pika, 2017; Rebout et al., 2020). This hypothesis considers the effect of risk in interactions at a species level, rather than at the level of individual interactions. Communication in more egalitarian species is more varied and less predictable, with the opposite found in more despotic species, where the risk of an agonistic outcome as a result of miscommunication may be higher (Maestripieri, 2005; Rebout et al., 2020).

6. Complexity, risk, and physical contact

Complexity can be measured at the level of a single interaction, for example by measuring the interaction's event size (i.e., number of signals used in a signalling bout), number of transitions between different signals within one signalling bout, or number of modalities involved (e.g., vocal, orofacial, or physical) (Clark et al., 2022; Hebets & Papaj, 2005). Alternatively, it can be measured at the level of an entire system (e.g., an entire species, or a group or class of interactions) by measuring the repertoire size within a system, the system's entropy, the diversity of signal combinations used, or the flexibility of signal use (Clark et al., 2022; Freeberg et al., 2012; Hebets, 2011; Pika, 2017; Rebout et al., 2020; Shannon, 1948). Similarly, there are many ways of measuring risk or social complexity, all of which rely on assumptions about individuals' perceptions of interpersonal relationships or about the required underlying cognitive skills (Peckre et al., 2019).

In this study, we investigated whether differences existed in signalling variability, complexity, and rates of physical contact between higher risk and lower risk interactions in chacma and olive baboons. In baboons, signals are often studied in isolation (e.g., the grunting literature: Silk et al., 2018), or with only minimal consideration of how they are combined (e.g., the greeting literature: Dal Pesco & Fischer, 2020). The non-vocal communication of baboons, like that of most other monkeys, has been understudied in comparison to that of apes (Meguerditchian, 2022). However, to better understand the evolutionary origins of aspects of communication that may share properties with human language, a broader comparative approach is needed (Meguerditchian, 2022). Baboons have a rich signalling repertoire (Molesti et al., 2020) and should not be disregarded, in particular due to their many evolutionary parallels with early hominins (Elton, 2006; Fischer et al., 2019; King, 2022) (see Chapter 2). Here, we compared features of approaches in interactions where the assumed perceived risk to the approacher was high versus low. While much of the existing literature on risk and signalling focuses on differences between species (i.e., the social complexity hypothesis), we focus here on the level of the interaction. We expected that interactions which

pose a higher risk to the approacher should lead to signalling which involves less contact behaviour and clearer signalling to avoid miscommunication.

We hypothesised that:

1. Approachers in higher risk proximity events would be less likely to exhibit physical contact than in lower risk proximity events.

2. Approachers in higher risk proximity events would exhibit less complex (i.e., fewer unique elements) signalling during their approach to aid with signal clarity.

3. Approach behaviour in riskier proximity events would be more predictable (i.e., lower entropy/entropy ratio) than in less risky events.

Risk, like complexity, is difficult to define and measure. Baboons are useful in this regard, as they are highly sexually dimorphic (Plavcan, 2001; Thorén et al., 2006) and exhibit male-dominated, linear dominance hierarchies (Fischer et al., 2019; C. J. Jolly, 2020). Males generally exhibit high levels of aggression towards both males and females (Kalbitzer et al., 2015; Kitchen et al., 2005; Packer et al., 1995; Smuts, 1985). While rank and rank differentials likely play a significant role in the perception of risk for approachers during same-sex interactions (e.g., Clark et al., 2022), we expect that individuals approaching a male baboon would generally be at higher risk of aggression or injury than those approaching a female baboon (Kitchen et al., 2009). As such, comparing approaches towards males and approaches towards females may provide insight into the relationship between risk and signalling even where individuals' ranks are unknown.

Infanticide and feticide are common strategies by immigrant males in savannah baboons (Bailey et al., 2021; Palombit et al., 2009; Palombit, 2000; Palombit, 2003; Weingrill, 2000), and as such, a female who is pregnant or has an infant should perceive a higher level of risk than a cycling female does when approaching a male. However, there is evidence indicating that cycling females experience aggression from and injury by adult males at a higher hourly rate than pregnant or lactating

females (Baniel et al., 2017). Baniel, Cowlishaw, and Huchard hypothesise that this is a form of sexual intimidation as males are more likely to experience long-term mating success with cycling females they intimidate (2017). Even so, we expect that while the rates of male aggression may be higher towards cycling females, sustained injuries would be less likely to directly influence female reproductive success than the death of an infant. As such, comparing approaches by females with and without infants may be a second proxy for risk in interactions between female and male baboons.

By investigating contact behaviour, event size, and entropy across sex combinations and by infant presence, we gain insight into the impact of interpersonal risk on approacher signalling, even where more conventional measures of risk (e.g., rank differential) are unavailable.

6.2 Methods

6.2.1 Subjects

This study incorporated video data from two groups of baboons: one troop of chacma baboons (*Papio ursinus griseipes*) from Gorongosa National Park, Mozambique, and one troop of olive baboons (*Papio anubis*) from Gombe National Park, Tanzania.

Gorongosa National Park: Video footage in Gorongosa National Park was recorded between October and November 2018 and July and November 2019 (Baehren & Carvalho, 2022; Muschinski et al., Preprint). Gorongosa National Park lies in the southern reaches of the East African Rift System and spans approximately 3770 km^2. The park's mosaic ecosystem supports high levels of biodiversity and has a rebounding population of megaherbivores and carnivores (Daskin et al., 2016; Stalmans et al., 2019, 2020). Approximately 230 troops of baboons range throughout the park (Stalmans et al., 2022), with variation in phenotype suggesting that the park may lie in a hybridisation zone between northern chacma baboons and southern yellow baboons. The Chitengo Troop ranges primarily in the forested area

surrounding the tourist lodge and research centre and is therefore highly habituated to the presence of humans. During the final week of filming in November 2019, the troop consisted of eleven adult females, one subadult/large juvenile female, eight resident adult males, three peripheral adult males, one subadult/large juvenile male, approximately 15 unidentified juveniles, and an indeterminate number of infants. Videography was completed by Lucy Baehren in 2018 and JM in 2019 (Baehren & Carvalho, 2022). Videos were taken opportunistically of groups of individuals, with focal group rotated throughout the day. The troop often spreads across large sections of the research centre, with some individuals staying behind at a resource, following those who move on later. All troop members typically rejoin by the late afternoon before moving outside of the research centre area to return to other foraging and sleep sites in the surrounding savannah woodland. Further randomisation could not be done because troop members had not yet been identified at the time of filming. However, individuals were identified over the course of the 2019 field season and could be identified in video footage, making it possible to control for individual identity *post hoc*. Research permits were approved by Gorongosa National Park (PNG/DSCi/C145/2019 (J. Muschinski) and PNG/DSCi/C110/2018 (L. Baehren)) and ethics approved by the University of Oxford Animal Welfare and Ethical Review Board (APA/1/5/ACER/10Dec2018).

Gombe National Park: Video footage in Gombe National Park was collected through collaboration with Mr Nuhu Buke and Dr Anthony Collins between January and May 2021 and between August and September 2021. The national park covers approximately 52 km^2 of savannah woodland, dense gallery forests, open deciduous woodland, and fishing beaches running along Lake Tanganyika (Müller-Graf et al., 1996; Nash, 1976; Ransom, 1981; Van Lawick-Goodall, 1968). The park has a length north to south of approximately 16 km and has ten main valleys that span it from east to west (Ransom, 1981). Primates (including baboons, chimpanzees, vervets, red colobus monkeys, red-tailed monkeys, and blue monkeys) are the most common fauna in the park and experience relatively high food and sleeping site availability along with low predation pressure (Ransom, 1981). The

baboons in the park are classified as olive baboons (*P. anubis*), with genomic evidence suggesting they belong to the central olive baboon clade (Roos et al., 2018, 2021). Videos were recorded of the AC Troop by Nuhu Buke as part of the long-term data collection project at the field site (permit numbers 2020-287-NA-1990-170 and 2021-447-NA-1990-170 (Anthony Collins)). The troop ranges around the research camp, similarly to the Chitengo Troop in Gorongosa, and consists of 36 individuals, four being adult males, nine adult females, three subadult females, four subadult/large juvenile males, one large juvenile female, and 15 small/medium juveniles (personal comm., A. Collins). Individuals followed were randomised, with videos taken opportunistically of any proximity events occurring in the followed subgroup when the dense vegetation would allow.

6.2.2 Data collection and preparation

Observational data were collected from video recordings any time a proximity event was identified. Proximity events were defined as any instance where an individual approached a conspecific from outside of five meters to within two meters [estimated based on body length; Rutenberg et al. (1987); J. Altmann et al. (1993); Levy et al. (2023); Leigh (2009)]. All adults, subadults, and large juveniles (cut-off of four years for females and five years for males) were included, with ages estimated based on physical features where age was unknown (Alberts & Altmann, 1995; J. Altmann et al., 1981; J. Altmann & Alberts, 1987; J. Altmann & Alberts, 2005; Charpentier et al., 2008; C. J. Jolly & Phillips-Conroy, 2003; Packer, 1979). Data collection began when the approacher entered a five meter radius of the recipient and the "initial interaction" of the proximity event was considered to have been completed when the approacher had arrived at the recipient and either sat down, begun walking away, foraging, grooming, resting, or being groomed, or had again begun distancing after having diverted, stopped-short in their approach, or passed by the recipient without interaction. Events were excluded where less than half of the total event had been filmed, where the interaction was triadic, or where the approacher signalled towards

more than one recipient. Following these exclusions, a total of 379 observations from Gorongosa and 133 observations from Gombe remained.

The ethogram used to collect data for this project was developed previously and is publicly available (Muschinski & Carvalho, 2023a). See Figure 6.1 for examples of signalling during recorded approaches. Ethogram items were removed for the event size and entropy analyses if they were highly likely to be primarily functional (e.g., foraging while approaching, bipedal locomotion due to using arms to carry an item, nursing an infant) or could be considered an outcome (e.g., arriving or grooming the recipient's infant). A total of 54 ethogram items were included in the event size and entropy analyses. Video coding was completed using BORIS version 7.10.2 (Friard & Gamba, 2016). Both Gorongosa and Gombe datasets were coded by JM. The observations were then filtered based on the identifiability of the approacher, facial visibility, and audibility of vocalisations depending upon analysis (see below). The recipient sex data subset included interactions among and between females and males (referred to as "sex combination" below). All interactions involving females with sexual swellings, who were likely pregnant (identified by red paracallosal skin (S. Altmann, 1973)), or carrying an infant were removed from this subset, as these factors may significantly alter the level of risk for the approacher. The second set of analyses (referred to as "infant presence" below) compared approaches towards adult males by females with infants (either carrying or within five meters). Females with visible swelling and those for which maximum sexual swelling could not be ruled out were excluded from analysis. Approaches by pregnant individuals (exhibiting red paracallosal skin) towards males were removed from the analysis as the sample size was too small (n = 3). All data cleaning and analysis were performed using Python version 3.8.5 and R version 4.3.0.

6.2.3 Contact probability

Sex combination prediction: *Individuals approaching males are less likely to participate in contact behaviour than those approaching females.*

Figure 6.1: Examples of signalling during approaches in chacma and olive baboons. From top left to bottom right: two types of hind-quarter touch, presenting, mounting, infant observation, and ear-flattening

Infant presence prediction: *Females with infants are less likely to participate in contact behaviour upon approach towards males than are females without infants.*

For this analysis we included all interactions where identity of the approacher was known, regardless of facial visibility or audibility level. In the sex combination analysis (n = 134), we included only approaches involving males or females without infants. In the infant presence analysis (n = 61), we included only approaches by females with or without infants towards males. Swelling females were excluded from both datasets. We collapsed all physical contact behaviours occurring during the proximity event's initial interaction into one binary output variable and used a Bayesian hierarchical logistic regression model with a Bernoulli distribution and logit link function [*brms* package; Bürkner (2018)]. For the sex combination analysis, our model included fixed effects of approacher's sex, recipient's sex, an interaction between approacher's sex and recipient's sex, and a random effect of approacher identity to account for repeated sampling. Weakly regularising priors were set for the β_0, β_1, and β_3 coefficients (Gelman et al., 2020; Kurz, 2023;

McElreath, 2020), as no relevant published data could be identified to set priors. The prior for β_2 was weakly informative, set based on the odds ratio of "contact greetings" in male-male versus male-female interactions calculated from rates of greeting reported by Kalbitzer et al. (Kalbitzer et al., 2015). This paper compared approach interactions across sexes in Guinea and chacma baboons, providing information on rates of contact in the supplementary material (Kalbitzer et al., 2015).

$$
\begin{aligned}
\text{Contact}_i &\sim \text{Binomial}(n = 1, p_i) \\
\text{logit}(p_i) &= b_{0i} + \beta_1 \text{approacher\_male}_i + \beta_2 \text{recipient\_male}_i + \\
&\quad \beta_3 \text{recipient\_male}_i \text{approacher\_male}_i \\
\text{b}_{0i} &= \beta_0 + u_{0i} \\
u_{0i} &\sim \text{Normal}(0, \sigma_0) \\
\beta_0 &\sim \text{Normal}(0, 1.25) \\
\sigma_0 &\sim \text{Exponential}(1) \\
\beta_1 &\sim \text{Normal}(0, 1) \\
\beta_2 &\sim \text{Normal}(-1.087, 1) \\
\beta_3 &\sim \text{Normal}(0, 1)
\end{aligned}
$$

For the infant presence analysis, our model included a fixed effect of approacher infant presence and a random effect of approacher identity. All priors were set to be weakly regularising as no prior information was available regarding probability of contact in interactions with versus without the approacher's infant.

$$
\begin{aligned}
\text{Contact}_i &\sim \text{Binomial}(n = 1, p_i) \\
\text{logit}(p_i) &= b_{0i} + \beta_1 \text{approacher\_infant}_i \\
\text{b}_{0i} &= \beta_0 + u_{0i} \\
u_{0i} &\sim \text{Normal}(0, \sigma_0) \\
\sigma_0 &\sim \text{Exponential}(1) \\
\beta_0 &\sim \text{Normal}(0, 1.25) \\
\beta_1 &\sim \text{Normal}(0, 1)
\end{aligned}
$$

Additionally, we attempted to account for recipient identity and species (chacma or olive) for both models, but these more complex models did not converge due to the small sample size. Prior predictive checks were run before analysis to ensure priors were appropriate. For both sets of models we ran four sampling chains, each with a total of 2000 iterations (1000 warm-up iterations, 1000 post-warm-up samples). Model fit was assessed via graphical posterior predictive checks (grouped bar plots; see Appendix G). Model convergence was assessed using trace plots, R-hat values, and bulk and tail effective sample sizes. The *brms* package (v. 2.20.4: Bürkner, 2018) was used for all analysis, along with *tidybayes* (v. 3.0.6: Kay, 2023), and *bayesplot* (v. 1.10.0: Gabry et al., 2019) for plotting and further model checks. Analysis scripts were modelled after Kurz (2023) both for the contact analyses and for the following event size analyses.

6.2.4 Event size

Sex combination prediction: *Individuals approaching males are likely to use less complex signalling (smaller event size) during their approach than those approaching females.*

Infant presence prediction: *Females with infants are likely to use less complex signalling (smaller event size) during their approach towards males than are females without infants.*

Repertoire size is an often used, simplified measure of the communicative complexity within a system (Freeberg et al., 2012). We here used event size as a measure of the communicative complexity within an individual observation, with event size defined as the number of unique elements exhibited by the approacher before and during the initial interaction. As we limited this analysis only to proximity events with high visibility (i.e., facial expressions were visible and audibility high enough to identify vocalisations), sample sizes were reduced (sex combination: n = 69; Infant presence: n = 35). Following calculation of each observation's event size, we used Bayesian hierarchical regression models with Poisson distributions and log

link functions to model the event size in each of the two analyses (*brms* package: Bürkner, 2018). The model for the sex combination analysis was as follows:

$$
\begin{aligned}
\text{Event\_size}_i &\sim \text{Poisson}(\lambda_i) \\
\log(\lambda_i) &= b_{0i} + \beta_1 \text{approacher\_male}_i + \beta_2 \text{recipient\_male}_i + \\
&\quad \beta_3 \text{approacher\_male:recipient\_male}_i \\
\text{b}_{0i} &= \beta_0 + u_{0i} \\
u_{0i} &\sim \text{Normal}(0, \sigma_0) \\
\beta_0 &\sim \text{Normal}(0.7520, 0.8326) \\
\beta_1 &\sim \text{Normal}(0, 0.5) \\
\beta_2 &\sim \text{Normal}(0, 0.5) \\
\beta_3 &\sim \text{Normal}(0, 0.5) \\
\sigma_0 &\sim \text{Exponential}(1)
\end{aligned}
$$

And the model specification for the infant presence analysis was:

$$
\begin{aligned}
\text{Event\_size}_i &\sim \text{Poisson}(\lambda_i) \\
\log(\lambda_i) &= b_{0i} + \beta_1 \text{approacher\_infant}_i \\
\text{b}_{0i} &= \beta_0 + u_{0i} \\
u_{0i} &\sim \text{Normal}(0, \sigma_0) \\
\beta_0 &\sim \text{Normal}(0.7520, 0.8326) \\
\beta_1 &\sim \text{Normal}(0, 0.5) \\
\sigma_0 &\sim \text{Exponential}(1)
\end{aligned}
$$

Weakly regularising priors were used for non-intercept coefficients for both analyses due to a lack of relevant prior information. The intercept prior was set assuming a mean of four and a variance of three on a count scale (lognormal distribution) based on the numbers of signals mentioned in previous descriptions of male-male greeting behaviour (Colmenares, 1990; Dal Pesco & Fischer, 2018, 2020; Kalbitzer et al., 2015; Smuts & Watanabe, 1990). The parameters of the

prior Normal$(0.7520, 0.8326)$ were estimated using the method of moments (Kurz, 2023) and checked via prior predictive simulation checks.

As above, graphical prior predictive checks, posterior predictive checks, and model convergence assessments were performed (see Appendix G). Posterior predictive checks of sample mean and variance were used to check for overdispersion and to confirm that a Poisson model was appropriate.

6.2.5 Entropy

Sex combination prediction: *Individuals approaching males have more predictable (lower entropy ratio) signalling during approach than individuals approaching females.*

Infant presence prediction: *Females with infants have more predictable (lower entropy ratio) signalling during approach towards males than females without infants.*

Entropy is a measure of the potential information and diversity of signal combinations contained in a system (Freeberg et al., 2012; Peckre et al., 2019; Pika, 2017; Shannon, 1948). It can be used to measure the uncertainty or randomness in a set of possible outcomes. Shannon entropy is calculated as follows:

$$H(X) = -\sum_{i=1}^{n} P(x_i) \log_2 P(x_i)$$

where:

- $H(X)$ is the entropy of the random variable X,
- $P(x_i)$ is the probability of the outcome x_i, and
- n is the number of possible outcomes.

The entropy and entropy ratio for each group of interest's approach interactions were calculated using the *NetFACS* package (Mielke et al., 2021). *NetFACS* is a package that allows for the analysis of the co-occurrence of behaviours using permutation tests and network analysis. The package uses simplified presence/absence

data for each element of interest for each observation and cannot be used to analyse order, length, intensity, or repetition of those elements (Mielke et al., 2021). Given a set of events, *NetFACS* calculates the observed entropy for the system using the above formula, and then also provides an "entropy ratio". The ratio is the observed entropy, calculated using the Shannon entropy formula above, divided by the "expected entropy". The expected entropy is the entropy of a randomised version of the dataset where the event size for each observation remains the same as the original dataset, but the signals are shuffled randomly between observations. Therefore, the expected entropy represents the maximum possible entropy in a system given the predetermined event sizes and the available signal repertoire. The ratio of observed entropy to expected entropy would then be very low in systems that are highly predictable, and closer to one in more complex systems that are less predictable.

As for the event size analyses, this analysis was limited to observations where facial visibility and audibility were good and where the identity of the approacher was known (sex combination: $n = 69$, infant presence: $n = 35$). To test the entropy-related hypothesis, we resampled each dataset with replacement 200 times and calculated the entropy ratios for each subpopulation (e.g., approacher females with infants versus approacher females without infants). Subtracting the entropy ratio of the "test population" from that of the "control population" for each resampled dataset allowed us to determine a 95% confidence interval for the difference in entropy ratios between conditions.

6.3 Results

6.3.1 Contact Probability

Models included random effects of approacher identity but did not account for species or recipient identity as this caused conversion issues for both datasets. For both models (sex combination and infant presence), chains mixed well, all R-hat

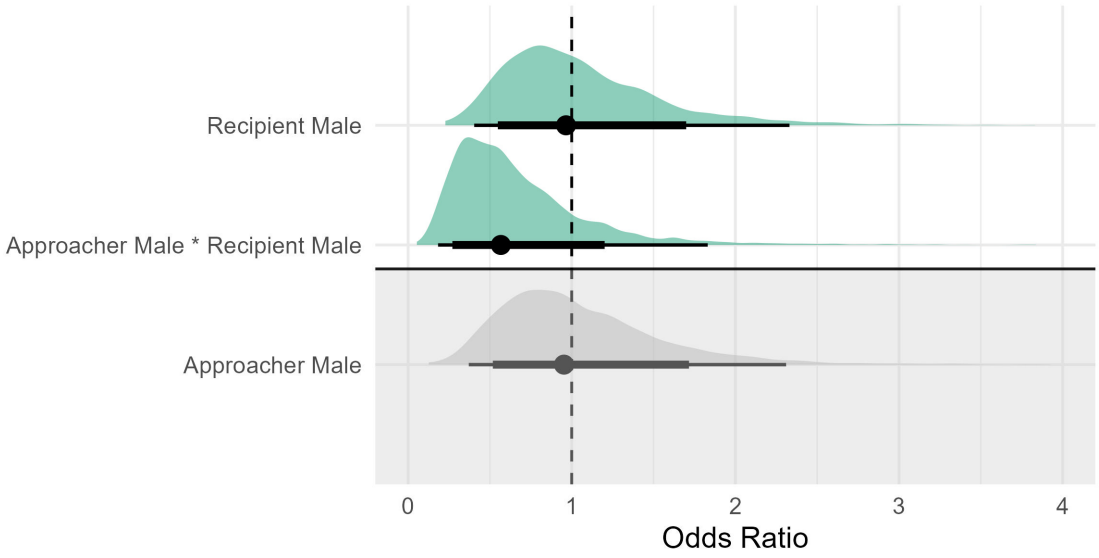

Figure 6.2: Posterior distribution of the odds ratios for model population-level effects. Thick and thin lines denote 80% and 95% credible intervals respectively. Hypothesis related odds ratios (i.e., recipient sex (reference category: male) and the interaction between recipient and approacher sex) are highlighted, while approacher sex (reference: male) is in grey.

values were below 1.01 (Vehtari et al., 2021), and bulk and tail effective sample sizes were acceptable (above 2190 for tail ESS and above 2900 for bulk ESS for fixed effects, and above 1830 for tail ESS and above 1550 for bulk ESS of random effects). For further model diagnostics, see Appendix G.

Contact by Sex Combination:

While the sex of the approacher and recipient individually did not appear to affect the likelihood of physical contact, results indicate that the interaction of approacher and recipient sex (i.e., where both approacher and recipient are male) may have had an impact on the probability of physical contact. While the 95% credible interval (CI) for the odds ratio of the interaction term included one (estimate: 0.569, CI: 0.183 to 1.836), 83.5% of the total posterior distribution was concentrated below one (see Figure 6.2). This indicates that under the assumptions of the model and the given data, there is an 83.5% probability that the true odds ratio for the interaction term falls under one.

This effect can be seen in the probability of contact for each sex combination,

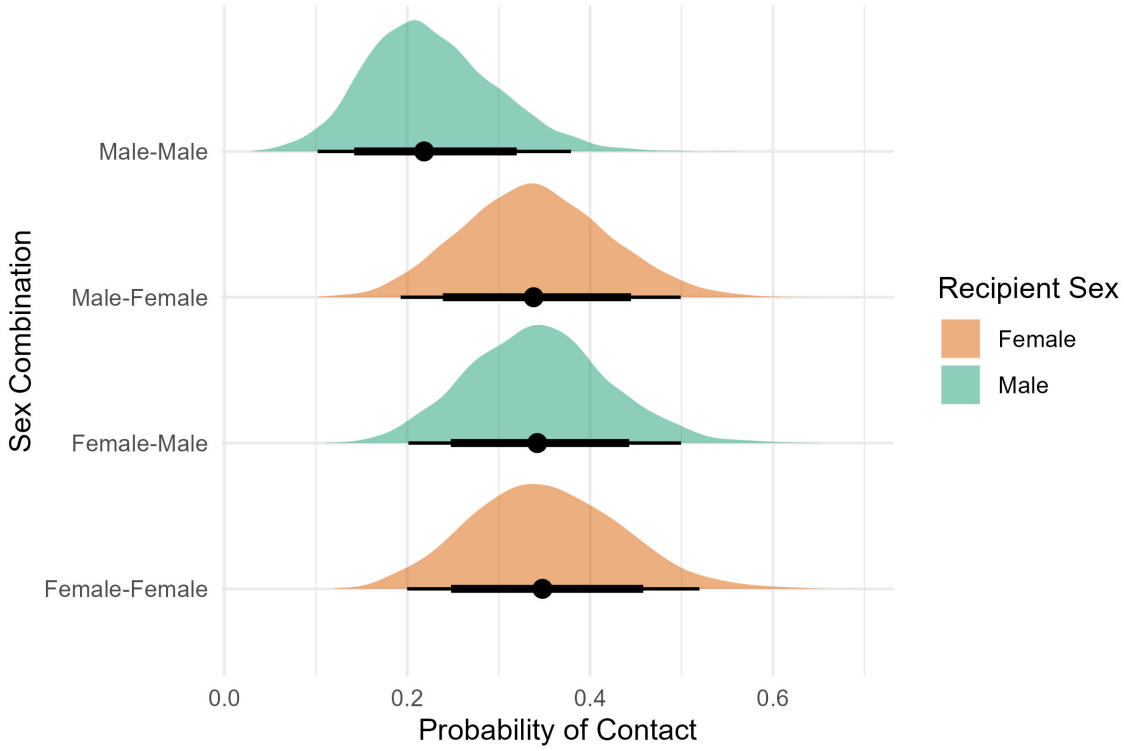

Figure 6.3: Posterior distribution of the probability of contact for each sex combination. Thick and thin lines denote 80% and 95% credible intervals respectively.

with the posterior distributions of the probability of contact in male-female, female-male, and female-female overlapping completely, but the probability of contact in male-male encounters being shifted lower (see Figure 6.3). However, overlap in the credible intervals (80% denoted by thick line and 95% denoted by thin line) for each sex combination indicates the limited confidence in these conclusions.

Contact by Approacher Infant Presence:

The odds ratio estimate for approacher infant presence was 0.539 (CI: 0.189 to 1.504). The credible interval for the odds ratio includes one, indicating that there is no strong evidence of an effect of infant presence (see Figure 6.4). We found that 87% of the posterior distribution of the odds ratio falls under one. As with the previous contact model, this indicates that given the model assumptions and data, there is an 87% probability that the true odds ratio for infant presence falls below one.

This was reflected in the posterior distributions of the probability of contact for

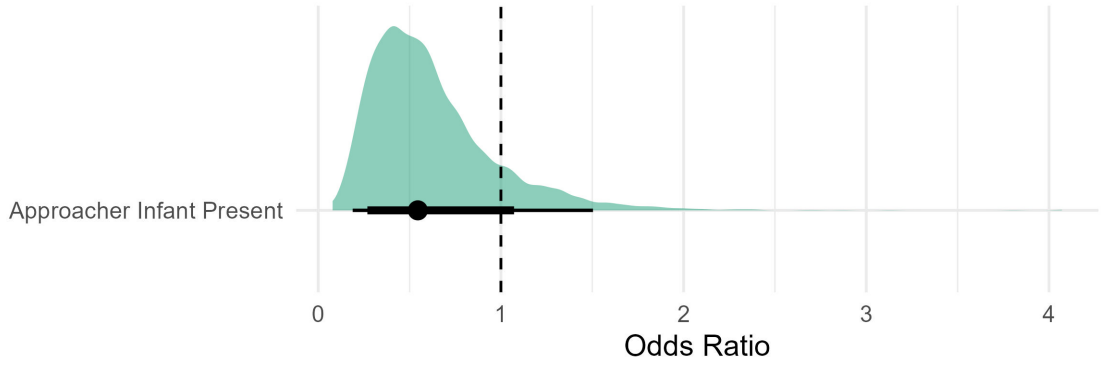

Figure 6.4: Posterior distribution of the odds ratios for approacher infant presence. Thick and thin lines denote 80% and 95% credible intervals

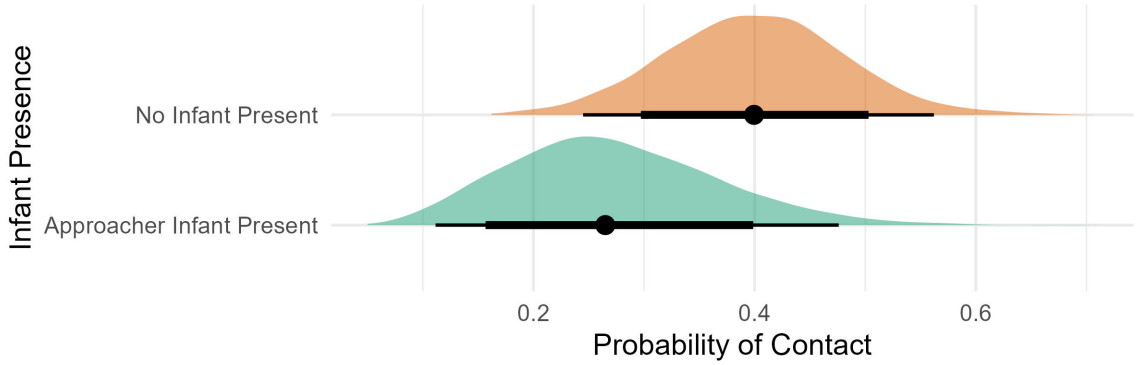

Figure 6.5: Posterior distribution of the probability of contact for approachers with and without infants. Thick and thin lines denote 80% and 95% credible intervals respectively.

approachers with and without infants. The estimate for the probability of contact was 0.273 (CI: 0.111 to 0.476) in interactions involving approachers with infants and 0.400 (CI: 0.245 to 0.562) where the approacher did not have an infant (see Figure 6.5). The large overlap in credible intervals indicates limited confidence in the effect of infant presence on contact behaviour. The width of the posterior distributions' credible intervals (see Figure 6.5) indicates that the precision of the estimates is low.

6.3.2 Event Size

Final event size models included random effects of approacher identity. Adding any further random effects (species or recipient identity) caused conversion issues for both datasets. Final models for both datasets converged well; all R-hat values were below 1.01, chains mixed well, and bulk and tail effective sample sizes were

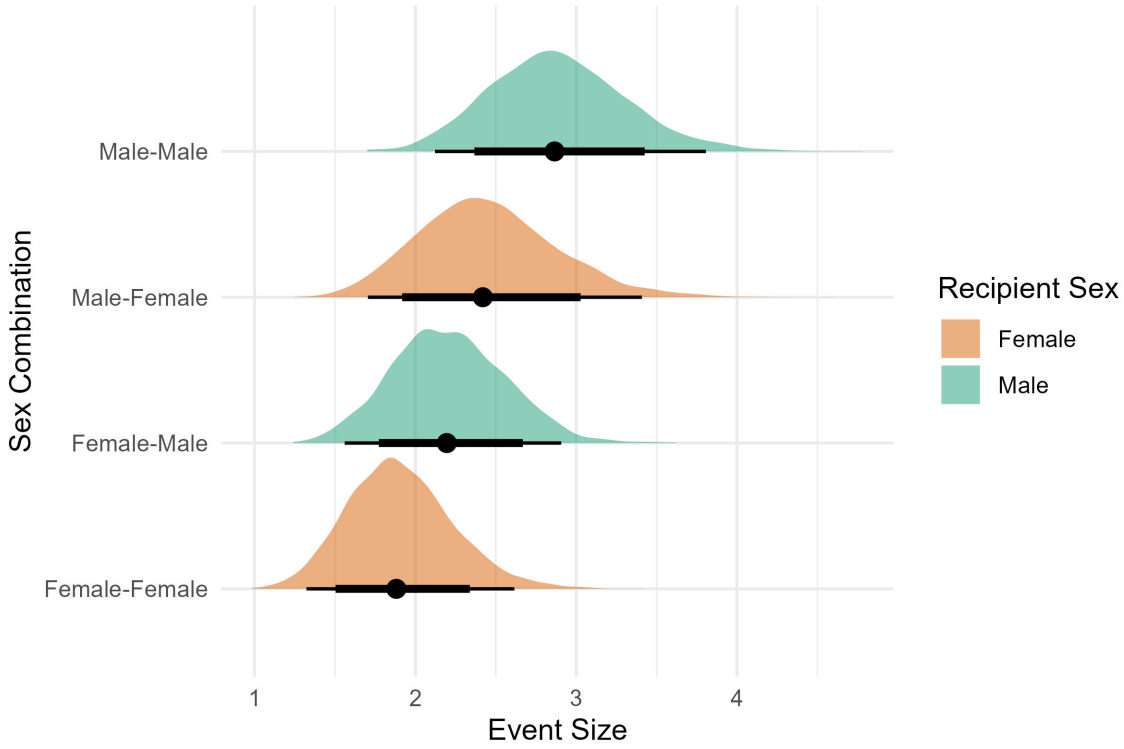

Figure 6.6: Posterior distribution of event size by sex combination. Thick and thin lines denote 80% and 95% credible intervals respectively.

acceptable (above 1300 for bulk ESS and above 1800 for tail ESS for random effects and above 1800 bulk ESS and 2200 tail ESS for fixed effects). Data were not overdispersed and a Poisson model was appropriate for both datasets. Further detail regarding model diagnostics can be found in Appendix G.

Event Size by Sex Combination:

Posterior distributions of event size by sex combination exhibited no clear differences by sex combination or by recipient sex (see Figure 6.6). Estimates for all coefficients were near zero (see Table 6.1).

Table 6.1: Coefficient estimates for event size by sex combination model.

Coefficient	Estimate	Est.Error	Q2.5	Q97.5
Approacher Male	0.251	0.222	-0.173	0.676
Recipient Male	0.149	0.208	-0.261	0.555
Approacher Male : Recipient Male	0.019	0.259	-0.487	0.519

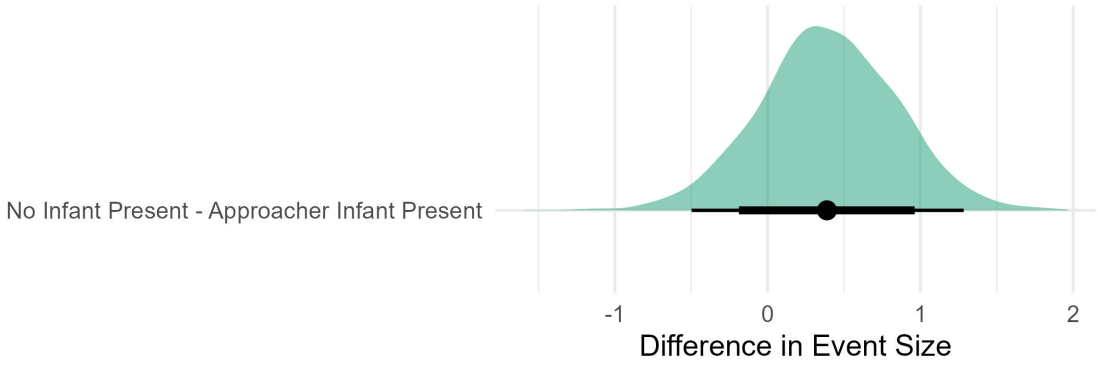

Figure 6.7: Posterior distribution of difference in event size between approaches without and with infants. Thick and thin lines denote 80% and 95% credible intervals.

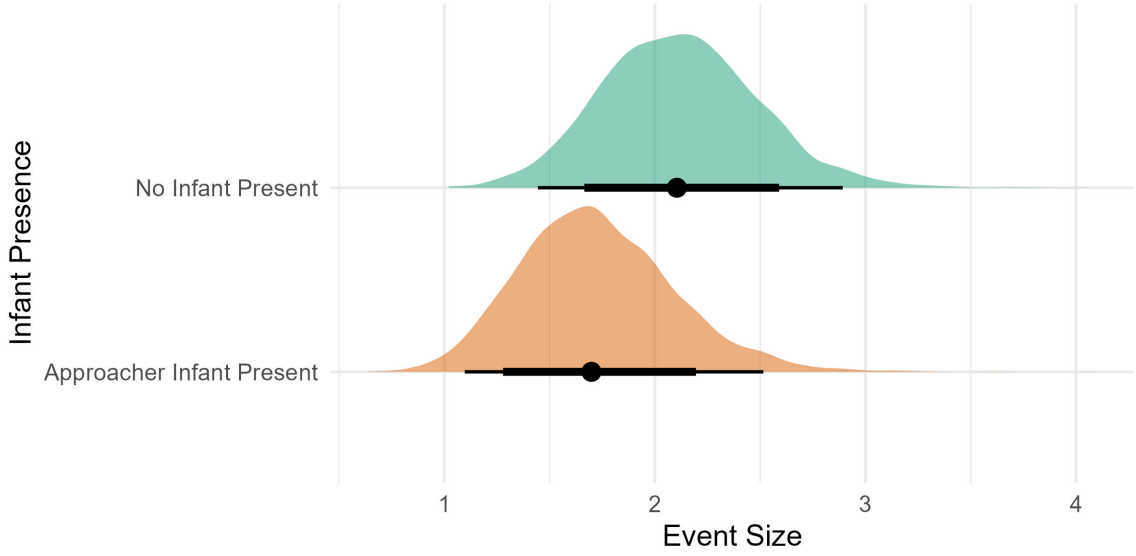

Figure 6.8: Posterior distribution of event sizes with and without approacher infant presence. Thick and thin lines denote 80% and 95% credible intervals.

Event Size by Approacher Infant Presence:

Posterior distributions of event size by approacher infant presence provided weak to no support for a potential effect of infant presence. The mean difference between the event size of approaches without infants versus with infants was 0.394 (CI: -0.498 to 1.284; see Figure 6.7).

The mean estimated event size for approaches with infants was 1.724 (CI: 1.097 to 2.515) and without infants was 2.118 (CI: 1.444 to 2.892) (see Figure 6.8). Again, the level of overlap indicates limited confidence in the effect of infant presence.

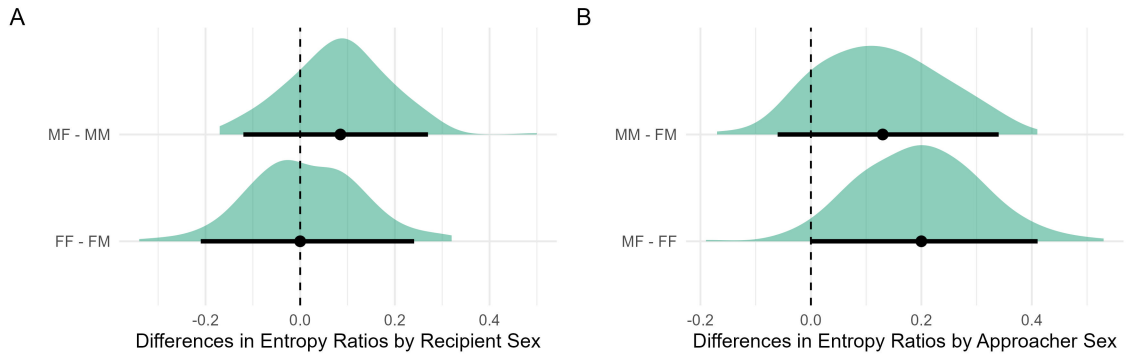

Figure 6.9: Bootstrapped differences in entropy ratio by recipient sex (A) and approacher sex (B). The thick line denotes the 95% confidence interval. The dashed line provides a reference for a difference of zero between sex combinations. A significant difference can be seen in (B) comparing male-female approaches to female-female approaches.

6.3.3 Entropy

Entropy by Sex Combination:

Contrary to expectation, there were no significant differences in entropy ratio by recipient sex, but differences did exist by approacher sex (see Figure 6.9). The mean difference in entropy ratio between male approaches and female approaches towards females was 0.20 (95% confidence interval: 0.00 to 0.41) and between male approaches and female approaches towards males was 0.13 (95% confidence interval: -0.06 to 0.34). Bootstrapped entropy ratio estimates by sex combination can be seen in Table 6.2. These findings indicate the entropy of male approaches tended to be higher than the entropy of female approaches (when recipient sex remained constant).

Table 6.2: Bootstrapped entropy ratio estimates by sex combination.

Sex combination	Mean	SD	CI lower	CI upper
Female-female	0.60	0.09	0.44	0.78
Female-male	0.59	0.08	0.45	0.73
Male-female	0.80	0.06	0.68	0.91
Male-male	0.72	0.08	0.58	0.84

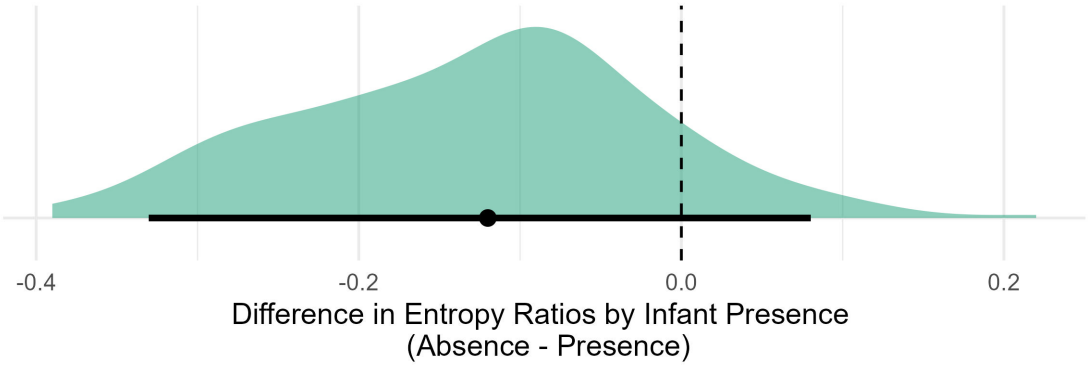

Figure 6.10: 95% confidence intervals of entropy ratio differences by infant presence.

Entropy by Approacher Infant Presence:

As for sex combination, no significant differences in entropy ratio were found comparing approaches with and without infants (see Figure 6.10). The 95% confidence intervals for the entropy ratio estimates for infant presence (mean: 0.71; CI: 0.58 - 0.87) and infant absence (mean: 0.59; CI: 0.40 - 0.72) provide no support for differences in entropy ratios between the two conditions.

6.4 Discussion

We hypothesised that the level of risk posed by the recipient to the approacher would affect the approacher's signalling, with higher levels of risk associated with clearer and less physical signalling to avoid miscommunication or unintended altercations. We considered two types of risk: first, risk posed by the sex of the recipient (i.e., a male recipient would pose a higher risk than a female recipient), and second, by the approacher's infant status (i.e., a female with an infant should perceive greater risk when approaching a male than does a female without an infant). While some previous studies have found support for more stereotyped, less variable communication in higher risk scenarios (e.g., Clark et al., 2022), other studies have suggested that redundant signalling (i.e., using multiple signals with the same underlying message) can be used to ensure intended messages are received (Higham & Hebets, 2013; Johnstone, 1996; Partan & Marler, 1999, 2005).

6. Complexity, risk, and physical contact

Comparing the likelihood of physical contact between approachers interacting with males versus with females provided weak evidence indicating that male-male encounters may be less likely to include contact than male-female or female-female encounters (even when females were not in oestrus or nursing). In line with our hypothesis, this "special case" of male-male encounters is likely due to the high level of male competition present in baboons, chacma baboons in particular, which would translate to increased risk during approach (Barrett & Henzi, 2008; Kalbitzer et al., 2015). The likelihood of contact in approaches by non-swelling females without infants did not differ depending on the sex of the recipient.

When we compared how females with infants differed from those without infants in their approaches toward males, we found limited to no evidence for a difference in the likelihood of contact by infant presence. The odds ratio estimate for approacher infant presence was 0.539, indicating a potential decrease in the likelihood of contact when the approacher has an infant with them. However, as the credible interval included one, with 87% of the posterior distribution falling below one, evidence for this effect is weak. Beyond the limited sample size, this could also be a result of which males females choose to approach. Females with infants have been shown to approach males who are "friends" more often than those who are not (Smuts, 1985). Male-female friendships have been reported across several *Papio* species and provide protection to the female's infant and may be a form of male parental care (Lemasson et al., 2008; Moscovice et al., 2010; Nguyen et al., 2009; Palombit, 2015; Smuts, 1985). While friendship status has been reported to be positively associated with physical contact such as grooming, it has also been shown to be negatively associated with presenting (Smuts, 1985). As such, friendship-status and differences in the likelihood of approaching friend versus non-friend males may influence our findings. Future studies should investigate how signal use, physical contact, and partner choice relate to male-female friendships. Identifying consistent signalling differences associated with friendship status could help identify female-male friendships in new study troops where long-term association data has not yet been collected. Completing a study similar to the one here but comparing across

the phases of cycling females could provide additional insight into the dynamics of risk and approach behaviour, as past studies have shown that cycling females are at highest risk of injury by males around the time of ovulation (Archie et al., 2014).

We found little support for our hypotheses regarding event size. There was no difference in event size by recipient sex, with substantial overlap in the 95% credible intervals of all sex combinations. Similarly, the evidence for a difference in event size with the presence and absence of an approacher's infant was weak. Females with infants had an average event size of 1.7, while females without infants on average used 2.1 unique signals, but the 95% credible intervals overlapped considerably. Based on the average event sizes for each category of approaches, it appears approaches between baboons in general have low event sizes. This, combined with the small sample size and lack of prior information likely contributed to the wide credible intervals.

We hypothesised that the entropy ratio would be lower in interactions where the risk posed to the approacher was higher. A lower entropy ratio would indicate that signalling in that condition was more predictable. We expected that the need for signalling clarity to avoid miscommunication would result in higher predictability, and therefore a lower entropy ratio. Results for both datasets showed no identifiable differences between higher and lower risk conditions. While we did not find reliable differences by recipient sex as initially hypothesised, we did note differences in entropy ratio by approacher sex. Male approachers tended to have a higher entropy ratio than female approachers, regardless of whether they were approaching males or non-swelling females without infants. This runs contrary to our expectations, as we predicted that male-male events, which have been described as "ritualised" (Colmenares et al., 2000; Dal Pesco & Fischer, 2018, 2020; Smuts & Watanabe, 1990; Whitham & Maestripieri, 2003), would be highly predictable. Our results indicate that males tend to use signals less predictably in their approaches towards conspecifics than non-swelling females do, where neither a recipient's nor approacher's infant is present. It is possible that males may be more likely to change their signalling due to other factors such as a recipient male's rank or

their friendship or lack thereof with a recipient female. The difference in entropy ratios between female and male approachers was stronger in approaches towards females. It may be that the complexity of signalling is also affected by the level of familiarity between individuals, with females in a female philopatric species already having enough security about the outcome of interactions due to their extensive interaction history and secure rank relationships that fewer signals are required. For example, while females approaching other females with infants tend to grunt, this is less common in interactions between mothers and daughters (Silk et al., 2016, 2018). Individuals who are less familiar with each other, on the other hand, may combine multiple benign intent signals to reassure the recipient. While 95% credible intervals overlapped, female-female events in our sample also had the lowest average event sizes. Males may combine affiliative signals more broadly and in more combinations as a result of less secure relationships. Males also might adjust their signalling repertoire when immigrating. As such, when considering signalling in a troop's males, we might see more variable signal combinations compared to a troop's females, who remain in the same troop throughout their lives. We should note here that the small sample size for both datasets is particularly problematic for entropy calculations given the relative complexity of this type of metric compared to identifying event size or the presence of physical contact.

Overall, our results provide some support for the hypothesis that level of risk posed by the recipient to the approacher is related to the complexity and physicality of approacher signalling. Given the limited sample sizes for both the infant presence and approacher sex analyses, the differences in contact between sex combinations (in particular male-male approaches), along with the differences in entropy ratio by approacher sex, though not recipient sex, are notable. A larger sample size in future would give further insight into whether any of the identified trends represent consistent differences. Analyses were also limited by the inability to account for observations with repeated recipients, meaning that some non-independence between observations could not be accounted for. Rank and familial relationships were unknown for the study troop and therefore could not be included in analysis.

Rank has been shown to influence inter-individual encounters and signalling in baboons, for example wahoo displays differ by rank and males are more likely to engage in a wahoo display with a similarly ranked opponent (Fischer et al., 2004; Kitchen et al., 2003; Kitchen et al., 2005). Future studies should incorporate rank, familial relationships, and data on between-sex and within-sex friendships, as we would expect risk to stratify within our suggested risk categories based on these variables. Further work is also needed on how to measure or identify appropriate proxies for risk within interactions. Risk may also need to be considered both in regard to immediate outcomes (i.e., injury or access to resources) and ultimate outcomes (reproductive success). We argue that while the frequency of aggression by males towards cycling females may be higher than towards those that are nursing or pregnant (Baniel et al., 2017), the average ultimate risk outcome is still higher for pregnant or lactating females as they may quickly lose an infant to male aggression.

Even accounting for these limitations, this study provides a valuable proof of concept, indicating intra-troop signalling is variable with infant presence and sex combination, both proxies for different types of risk. Physical contact was found to be least likely in male-male encounters compared to other sex combinations and signalling in approaches by males appeared less predictable than approaches by females, particularly towards female recipients. Differences in event size were unclear both for sex combination and infant presence, as were differences in the likelihood of contact and entropy ratio for infant presence. The results of this study show that these measures could be useful ways of investigating the impact of risk on signalling modality and complexity and should be further explored, in particular considering the effects of relationship strength, rank, and kinship between individuals.

6.5 Acknowledgements

We greatly appreciate the work of our collaborator Lucy Baehren, who recorded many hours of footage in Gorongosa National Park. We would also like to thank the

staff of Gorongosa National Park, in particular Marc Stalmans, Jason Denlinger, and all rangers who worked with us in the field, including Ernesto Xavier and Sérgio Joao Amaral, without whom this work would not have been possible. The authors are most grateful for the vision of Greg Carr and support of the Gorongosa Restoration Project. This work was funded through grants from the Boise Trust Fund administered by the Oxford University Department of Zoology, the Owen Aldis Scholarship awarded by the International Society for Human Ethology, and further grants from St John's College, University of Oxford and the Clarendon Fund, University of Oxford. Alexander Mielke was funded by a Leverhulme Trust Early Career Fellowship.

7 Discussion

The overall objective of this thesis was to identify how risk shapes communication at the individual and species level, using baboons as a model. Communication during approaches between conspecifics was used as a test case, as this is when interactions are opened and access to personal space negotiated. Sex combination and infant presence were used as proxies for risk throughout the thesis, with expected risk differing due to the high level of sexual dimorphism, male-male competition, and infanticide exhibited in baboons (Dal Pesco & Fischer, 2020; Palombit, 2003). The research considered signals in combination and across signalling modalities, rather than focusing on gestural, vocal, or orofacial signals separately (Amici et al., 2022). This provides a more integrated perspective than previous research on baboon signalling and complements ongoing work into multimodality and compositionality across primate communication (Amici et al., 2022).

7.1 Summary of findings

This thesis has presented three empirical chapters, each focused on a different aspect of baboon approach behaviour. Within baboons, the existing approach behaviour literature is splintered, with many studies focused on specific sets of signals (e.g., stereotyped male greetings: Smuts & Watanabe, 1990) or on individual signals

(e.g., grunting: Cheney et al., 1995; Faraut et al., 2019), rather than considering how signals are combined (Amici et al., 2022), how these combinations may differ depending on social factors such as sex of the approacher/recipient or infant presence, and how combinations may be related to differences in the outcomes of interactions. The overall aim of this thesis was to re-examine baboon approach behaviour, addressing these gaps and considering how risk impacts signalling.

The first empirical chapter (Chapter 4) addressed this on a species level, situating male-male greeting behaviour of chacma baboons within that of *Papio* at large. The study used video footage from Gorongosa National Park, Mozambique. There has been considerable discussion elsewhere of how various aspects of male-male sociality in baboons may be related to greeting behaviour (Dal Pesco & Fischer, 2020). Dal Pesco et al. suggest there is a link between lack of coalition formation or quality of male-male relationships with stereotyped male-male greeting behaviour on a species level (Dal Pesco & Fischer, 2020). Contrary to expectations based on previously published work, male-male encounters in Gorongosa National Park chacma baboons exhibited the same signals as those in olive, yellow, and hamadryas baboons, with similar rates of physical contact and reciprocity across greetings (see 7.3.2). The same signals identified in other male-male greeting literature were present at comparable rates across identified chacma baboon approaches, with ear-flattening occurring in 89% and lip-smacking in 42% of approaches by prime males. Of all identified greetings, 31% were found to involve physical contact, 13% intense physical contact (mounting, embracing, or genital contact), and 50% of completed greetings were physically reciprocal. I discussed the relevance of this within *Papio*, highlighting the Guinea baboon as the outlier among baboons, but also noting that what sets chacma baboons apart may be the high percentage of incomplete greetings (65%) that incorporate no signals besides ear-flattening, lip-smacking, and direct gaze. Towards the end of the chapter, I highlight the issues with the framework typically used to study male greeting in baboons, noting in particular the lack of consistent definitions and the circularity of defining a greeting as "any instance where a greeting behaviour occurs". I propose a new framework

for the study of male greeting in baboons, widening data collection to include all approaches where a distance-based proximity threshold is crossed. This type of framework would make more standardised comparison across field sites and species possible and would allow for data collection on the instances where males come in close proximity but do not exhibit the typical male greeting signals. I then apply such a framework in the following chapter, but widen the scope to include all sex combinations to study signal use during approach more broadly.

In the second empirical chapter (Chapter 5), we focused on signals used in individual interactions, comparing them across sex combinations and by recipient infant presence/absence. This chapter incorporated video footage from chacma baboons in Gorongosa National Park, Mozambique and olive baboons in Gombe National Park, Tanzania. We used a network analysis method (community detection) to identify groups of signals that were likely to occur together. We then compared these across sex combinations. We predicted there may be similarities in male-male and female-female encounters, as within these interactions individuals are interacting within their respective dominance hierarchies. In both of the included baboon species, male dominance hierarchy is established through competition, while female hierarchy is linked to matrilines (Fischer et al., 2019). Results for female-male and female-female interactions without a recipient's infant present were inconclusive, but the cluster of ear-flattening together with lip-smacking was identified in both same-sex combinations. Across all interactions, we identified three main themes in signalling - the first being ear-flattening co-occurring with lip-smacking, the second being a link between direct gaze or gaze avoidance with direct interaction versus passing without contact, and the third linking grunting and infant contact.

Based on these findings, we developed hypotheses regarding how these signals or signal combinations were associated with changes in the likelihood of physical contact with the recipient or recipient's infant where appropriate. We then used logistic regression models to test these hypotheses. We found that continued observation of an individual was predictive of making physical contact with that

individual, whether an adult or an infant. We discussed the relevance of this in relation to primates' ability to follow and detect gaze. Unexpectedly, grunting and the combination of ear-flattening with grunting were not associated with infant contact in our sample, but this could be due to other social factors (i.e., kinship) which we were unable to account for. Perhaps most interestingly, in interactions without recipient infants, combining ear-flattening and lip-smacking in the same approach was associated with a decrease in the likelihood of physical contact. This is in contrast to use of the individual signals, which are associated with an increase and no change in contact respectively. This could be an example of componentiality, discussed more below (see 7.3.1).

In the final empirical chapter (Chapter 6) we compared two measures of complexity (entropy and event size) and the likelihood of physical contact between different risk conditions in two datasets. We hypothesised that signalling would be clearer (fewer signals used, combined in predictable ways) in interactions where perceived risk to the approacher is higher. Repertoire size has been used in previous communication studies (Freeberg et al., 2012; Pika, 2017) to compare complexity of communication across species. Here, we used event size (number of unique signals used within one approach interaction) as a measure of complexity of the given signalling bout (Mielke et al., 2021). By comparing event sizes of interactions across risk conditions, we assessed whether interactions that pose higher or lower risk tended to involve more or fewer signals. Entropy, the second measure used, is a reflection of how predictably signals are combined across a group of observations, with a lower entropy indicating all observations are very similar, and a higher entropy indicating signals are used and combined more variably.

The first dataset included interactions between males and females without any infants present. We used recipient sex as a proxy for risk, with the assumption that perceived risk would be higher when approaching a male than a female. The second dataset included approaches towards males by females either with or without an infant. Here infant presence was used as a proxy for risk as we expected that approaching a male should pose higher risk to those females with infants than without

(Palombit, 2003). Bayesian posterior distributions provided limited evidence for differences in the likelihood of physical contact for both datasets, with contact less likely in male-male approaches than other sex combinations and in interactions with an approacher's infant present compared to absent. Models provided no support for differences in event size by infant presence or by sex combination. No differences in entropy ratio were found by recipient sex, but approaches by males exhibited a higher entropy ratio than those by females, suggesting male approachers may combine signals more flexibly than females. However, this could also be a result of differences in average event size, with mean event sizes being greater for male approaches than female approaches. No differences in entropy ratio were found by infant presence. While hypotheses regarding contact were weakly supported, hypotheses regarding complexity were mostly unsupported. This could be a result of sample size limitations, but could also indicate that other factors are the primary drivers of signalling complexity, that risk may increase signalling complexity as more redundant signals are combined to increase signal strength, or that the selected proxies for risk were not suitable.

7.2 Limitations

7.2.1 Video data

Use of video footage has many advantages, but collecting video footage and use of video archives can also present methodological issues. Video footage for this thesis was gathered from three sources, two of which (filmed by Lucy Baehren and myself) were recorded prior to the inception of this project. As discussed in Chapter 3, the largest source of footage was the video archive of a former PhD student (Lucy Baehren), who was recording for the purpose of studying leave-taking behaviours. While the filming methods were very similar to those that would have been implemented if the archive had been purpose made for this project, it came with several limitations. At the time of filming, individuals had not yet been identified, so videos could not be recorded in a way that was fully randomised

or independent. Similar issues were present in the footage recorded by myself in 2019, as I did not fully identify all individuals until towards the end of the field season. The field technician in Gombe, Nuhu Buke, faced severe visibility issues as a result of the vegetation, also making it difficult for him to follow the randomised list we created for focal follow videos. As such, video recording for this project were only pseudo-randomised, with efforts made to rotate through different sub-groups of individuals. I partially accounted for this by identifying individuals from footage *post hoc* where possible, and completing several sets of analysis (Chapter 6) incorporating a random effect of approacher identity using a Bayesian approach, which handles small sample sizes more effectively. However, individual identity could not be accounted for in Chapter 4, as many of the male-male encounters involved unidentified individuals from the Montebelo troop, or in Chapter 5, as the randomisation in NetFACS cannot account for repeated measures and because singularity issues arose in modelling when random effects were included due to the sample size. This may introduce issues of pseudoreplication (J. Whitehouse et al., 2023), which are clearly mentioned within the relevant papers. Observations are not evenly spread across all individuals, with what may be a bias in observations towards individuals who are higher ranked or currently very socially attractive (e.g., new mothers). Similarly, the small overall sample size poses limitations, in particular for behaviours or types of interactions that are very rare. Sample size limitations are partially addressed by using bootstrapping methods in Chapters 4 and 5 and by taking a Bayesian approach in Chapter 6. However, the underlying issue remains, as bootstrapping for example cannot account for events that simply are not observed due to how rare they are, but that do exist in the population. The sample size limitations are handled as well as possible given the limitations on data collection posed by the Covid-19 pandemic.

7.2.2 Lack of contextual data

The second set of limitations centre on data that was unavailable due to the relatively recent start to primatological study of the troops at Gorongosa National

Park. Prior to the start of my PhD, no members of the Chitengo troop in Gorongosa had been identified and no long-term behavioural data collected. Therefore, I did not have access to reliable rank, kinship, or social affiliation data. As detailed in Chapter 3, I began collecting dyadic interaction data (e.g., displacements) and social network data (i.e., nearest-neighbour, 5 m chain scan, and 10 m scan) once all individuals had been identified in 2019. However, data collection was unable to go on long enough to reliably assess rank or social affiliation (see Chapter 3). Bootstrapping of Elo rating results indicated rank data were not robust enough to be included in analyses. Similarly, social affiliation data collection did not go on long enough to allow for inclusion.

Missing rank, kinship, and social affiliation data are particularly relevant when comparing individual interactions. For example, in female-female interactions we expect kinship to influence grunting in approaches towards infants (Silk et al., 2018) or in female-male interactions friendship-status may affect the likelihood of a female avoiding an approach (Smuts, 1985). These types of factors would be expected to potentially have a strong effect on analyses focused on the use of individual signals, for example when investigating the relationship between grunting and infant contact in Chapter 6. The hypotheses of papers included here were designed to limit the effect of these factors where possible by focusing on larger categories such as sex combination and infant presence. We expect the many varying social and kinship relationships to introduce noise into the analyses, but that overall identified patterns should remain relevant. For example, in entropy analyses, we hypothesised that male-male approaches would show more predictable signal use because there is generally less variability in the types of relationships two males can have with each other compared to two females.

7.2.3 Theory and generalisability

The thesis centres on the concept of "risk", but risk itself is not directly measurable and perception of risk will differ between individual members of a population. I focus primarily on sex combination, sex of the recipient, and infant presence as

indicators of risk for the approacher on an individual level. On the species level, male-male interactions in chacma baboons are assumed to be riskier than those in other species due to the higher general rates of competition and aggression (Henzi et al., 1999; Henzi & Barrett, 2003; Henzi & Barrett, 2005). However, when considering differences between individual troops of chacma baboons and troops from other species, other factors such as resource density, troop sex ratio, and troop size may play a significant role. Even on an individual level, perception of risk may not align with selective pressure that would affect the evolution of signalling. Especially when unable to account for personal relationships, measuring risk in an individual interaction becomes very difficult. I attempted to circumnavigate this by focusing on differences in risk which would be expected to hold regardless of interpersonal relationships; for example, a female baboon should be more concerned about risk of aggression when having an infant to care for than when she is alone, regardless of whether the male she is approaching is a friend or not. Even so, it is possible that these are not well-suited proxies for risk and that results should be interpreted primarily within the context of the measures themselves (i.e., sex combination and infant presence), rather than within the context of "risk".

As is the case with most primatological studies, it is difficult to know how generalisable the findings of the studies within this dissertation are beyond the field sites and populations in question. Throughout the history of primatology, there have been many instances where findings from individual field sites revealed differences with other study populations, and indeed this variation across populations is of interest in itself, highlighting the behavioural flexibility of the species we study (McGrew, 2004). The primary study population of this dissertation is classified as *Papio ursinus griseipes*, but phenotypic similarities and genetic evidence suggest previous gene flow with *Papio cynocephalus* (Santander et al., 2022). As such, it is possible that behaviour of the study troop is not typical for chacma baboons, but this in turn raises the question of what it means to be "typical." Without further study of additional baboon populations both within Gorongosa National Park and moving south further away from the hybridisation zone with yellow baboons, this

is not a question that can be answered yet. The papers in this thesis provide data points which help in triangulating answers to larger research questions which will only be answered across many years of research spanning multiple sites and species (Heale & Forbes, 2013). The theoretical and methodological contributions of this thesis also provide useful starting points for further study, highlighting promising areas of future research.

Finally, this thesis does not and cannot test causal relationships. Causal inference is an analytical framework which has gained a significant foothold in randomised control trial research and in epidemiology (Tennant et al., 2021), but is only now starting to enter ecological and behavioural sciences (Arif & Massey, 2023; Laubach et al., 2021). While in primatology we discuss findings in terms of "associations" and "correlations," we are fundamentally still primarily interested in causal relationships. Causal inference involves specifying a model based on confounders identified by developing a structural causal model that clearly outlines all variables which may influence the variable of interest (the exposure) and the outcome. These structural causal models can be visualised using directed acyclic graphs (DAGs), which are non-parametric diagrams depicting directional relationships between all involved variables. Figure 7.1 provides a very simplified depiction of what a DAG may look like for the outcome of a signal's use.

As can be seen from the DAG, there are many variables that would need to be accounted for to identify the causal effect of the signal of interest on the outcome, requiring both a substantial sample size and the ability to measure many variables that may in reality be very difficult or impossible to measure. In signalling research in particular, applying causal inference will prove very difficult, as the entire preceding signal exchange would need to be considered in analysis. While causal inference is likely to, and should, be integrated into aspects of primatological research in the future, the purpose of this brief explanation is to reinforce the issues associated with interpreting the results of these studies causally. This is particularly relevant when considering Chapter 5; while there was a negative association between the combined use of ear-flattening with lip-smacking and physical contact, this does

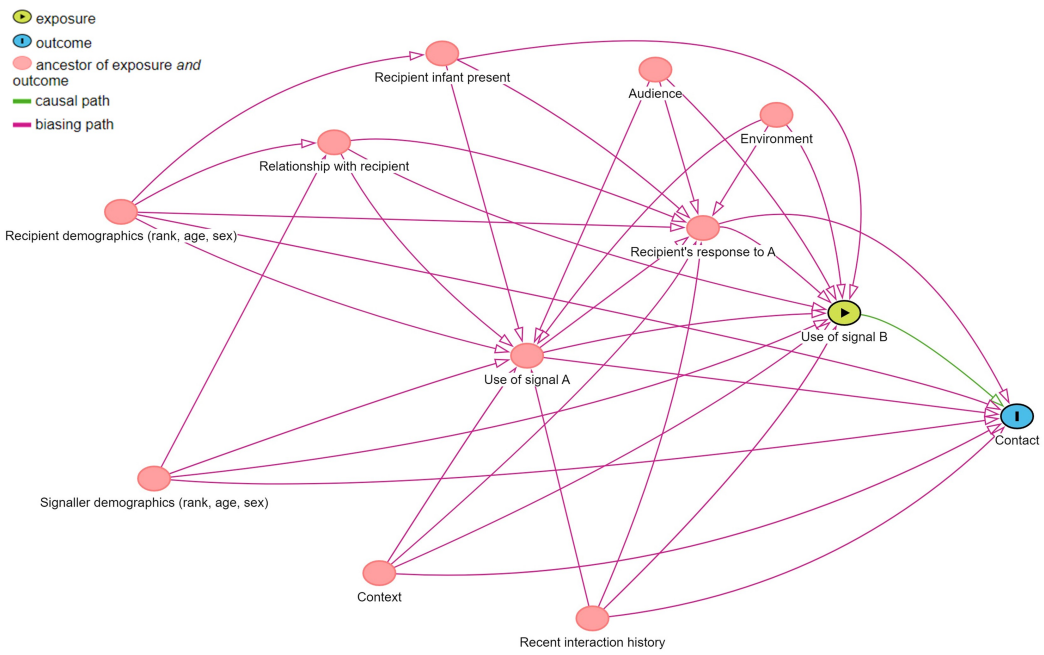

Figure 7.1: An example of a simplified directed acyclic graph focused on the causal relationship between use of signal B and resulting physical contact. Created using Dagitty (Textor et al., 2011).

not imply that the use of the two signals together necessarily caused this reduction in contact. It may be, for example, that the use of the two signals within the same interaction is more likely in particularly tense interactions, where physical contact is already much less likely to occur. These types of causal interpretations are outside of the scope of this thesis.

7.3 Contributions to the literature

The existing literature on approach interactions and greetings in baboons, along with much of the communication literature across other primate species, typically focuses on individual signals or modes of signals (Amici et al., 2022). The three empirical chapters of this thesis demonstrate the additional insight provided by considering how signals are combined. We also consider what larger-scale features of signalling bouts can tell us about communication, for example by investigating complexity through event size and entropy. No other study has done so for baboon

signalling, and the findings presented here complement existing work on how risk at a species level (e.g., steepness of dominance hierarchies in macaques: Maestripieri, 2005) and at an individual level can affect signalling. The three empirical studies also highlighted the usefulness of video footage in studying the details of approach signalling. When coding interactions *in situ*, it can be difficult to capture detailed information on signal use and order, making analyses such as those in Chapter 5 in particular, difficult. Baehren and Carvalho's (2022) use of the same video footage to study behaviours which occur prior to leave-taking highlights similar strengths, as leave-taking cannot be easily predicted and therefore is most efficiently studied retroactively from video footage.

7.3.1 Signal combinations and language

Chapter 5 highlighted how using a network-based approach extends what we currently know about negotiating access to interaction partners. We found evidence that combining of signals may be associated with a change in meaning compared to the use of the signals individually. When combinations matter, it does not suffice to understand the relationship between single signals and interaction outcomes, otherwise we are left only with a partial picture. In Chapter 5 the combination of lip-smacking together with ear-flattening was associated with a severe reduction in the likelihood of contact in the resulting interaction. This could be considered an example of componentiality, considered to be a precursor of compositionality (Oña et al., 2019). Oña et al. define componentiality as the "recombination of signals with different effects" (Oña et al., 2019). However, as discussed above, more research would be needed to identify the causal effect of combining the use of the two signals and the interaction outcome.

Compositionality is a fundamental feature of human language, reflecting the ability to convey complex meanings by combining simpler elements (Amici et al., 2022). This linguistic principle allows speakers to structure new expressions by arranging elements of a language. In the evolution of language, compositionality allowed for the communication of increasingly sophisticated concepts, fostering

social cohesion, and contributing to the adaptability and richness of language over time (Corballis, 2017). The underlying cognitive skills required for compositionality are however also relevant to communication through gestures (Goldin-Meadow & Brentari, 2017). Much of primate communication is multimodal, incorporating tactile or visual signals in addition to vocalisations, similarly to human communication (Arbib et al., 2008). In primates, vocalisations tend to be used less flexibly than other signal modes and gestural communication may have been a critical part of the evolutionary pathway of cognitive capacities necessary for language (Arbib et al., 2008; Rodrigues et al., 2021). Prototypical languages may have heavily or even primarily involved gestures rather than vocalisations (Armstrong, 2008).

The results of Chapter 5 complement findings in other species, indicating that combining signals may modify meaning. For example, in crested macaques, lip-smacking is combined variably with other visual or vocal signals, with the likelihood of affiliative contact by the recipient changing depending upon signal combination (Micheletta et al., 2013). When lip-smacks are combined with soft grunts, the likelihood of affiliative contact is higher, while it is decreased when combined with exposure of teeth (Micheletta et al., 2013). A study of how chimpanzees combine two gestures (stretched arm gesture and bent arm gesture) and two facial expressions (funnelled lip face and bared teeth face) found evidence for precursors to compositionality (Oña et al., 2019). Combining the bared teeth face with gestures in positive contexts impacted the receiver's likelihood of affiliation behaviour compared to use of the two gestures alone. The effect of adding the bared teeth face did differ, however, between the two gestures, which is at odds with definitions of compositionality that require that components have consistent meanings across combinations (Oña et al., 2019). The findings of Chapter 5 on the combination of lip-smacking and ear-flattening present similar evidence, though intentionality was not established. Research on signal combinations, together with investigating intentionality (see "Intentionality, gesture, and sequence") and turn-taking (Heesen & Fröhlich, 2022), can help identify which primate species

exhibit the cognitive skills that are fundamental building blocks required for human language (Rodrigues et al., 2021).

7.3.2 Risk at a species level

This thesis contributes substantially to what is known about male-male stereotyped greeting behaviour in chacma baboons, but also adds to the understanding of "male greeting" across primates more generally. Both through taking a more traditional approach to studying male-male greetings (Chapter 4) and by using a network-based analysis to identify clusters of signals that tend to co-occur (Chapter 5), the empirical work of this thesis identified similarities in male-male greetings of chacma baboons and the other baboon species (see summary above). Setting these findings into the larger context of *Papio*, we find rates of physical contact and intense physical contact in male-male greetings of chacma baboons are similar to those of the other female-philopatric species, but that they differ drastically from the Guinea baboons. Guinea baboons, characterised by exceptionally tolerant relationships between males, exhibit a much larger signalling repertoire between males, considered to be one measure of communicative complexity. Unlike the other *Papio* species, Guinea baboons regularly use more elaborate contact behaviour such as prancing and polonaise in their interactions, and male greetings are much more likely to involve contact (93.4%), intense contact (59.2%) and to be reciprocal (81.9%) (Dal Pesco & Fischer, 2018). The function of male greetings appear to differ slightly across *Papio*, with male greetings in Guinea baboons serving primarily to "strengthen in-group affiliation and promote cooperation" (Dal Pesco & Fischer, 2018, p. 87), while in yellow baboons they function to signal status, in olive baboons to negotiate or confirm social relationships, and in hamadryas baboons to buffer tension.

Chacma baboons exhibit little to no male coalitionary behaviour (Henzi & Barrett, 2003), but were still found to exhibit a degree of greeting comparable to that of olive and yellow baboons, contrary to expectations. Compared to Guinea baboons, chacma baboons exhibit less cooperation and higher rates of between male

aggression (Kalbitzer et al., 2015), indicating that male-male interactions in chacma baboons can be considered higher risk than those of Guinea baboons. As such, it appears the overall quality of male-male relationships and risk posed by male-male interactions may be drivers of the form male greetings in baboons take, but that the presence or absence of male greeting is not inherently linked to coalition formation and cooperation specifically. These findings also aid us in making predictions, yet to be tested, about male greetings in Kinda baboons. Kinda baboons, while closely related to yellow and chacma baboons (Roos et al., 2021; Zinner et al., 2013), show marked differences in physiology and social behaviour compared to the other COKY baboons. The species is smaller in size and exhibits less sexual dimorphism and male contest competition, while often living in large multimale-multifemale groups numbering over 200 members (Petersdorf et al., 2019; Rogers et al., 2019; Singleton et al., 2017). Males show very little aggression towards new males joining the troop, with new males entering at the bottom of the dominance hierarchy and slowly increasing rank through increased tenure (Petersdorf et al., 2019). Male greeting would be particularly interesting to study in Kinda baboons given their unique male-male behaviour - there is little direct risk between males, but the social bonds between males are also weak, with as of yet no reported coalition formation, and no need for coalitions given the lack of contest-competition (Petersdorf et al., 2019).

Integrating the findings on *Papio* with the larger primate literature, we find that it mirrors findings in other species that exhibit male greetings (i.e., macaques), and aligns with the overall social complexity for communicative complexity hypothesis (Freeberg et al., 2012). As discussed above, the *Papio* species with the most tolerance between males (Guinea baboons) also exhibits the greatest greeting repertoire size (i.e., complexity). Male greetings are also a common feature in macaques (see Table H.1). While several species beyond the *Papionini* tribe also exhibit greetings between males, greetings within the tribe are particularly noteworthy due to their behavioural similarities (see Table H.1).

The function of male greetings across species (see Table H.1) appears to shift in line with the spectrum of male-male relationship quality. The function of male

greetings in many species with low social tolerance, highly linear dominance hierarchies, and high competition between males is often to reduce tension, especially between males close in rank. In female-philopatric species that exhibit greater male-male tolerance (e.g., Tonkean macaques), greetings appear to reinforce social bonds, while in species with particularly high social tolerance and strong male-male bonds (i.e., Guinea baboons) they can function to strength bonds or form coalitions. It is difficult to compare across studies, however, due to within-species differences that can arise due to differences in population density, resource availability, sex ratio, and captivity status. Overall, the findings here support the notion that risk at a species level (i.e., level of dominance linearity, egalitarianism, and tolerance in relationships) affects communication and is associated with communicative complexity and repertoire size.

7.3.3 Reconsidering risk at an individual or age-sex class level

In Chapter 6, I hypothesised that interactions that pose a higher risk to the approacher would involve clearer signalling by the approacher. However, "clarity" can be difficult to define and conceptualise. For example, in some cases miscommunication may be reduced by using multiple redundant signals to ensure a message is transmitted, while in other cases it may be clearer to simplify the signals used by reducing the overall number of signals. It may also be that further signalling (e.g., redundant signals of benign intent) is required in relationships that are more insecure, again leading to more complex signalling in riskier relationships (Grampp et al., 2023). Here, interactions across sex combinations were expected to differ in risk level, with approaches towards males (by both males and females) considered higher risk, and approaches towards females lower risk. We expected this risk to be reflected in the diversity of interactions individuals might have within those combinations and the predictability of signal use. For example, male-male interactions were expected to be highest risk and therefore exhibit the least diversity in signal combinations and the most predictable signalling. Female-female

interactions, at the other extreme, were expected to exhibit the greatest variability, due to the rich social lives and variety of interactions and relationships females can have with each other in a female-philopatric species that also has instances of female friendship (Silk, Altmann, et al., 2006; Silk, Alberts, et al., 2006). Similarly, approaches towards males by females with infants were expected to be less complex than those by females without infants, due to the extra risk resulting from the presence of their infant. Overall, results from the chapter were inconclusive with no strong evidence that signalling complexity was reduced where interpersonal risk was higher. Event sizes across all the interaction types tended to be small (2 - 3 unique signals per interaction), indicating approach signalling in general was relatively simple. Surprisingly, male-male interactions tended to have the highest event size, with female-female interactions the lowest, though credibility intervals overlapped heavily.

The entropy ratio results were counter to our predictions, with no differences in entropy ratio by recipient sex, but significant differences by approacher sex. It is possible that female-led interactions tend to be more simple, using a lower number of signals, and that while males always tend to use the same set of four signals when approaching other males (lip-smacking, ear-flattening, presenting, and contact) not all are used in every encounter, thereby producing more variability across encounters. In other words, maybe complexity for male-male encounters is higher because they have a greater "relevant repertoire" for that interaction type. If females tend to use fewer signals (one to two, compared to two to three for male-male events) this could also explain why the modularity for signal clusters was so low in the female-led approach interactions in Chapter 5, since signals would not often be combined.

The addition of more signals in male-male interactions may be due to a greater need for redundant signalling to ensure messages are transmitted successfully (e.g., signalling benign intent). While difference in entropy ratio by approacher sex was only significant for approaches towards females, there was also a trend in approaches towards males, with male-male approaches again exhibiting a higher overall entropy

ratio than female-male approaches. These entropy differences could indicate that the predictability of signalling by the approacher is more affected by risk posed to the recipient compared to risk posed to the approacher. Previous findings indicating that grunting is less common in approaches towards females with infants between mothers/daughters compared to two unrelated females (Silk et al., 2017, 2018) supports this interpretation. It also brings into question whether risk may simply play a smaller role in within-group communication than initially hypothesised, with other factors such as level of familiarity - separate, but related to risk - playing a more important role. This could also explain the differences in entropy ratio by approacher sex: Male-male approaches would, in chacma and olive baboons, be between individuals with lower familiarity than female-male interactions, which may often be between females and their male friends (Smuts, 1985). Similarly, male-female approaches, while perhaps between friends, would likely be between individuals with lower familiarity than female-female approaches which may often be between kin or at minimum between lifelong troop-mates.

Entropy ratio results could imply that signalling complexity is lower in more secure or predictable relationships. This aligns with recently published research on wild chimpanzees and mangabeys, where it was found that riskier social situations (e.g., directly following group fusion), were associated with more multisensory signals and more complex signal use (Grampp et al., 2023). Clark et al. (2022) also considered interpersonal risk, in the form of close rank differentials between individuals, in interactions between crested macaques. They predicted, similarly to our predictions in Chapter 6, that interactions in higher risk situations would be more stereotyped, with less variability, and higher intensity. Facial expressions were found to be more intense, but not any more or less variable, in interactions between closely ranked individuals (Clark et al., 2022). Additionally, signalling was most variable and least intense during affiliative contexts (Clark et al., 2022).

It is possible that higher interpersonal risk may actually result in clarity through use of redundant signals or signals that use multiple transmission channels (e.g., vocal and visual) (Grampp et al., 2023), rather than increasing clarity by reducing

the number of signals used to avoid miscommunication. This aligns with the ideas that riskier situations are more socially complex, and that social complexity is associated with communicative complexity (Grampp et al., 2023). However, when considering baboons, this would imply that the sex combination that is arguably most despotic (male-male interactions) has the highest risk and therefore social complexity, which is at odds with interpretations of complexity of social systems when comparing communicative systems of egalitarian versus despotic species (Rebout et al., 2020). Further detangling of what constitutes social complexity at both the level of the individual interaction and the species level will be critical for identifying the proximate and ultimate drivers of communicative complexity and is an ongoing debate (Bergman & Beehner, 2015).

7.4 Future directions

Beyond simply increasing sample sizes to gain a more in depth understanding of the questions posed here, there are five main avenues for future research: first, variation in approach behaviour between individuals, troops, field sites, and species; second, determining whether any of the identified signals can qualify as gestures; third, questioning whether familiarity (i.e., friendship and kinship) breeds complexity or complacency; fourth, investigating the development of approach behaviour, both from the perspective of ontogeny and of enculturation following migration; and fifth, further exploration of how studying relationships between risk and signalling in approach interactions gives insight into both perception of personal risk and ability to mentalise by considering risk to the recipient.

7.4.1 Inter-individual, troop, population, and species differences

Signalling may be expected to differ not just by species, but also by population (e.g., culture), dyad, or individual. Comparing approach signalling between species can help us match differences in signal use and structure with species-level characteristics such as dominance hierarchy linearity (Maestripieri, 2005) or social structure

(Kalbitzer et al., 2015). This thesis has situated male chacma baboons within this framework in Chapter 4. Similarly, comparing across populations could allow us to identify cultural variants (Whiten, 2000) or differences that may be due to environment (Cowlishaw, 1999; Ey et al., 2009) or social factors such as sex ratio or population density (Corewyn & Setchell, 2019). In groups that are much larger in size, approach behaviour may differ between individuals who are particularly familiar with each other and those who are not (McFarland et al., 2017). In species with very large group sizes, we might expect a difference between individuals who are not part of each other's social networks and those who have weak versus stronger social bonds (Lehmann et al., 2007; McFarland et al., 2017).

7.4.2 Does familiarity breed complexity or complacency?

In this thesis, I was unable to address the relationship between kinship or social affiliation and approach behaviour. Other work has indicated that such factors do play a role in approach behaviour, but these studies have typically focused on individual signals (e.g., grunting: Silk et al., 2018) or outcomes (e.g., displacement: Smuts, 1985) rather than considering how signals are combined. Applying a more holistic approach, as done in this thesis, would provide significantly more insight into how these factors shape signal content and structure. Understanding how these factors relate could also allow faster assessments of kinship or friendships in new populations where relationships are unknown (e.g. if certain signal combinations were to be seen primarily in friendship or kinship relationships). Familiarity, whether kinship or friendship based, may also provide further security in the relationship that affects signalling structure or complexity. Similarly, it has been shown that signalling may be more intense (i.e., faster rate of grunting and lip-smacking) in relationships which are less secure, for example individuals who are close in rank (Clark et al., 2022). This poses the question: does familiarity lead to complexity or complacency? It is possible that individuals who are more familiar with each other are more flexible in their signal use and interact in a wider variety of ways, but conversely it is also possible that less signalling is needed, which seems

to be the case for grunting towards individuals with infants during approaches between daughters/mothers (Silk et al., 2016, 2018).

7.4.3 Ontogeny, migration, and culture

Further research on the ontogeny and learning of signalling combinations is also necessary. This could provide insight into both the evolution of language (e.g., how responses by conspecifics shapes development of signalling) and the evolution of cultural variants in signalling. Not only does proximity provide opportunities for learning socially about other aspects of the physical or social environment (e.g., foraging opportunities: Carter et al., 2016), approach behaviour itself may be socially learned and may develop cultural variants (Sapolsky, 2006). As mentioned in the previous section, cultural variants in approach behaviour could exist between troops or sites, making the study of how migrant males integrate into a troop and how approach behaviour develops in juveniles within the troop valuable.

In fact, an olive baboon troop in Masai Mara Reserve, Kenya, whose most aggressive males had been killed off by a tuberculosis outbreak, was characterised by lower levels of aggression for over a decade following the original tuberculosis outbreak (Sapolsky, 2006; Sapolsky & Share, 2004). These changes (e.g., greater time spent in proximity to conspecifics and greater tolerance of lower ranking males by high ranking males) persisted even as new males joined the troop (Sapolsky & Share, 2004). No differences could be identified in the behaviour of new males when they first entered the post-tuberculosis Forest Troop versus a control troop, but observations suggested that how resident females responded to newly immigrated males was drastically different than in control troops, potentially helping to maintain the more peaceful group milieu (Sapolsky & Share, 2004). Studying approach behaviour involving migrating males (i.e., how resident males and females approach them, who new males chose to approach, what signals are used, how new males respond to approaches by others) could provide substantial insight into how signalling and compatibility of signalling relates to the success and failure of attempted migrations.

7.4.4 Intentionality, gesture, and sequence

Once signals used during approaches are identified, considering whether these signals could be considered intentional or classified as gestures is a productive next step when studying the evolution of language (Grund et al., 2023). In primatology, signals are considered gestural if they are used to intentionally transmit information with an aim of changing the receiver's behaviour or understanding, are goal-directed, and are used flexibly (i.e., it is not a hard-wired behaviour) (Aychet et al., 2020; Cartmill & Byrne, 2010; Roberts et al., 2013). Intentionality can be determined through a variety of means, for example assessing whether the signaller accounts for the attentional state of the recipient (e.g., performs the behaviour within the receiver's field of vision or uses attention-getting behaviours), whether they wait for a response, and/or if they repeat the signal if the desired response is not given (Roberts et al., 2013; Rodrigues et al., 2022). Gesture is understudied in monkeys compared to apes, even though previous studies indicate that primate species besides apes may have the cognitive skills required for gestural communication (Aychet et al., 2020; Molesti et al., 2020). A study in olive baboons identified a set of gestures including presenting, lip-smacking, "giving ground", and hand-body touch that were performed by nearly all troop members (Molesti et al., 2020). They found that gestures were more likely when the recipient was observing the signaller, and when the signaller was observing the recipient, further supported by findings from Chapter 5 of this dissertation. Considering the signals identified in this thesis from a gestural perspective would provide further insight into cognitive capacity of baboons in both producing and interpreting gestures (Cartmill & Byrne, 2010). Another valuable area of future study would be how such gestures are combined into sequences, which provides a further layer of complexity (Roberts et al., 2013). The same footage used for the empirical chapters has also been used in work on leave-taking behaviours (Baehren & Carvalho, 2022); combining the work here with Baehren's work in a sequence context could allow us to look at how interactions both open and close, and how these "bookends" relate to each other.

7.4.5 Perception of risk and perception of others

Studying approach behaviour and how individuals change their signalling based on the identity of the recipient also gives us insight into their perception of risk to self and others. The work of this thesis, focused on risk related to sex combination and infant presence, has just begun to scrape the surface. Risk can be measured in many ways, for example relating to threats in the environment (Mercier et al., 2017), species or troop level factors such as social organisation or level of despotism (Maestripieri, 2005), or interpersonal factors such as rank differentials (Clark et al., 2022), infanticide (Weingrill, 2000), interaction history (Cheney & Seyfarth, 1997), or familiarity. It is possible that only certain types of risk influence signalling, or that different types of risk result in different selective pressures and resulting changes in signalling. For example, high risk scenarios related to threats by predators (e.g., alarm calls) could result in less variable, clearer signalling to facilitate immediate, unencumbered understanding, whereas high risk related to rank could result in more variable signal use due to use of many redundant signals and higher variability in a signaller's potential goal. Further understanding of how these different factors influence complexity and variability of signalling may provide further insight into evolutionary drivers of the evolution of language (Freeberg et al., 2012; Pika, 2017).

There is substantial evidence already indicating that individuals change their signalling based on the identity of and their relationship with the recipient. For example, in baboons signalling changes based on the sex of the recipient, rank differential (Fedurek et al., 2019), kinship (Silk et al., 2018), friendship (Smuts, 1985; Städele et al., 2019b), recent interaction history such as altercations (Cheney & Seyfarth, 1997), and goal (Meunier et al., 2013). This indicates that baboons have an understanding of how the status of the recipient in relation to themselves may affect their own goals. However, the question remains whether baboons similarly have an understanding of how their own identity may be perceived by the recipient (Ensink & Mayes, 2010; i.e., ability to mentalise: Heyes, 1998).

While, for example, signalling "benign intent" through grunting could easily be learned through association, it is possible that a signaller modifying their approach behaviour could be a result of their ability to consider the receiver's mental state and the risk that they themselves pose to the receiver. Research into the development of such signalling differences and their application across settings could provide complementary information to more formalised studies and experiments on nonhuman primate theory of mind and mentalising (Heyes, 1998) (see also above section on gesture and intention).

7.5 Closing thoughts

This thesis has provided a new perspective on greeting and proximity events in baboons by taking an integrated, holistic approach. It highlighted gaps in the existing literature relating to approach behaviour, namely a lack of integration across sex combinations and modalities, with a focus on proximity itself and resulting interactions as resources. I started by providing new data on traditional "male greetings" in chacma baboons, adding to the little that is currently known about male greetings in this species and furthering the discussion on the relevance of these stereotyped greetings across *Papio* and primates more generally. From there the thesis widens in scope, considering the content and structure of signal bouts across sex combinations, investigating how signalling changes across sex combinations and perceived risk levels. Results of these chapters indicate that signals are used flexibly across sex combinations, but that certain signals (e.g., lip-smacking and ear-flattening) may be combined in reliable ways that alter meaning. Contrary to expectations, signalling complexity did not vary significantly with the proxies used to assess risk posed by the interpersonal interaction to the approacher. The thesis lays the groundwork for important future work relevant to studying the evolution of cognition and language, emphasising the importance of considering not just signal use, but signal combination when studying approach interactions.

Appendices

A

Troop Demographics

Troop	Age	Name	Sex	Birth or entry date	Rank	Comment
Gombe						
	Adult	Uhuru	M	entry 22.7.16	2	
	Adult	Donald	M	entry 8.1.18	1	
	Adult	New arrival 1	M	2nd+ transfer, older	unknown	more calm
	Adult	New arrival 2	M	1st transfer, age c8 ?	unknown	v nervous kid
	Adult	Yolta	F	2.6.05	12	Amenorhoeic
	Adult	Urusi	F	14.9.06	1	Cyling
	Adult	Unarasika	F	12.1.06	8	Weaning
	Adult	Ulaya	F	18.4.06	10	Suckling
	Adult	Usa	F	4.9.07	5	Pregnant
	Adult	Yambera	F	20.8.07	11	Cycling
	Adult	Ujeranga	F	21.2.08	4	Pregnant
	Adult	Usambara	F	8.6.08	7	Suckling
	Adult	Herena	F	25.7.11	3	Suckling

Troop	Age	Name	Sex	Birth or entry date	Rank	Comment
	Adult	Unyasa	F	12.2.14	9	Cycl adolesc
	Adult	Ukimbu	F	20.12.14	7	Cycl adolesc
	Adult	Upale	F	2.1.15	2	Cycl adoles
	Juv/ Subadult	Utani	M	23.11.12		small for age, late exit ?
	Juv/ Subadult	Hadson	M	19.1.14		
	Juv/ Subadult	Ulanga	M	27.1.15		
	Juv/ Subadult	Ufana	M	18.4.15		
	Juv/ Subadult	Yahoo 2	F	24.5.16		
	Juv/ Subadult	Udewa	M	25.8.16		
	Juv/ Subadult	Hombo	M	25.12.16		
	Juv/ Subadult	Ututa	F	13.1.17		
	Juv/ Subadult	Ulu	F	(mid'17) 1.7.17		
Gorongosa						
	Adult	Bulb	M			
	Adult	Aku	M		High	
	Adult	Arrow	M		High	
	Adult	Earl	M			
	Adult	Idoso	M		Low	
	Adult	Pao	M			
	Adult	Pequeno	M	entry Nov. 2018	1	
	Adult	Pez	M		Low	

A. Troop Demographics

Troop	Age	Name	Sex	Birth or entry date	Rank	Comment
	Adult	Quasimodo	M		Low	
	Adult	Avi	F	Prime adult	Low	
	Adult	Chapeu	F	Subadult 2018, young adult 2019 (first pregnancy)		Mother: Marge (guess); First pregnancy 2019, miscarriage or infanticide late September
	Adult	Gabriella	F	Prime adult	Low	
	Adult	Jane	F	Older adult	Low	
	Adult	Maizey	F	Subadult 2018, young adult 2019 (first pregnancy)	High	Mother: Matilda; first infant 14 Oct 2019
	Adult	Marge	F	Prime adult	Low	
	Adult	Matilda	F	Older adult	1	Offspring: Maizey
	Adult	Molly	F	Older adult		
	Adult	Nina	F	Older adult		
	Adult	Roxy	F	Older adult		
	Adult	Zoe	F	Prime adult		Offspring: Malcolm, Raisin (likely)
	Juv/ Subadult	Atrevida	F	Medium juvenile		
	Juv/ Subadult	Raisin	F	Large juvenile/borderline subadult		Mother: Zoe (likely)

Troop	Age	Name	Sex	Birth or entry date	Rank	Comment
	Juv/ Subadult	Patric	M	Large juvenile		
	Juv/ Subadult	Saad	M	Large juvenile		
	Juv/ Subadult	Malcolm	M	mid June 2019		Mother: Zoe

B
Ethogram

Category	Behaviour	Description
Aggressive contact	attack	Aggressive action targeted at a conspecific including grabbing, biting, hitting, and tackling
	bump	Individual pushes other individual with side of body
	hit	Individual uses a hand to quickly smack another outside the context of play
	push	Individual pushes another with its hands outside of the context of play
Body positioning	approach	Decrease distance between self and conspecific
	bend-away	Individual leans away from a passing higher rank individual
	bipedal	Standing or locomotion on hind legs
	chase	Individual runs after a conspecific who is fleeing from them
	distancing	Greeter increasing distance between themselves and greetee
	divert	Greeter diverts before reaching greetee
	follow	Individual follows closely behind the other
	sit	Individual goes from another position to sitting

Category	Behaviour	Description
Body positioning	stand	Individual standing quadrupedally
	turn_away	Greetee repositions entire body to be facing away from greeter
Contact	hind-quarter_touch	One hand is used to touch the hindquarters of a second individual
	hip-grasp	Both hands are used to touch the hips of a second individual, but neither individual moves forward
	inspect	Individual investigates by a combination of via sight, touch, and smell
	mount	The focal individual grasps the hips of another individual and positions their genitals facing the anogenital region of the conspecific. Does not involve thrusting or intromission
	penis-diddle	The focal individual touches the penis of another male
	polonaise	The focal individual touches the hips of a conspecific with both hands, and the two move forward with the focal individual maintaining contact.
	prancing	The focal individual moves the torso up and down rapidly, lifting both front legs off the ground repeatedly.
	scratch	The hand is placed in the fur of a conspecific and fingers are contracted several times. This is a brief behavior and not targeted with a focused gaze, unlike grooming.
	sniff	Sniffing of conspecific
	stroke	An open or slightly curved hand is briefly drawn along the fur of a conspecific.
	touch	The focal individual uses a hand to contact the body of a second individual, not including the genital, groin region, or hips

Category	Behaviour	Description
Contact	upside_down_embrace	Individual A stands in front of B, who is usually seated, bends forward with their rump and tail in the area, puts their head towards the ground and reaches their arms through their hind legs to touch or grasp individual B. B usually makes physical contact with A and sniffs or inspects A
	embrace	The focal individual wraps one or both arms around a conspecific from the front, side or rear
Event criteria	2_m_radius_start	Individual gets within 2 m of second individual
	2_m_radius_stop	Individual gets within 2 m of second individual
	arrive	Greeter arrives at point of greetee
	end	Event stop criteria are reached
	pass_no-contact	Individual passes another within 2m without making physical contact
	recipient_avoids	The approacher comes within two meters of the recipient but is unable to arrive or pass by because the recipient begins to move away from the recipient. This category includes displacements, but is broader.
	stops_short	The approacher comes within two meters of recipient but then stops short (e.g. begins foraging) and does not complete the approach.
Facial signal	ear-flattening	Ears are pressed against side of head
	glance_toward	Brief glance at another individual
	grimace	Lips are drawn back to expose teeth
	lip-smack	Lips and tongue moved rapidly repeatedly, often accompanied by audible smacking
	look_away	Head turned actively and sharply away from the direction of the conspecific
	observe	Continued watching of another individual
	threat_eyebrow_flash	Individual gazes directly at conspecific and raises eyebrows repeatedly
	threat_headbob	Individual gazes directly at conspecific and moves head forward and down repeatedly. Often paired with eyebrow flashing.

Category	Behaviour	Description
Facial signal	yawn	Mouth stretched wide open in yawn
Infant interactions	infant_carry	Infant is clutched to the chest with one or both arms while carrier is locomoting
	infant_grab	Individual reaches for or grabs infant; contact is not necessary if mother interferes
	infant_groom	Grooming infant
	infant_inspect	Sniffing and visually inspecting infant
	infant_observe	Watching a conspecific's infant in a focused way
	infant_release	When an individual holding or grasping an infant's limb releases the infant
	infant_touch	Touching infant without trying to lift
	nursing	A mother is carrying her natal coat infant ventrally and may or may not be feeding the infant. It was not always possible to determine whether the infant was acitvely nursing (i.e., nipple in mouth) and this should therefore not be considered equivalent to feeding time
Movement	displace	Individual approaches a conspecific who in turn moves to another location. The individual immediately assumes the conspecific's position once vacated.
	dodge_flinch	Dodging or flinching away from another individual, not in a context of play
	flee	Greetee moves away from greeter quickly
	lunge	A sudden movement toward a conspecific often finishing with an attempt to grab
	move_towards	Greetee moves towards greeter
	pause	Individual interrupts an approach and stops moving forward
	present	Individual approaches conspecific and positions posterior towards the conspecific, typically raising the tail. The presenter may lower the torso towards the ground.
	present_reach	Individual presents and reaches out with a hind foot towards the recipient

Category	Behaviour	Description
Movement	reach	Individual reaches out towards conspecific to touch, but doesn't make contact
	solicit_grooming	Individual moves towards a conspecific, positions self for grooming, and waits in position for several seconds until either successful (grooming begins) or unsuccessful (other individual ignores solicitation, typically avoids gazing at solicitor, and the solicitor sits down or moves off).
	walk-away	Greetee moves away from greeter OR greeter moves further away from the greetee prior to coming within 2 meters
Non-social	forage	Active acquisition, processing, and eating of food
	groom_self	Individual uses hands or mouth to groom itself
	head_shake	Individual shakes head rapidly
	rest	Individual stays in one place with little movement and no other primary activity state
	scratch_ground	Individual uses hand to scratch at or dig in ground, often foraging related
	scratch_self	All behavioral events directed towards one's own body and that have been interpreted in other studies as indicative of anxiety, including scratch, self-touch, nose touch, and body shake
	vigilant	Individual is tensely observing another individual, animal, human, etc. who may be a threat
Social affiliative contact	copulate	Mounting with intromission and thrusting. Often accompanied by a copulation call produced by the female
	groom	Individual uses fingers and potentially mouth in a focused manner to move conspecific's hair back and forth, removing loose hair, dirt, and pests. The groomer's gaze is focused on the area being groomed.
	groom_other	Groom an individual besides partner
	jump_on	Individual jumps on the other's back in play or frustration. Typically performed by juveniles

Category	Behaviour	Description
Vocalizations	bark	Short, loud, medium- or high-frequency vocalization that resembles a dog's bark (includes alarm barks and lost barks)
	chatter	Quickly move mouth and lips to produce repetitive sound that sounds like (and may be the result of) teeth chattering
	contact_call	Short call to locate other individual
	copulation_call	Long, guttural staccato vocalization produced by a female after copulating.
	grunt	Low-frequency vocalization, usually punctuated by silences, emitted with the mouth closed or slightly open
	keck	A cough-like, staccato medium frequency vocalization given with an open mouth (grimace), punctuated by silences between each syllable (usually occurs in a submissive context, in response to an approach, or in response to aggression or threat of aggression)
	scream	High pitched, continuous vocalization
	wahoo	A loud, two-part vocalization in which the syllables sounds similar to "wa" and "hoo"

C

BORIS Variables

Variable	Description	Options
Date	Date video was recorded	
Coding date	Date on which the video was coded	
Review date	Date on which the coding was reviewed	
Date correct	Whether the recording date listed is accurate	
Group	Troop recorded	Chitengo, AC Troop
Species	Baboon species recorded	Chacma baboon, olive baboon
Approacher	Identity of the approacher	See troop demographics
Recipient	Identity of the recipient	See troop demographics
Physicality	Whether approacher made physical contact with recipient or recipient's infant	No contact, recipient contact, infant contact, contact with both
Greeting type	Sex dyad combination	M-M, M-F, F-F, F-M
Infant presence	Whether an infant was present within a 5 meter radius of the recipient	No infant, recipient's infant, approacher's infant, both, other's infant

Variable	Description	Options
Approacher reproductive status	Female's reproductive status (none if male)	None, Nursing, Pregnant, Swelling, Unknown
Recipient reproductive status	Female's reproductive status (none if male)	None, Nursing, Pregnant, Swelling, Unknown
Approacher visibility	Visibility full when the approach and interaction end if visible, partial when part of the approach or interaction is obscured by vegetation or camera angle. Faces marked as visible when lip-smacking and ear-flattening could be identified	Full, full without face, partial, partial without face
Recipient visibility	See above	Full, full without face, partial, partial without face
Sound quality	Rating of sound quality based on when vocalizations and leaves rustling can be heard and sources identified (high), heard but source not confidently identified (medium), or whether it is unknown if sound could be heard if present (low)	Low, medium, high
Context known	Whether the preceeding 2 minutes are also on film, allowing for context to be identified	Yes, No
Context	Has there been an altercation, competition over food, or something surprising or causing alarm in the troop in the previous two minutes	Explicit conflict, food present, startled, not tense
Approacher prior activity	What was the activity of the approacher before the approach began	Resting, grooming, foraging, travelling, unknown
Recipient prior activity	What was the activity of the recipient before the approach began	Resting, grooming, foraging, travelling, unknown

Variable	Description	Options
Triadic	Are three individuals involved in this proximity event	Yes, No
Approacher ID certainty	ID should be entered under approacher if over 50% sure of identity. "No" if observer has doubts their ID is correct	Yes, No
Recipient ID certainty	ID should be entered under recipient if over 50% sure of identity. "No" if observer has doubts their ID is correct	Yes, No

D

Chapter 4 - Supplementary materials

Table D.1: Sample sizes for each type of signal and age group shown in Table 4.3.

Greeter age	Ear visibility	Full facial visibility	Total observations
Medium juvenile	8	7	8
Large juvenile	1	1	1
Subadult	6	4	6
Prime adult	28	19	30
Old adult	5	4	6

Table D.2: Proportion of greetings by each age category of greetee incorporating each signal of interest. Sample sizes for each category can be found in Table D.3.

Greetee age	Ear-flattening	Lip-smacking	Present	Embrace
Medium juvenile	0	0	1	0
Large juvenile	N.A.	N.A.	0	0
Subadult	1	0	0.25	0.25
Prime adult	0.66	0.32	0.05	0.03
Old adult	0.62	0.57	0	0
Greetee age	**Penis diddle**	**Hind-quarter touch**	**Hip-grasp**	
Medium juvenile	0	0	0	

Large juvenile	0	0	0
Subadult	0.25	0	0
Prime adult	0.08	0.14	0.08
Old adult	0	0.12	0

Table D.3: Sample sizes for each type of signal and age group shown in Table D.2.

Greetee age	**Ear visibility**	**Full facial visibility**	**Total observations**
Medium juvenile	1	1	1
Large juvenile	0	0	1
Subadult	3	2	4
Prime adult	35	31	37
Old adult	8	7	8

E

Chapter 5 - Inter-observer reliability checks

To complete inter-observer reliability checks, I recruited a research assistant (Reece Hammond), who was blind to the hypotheses of the study. He viewed and coded 50 randomized interactions from the Gorongosa database, amounting to approximately 14% of the dataset. Reece was new to behavioural coding in BORIS and to observational work with primates. He first completed a period of training that involved viewing videos to review the ethogram behaviours and then coding 15 interactions side by side with me. Following the training period, proximity events that were not used for training were randomized and the first 30 selected for use. Following this initial round of coding, we realised many behaviours occurred so rarely that a larger sample size was needed to capture more behaviours. We randomized the remaining list of observations and Reece coded a further 20 observations. I calculated Cohen's Kappa and Gwet's AC1 for each signal using the *irr* and *irrCAC* packages (Gamer et al., 2019; Gwet, 2019). Results are found in Table E.1 for most, but not all, signals identified in clusters during community detection. The values presented are calculated based on the full set of 50 observations coded by the research assistant. Given how rare many of the signals in the complete ethogram were, some did not appear in the 50 coded observations and as such

inter-observer reliability could not be calculated for all variables (excluded from the table). Similarly, some Cohen's Kappa results below are strongly affected by the small number of observed events, which, when missed by a second rater, can easily lead to a very poor coefficient. We calculated Gwet's AC1 values in addition to Cohen's Kappa values due to the known issues of using Cohen's Kappa for imbalanced dichotomous data (Bakeman & Goodman, 2020; Gamer et al., 2019; Giammarino et al., 2021; Xu & Lorber, 2014).

Table E.1: Interobserver reliabilty measures for all behaviours identified in clusters during community detection in Chapter 5. Both Cohen's Kappa and Gwet's AC1 values are presented.

Behaviour	Cohen's Kappa	Gwet's AC1	Proportion Agreement	Proportion Chance Agreement	Confidence Interval (Gwet's AC1)
arrive	0.67	0.76	0.86	0.43	(0.57,0.941)
dodgeFlinch	0.00	0.96	0.96	0.04	(0.897,1)
earFlattening	0.48	0.55	0.76	0.46	(0.311,0.799)
glanceToward	0.48	0.67	0.80	0.38	(0.464,0.886)
grimace	0.00	0.94	0.94	0.06	(0.86,1)
grunt	0.50	0.84	0.88	0.24	(0.706,0.978)
hindQuarterTouch	0.65	0.95	0.96	0.11	(0.889,1)
infantCarry	0.48	0.96	0.96	0.08	(0.893,1)
infantGrab	0.48	0.96	0.96	0.08	(0.893,1)
infantObserve	0.20	0.86	0.88	0.15	(0.737,0.982)
inspect	1.00	1.00	1.00	0.04	(1,1)
lipSmack	0.55	0.80	0.86	0.31	(0.637,0.958)
observe	0.57	0.63	0.80	0.46	(0.404,0.855)
passNoContact	0.65	0.82	0.88	0.34	(0.663,0.972)
present	0.80	0.87	0.92	0.40	(0.73,1)
scratchSelf	0.79	0.98	0.98	0.09	(0.933,1)
solicitGrooming	0.19	0.86	0.88	0.15	(0.737,0.982)

F

Chapter 5 - Supplementary results

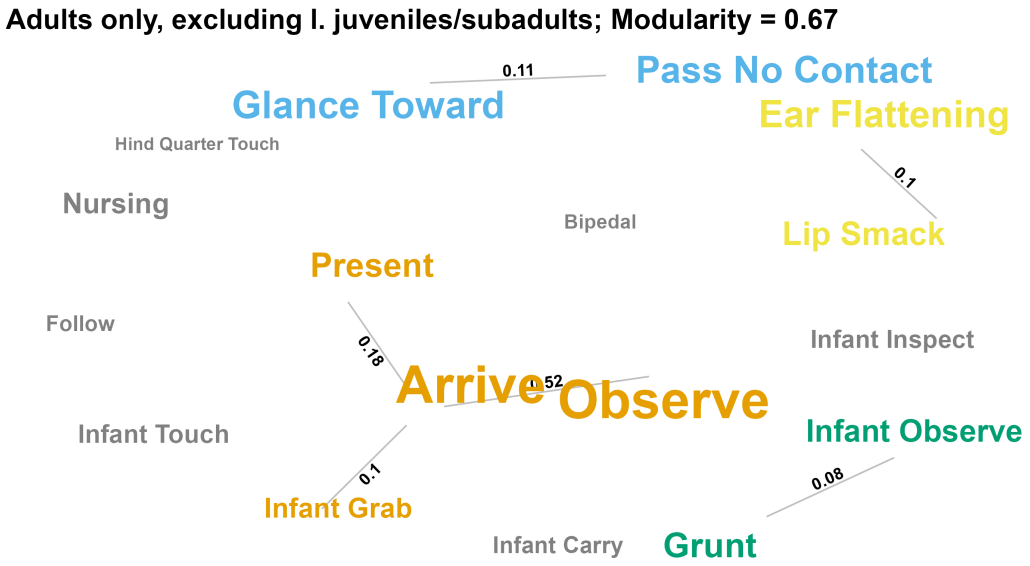

Figure F.1: Community detection across all observations excluding interactions with large juveniles or subadults. Linked and coloured behaviours are detected clusters, with edges labelled with the combination's observed probability

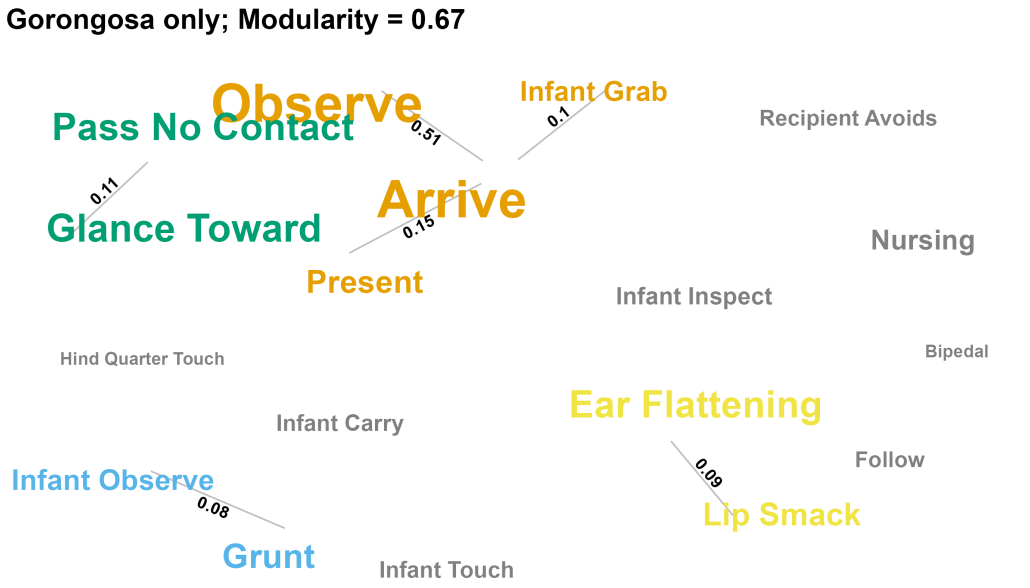

Figure F.2: Community detection across all Gorongosa observations. Linked and coloured behaviours are detected clusters, with edges labelled with the combination's observed probability

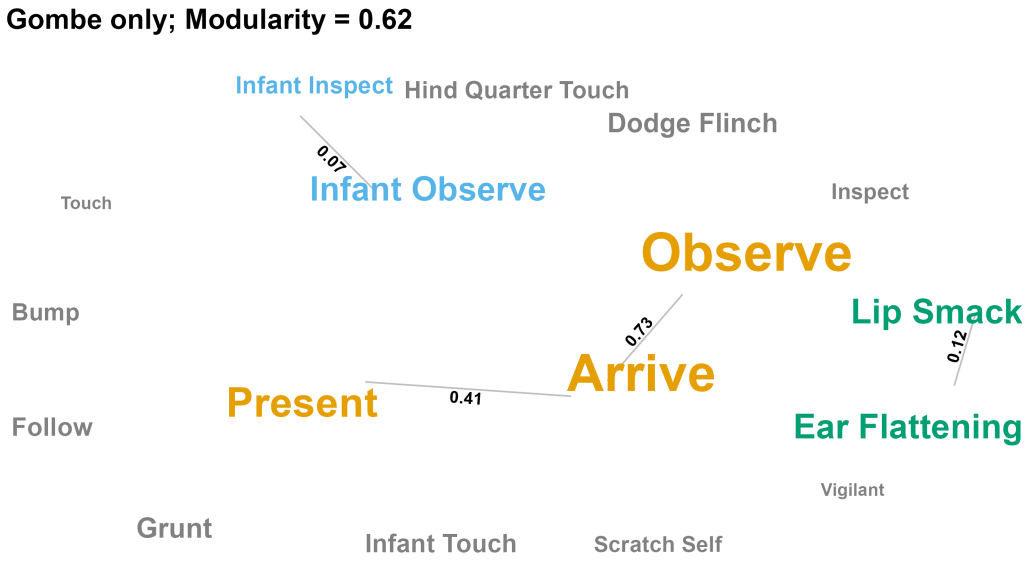

Figure F.3: Community detection across all Gombe observations. Linked and coloured behaviours are detected clusters, with edges labelled with the combination's observed probability

G

Chapter 6 - Supplementary materials

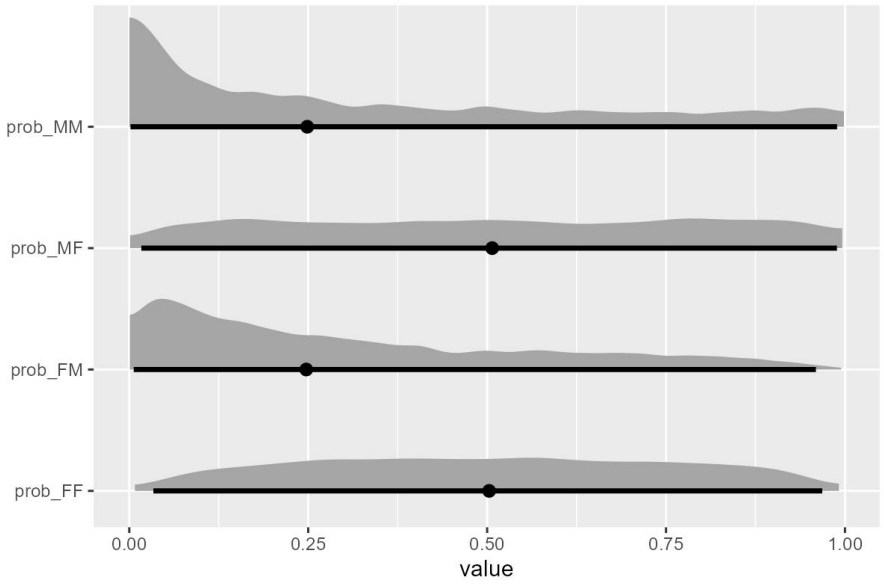

Figure G.1: Prior predictive checks for the contact model for sex combination

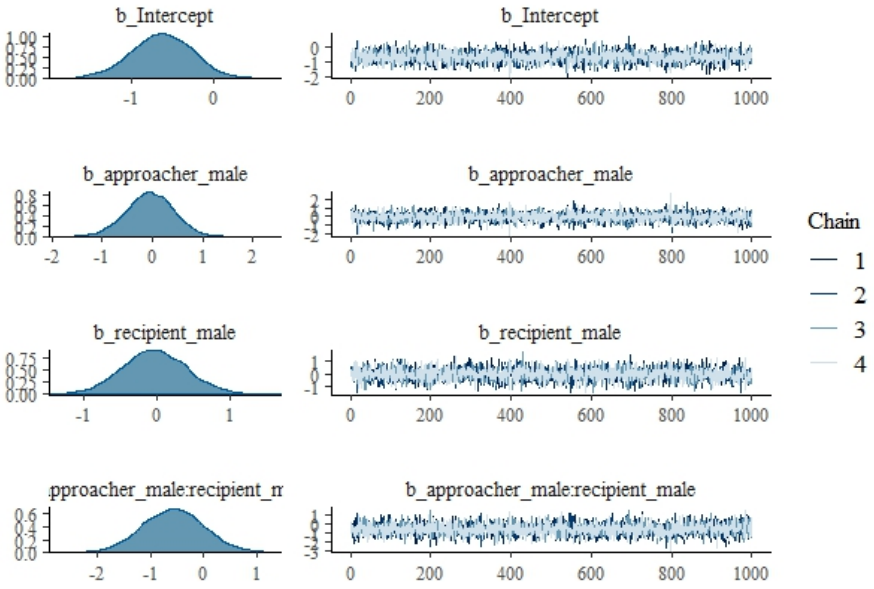

Figure G.2: Model diagnostics showing chain mixing for contact model for sex combination

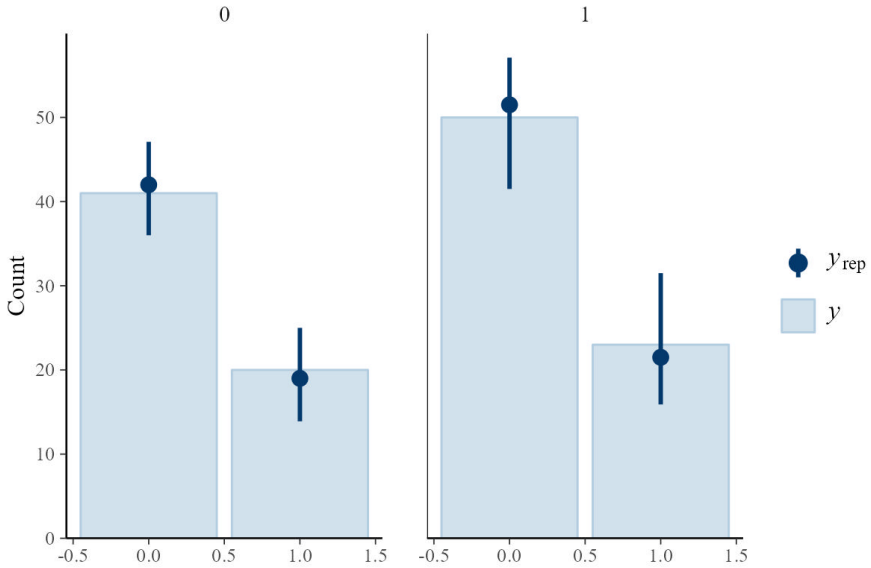

Figure G.3: Posterior predictive checks for the contact model for sex combination

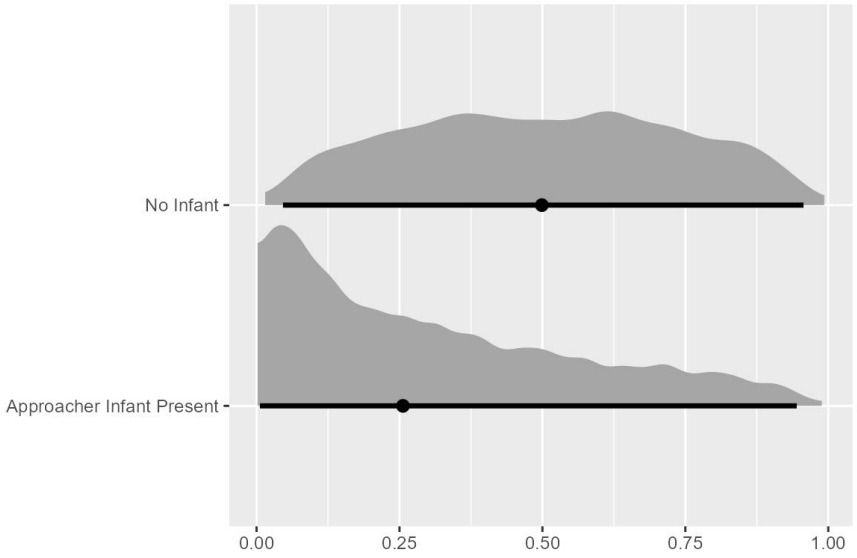

Figure G.4: Prior predictive checks for the contact model for infant presence

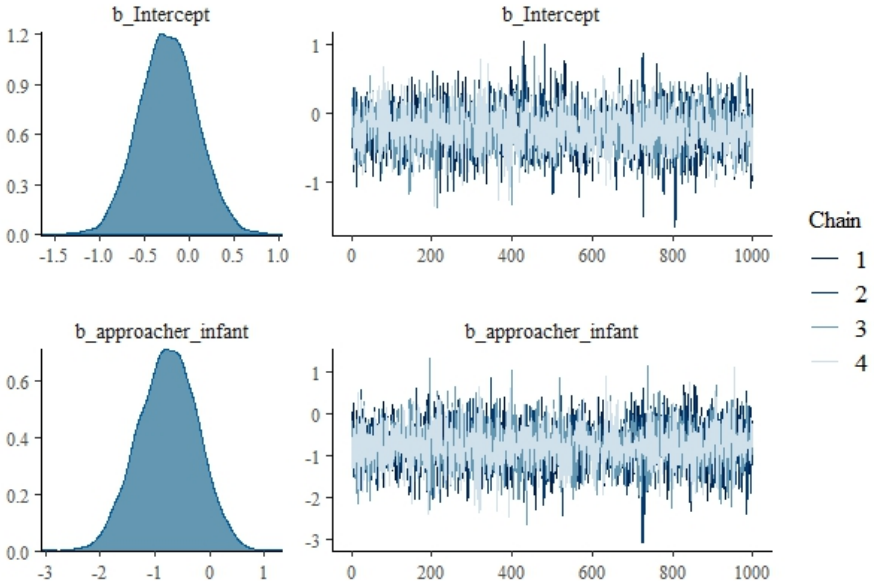

Figure G.5: Model diagnostics showing chain mixing for contact model for infant presence

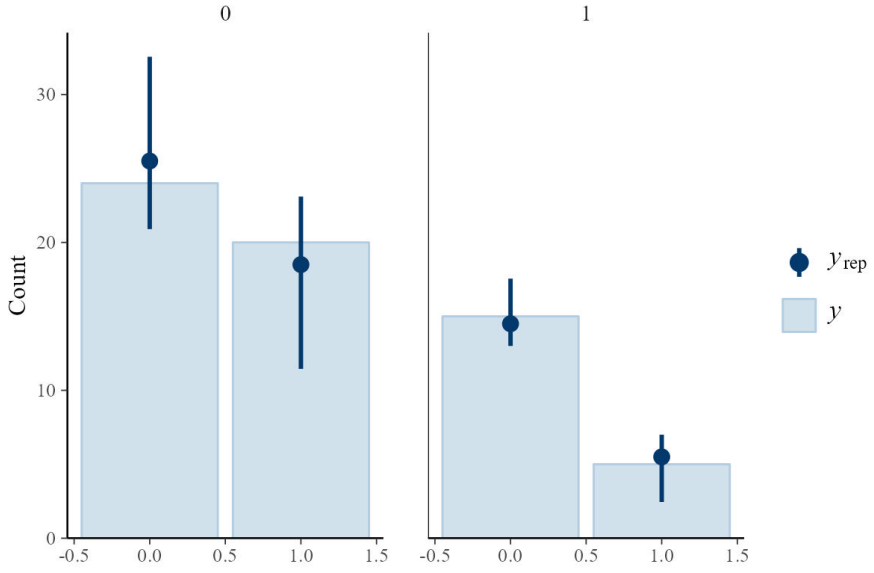

Figure G.6: Posterior predictive checks for the contact model for infant presence

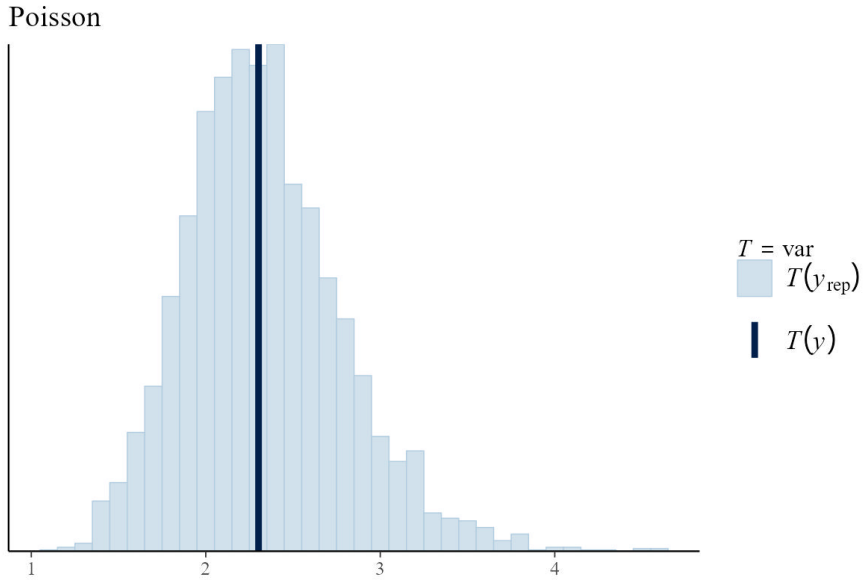

Figure G.7: Variance check for Poisson model for event size by sex combination

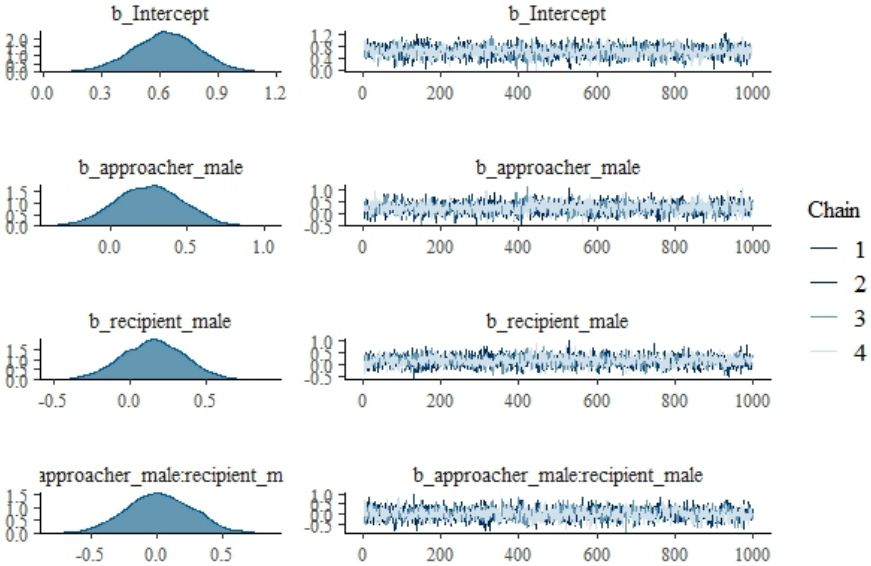

Figure G.8: Model diagnostics showing chain mixing for event size model for sex combination

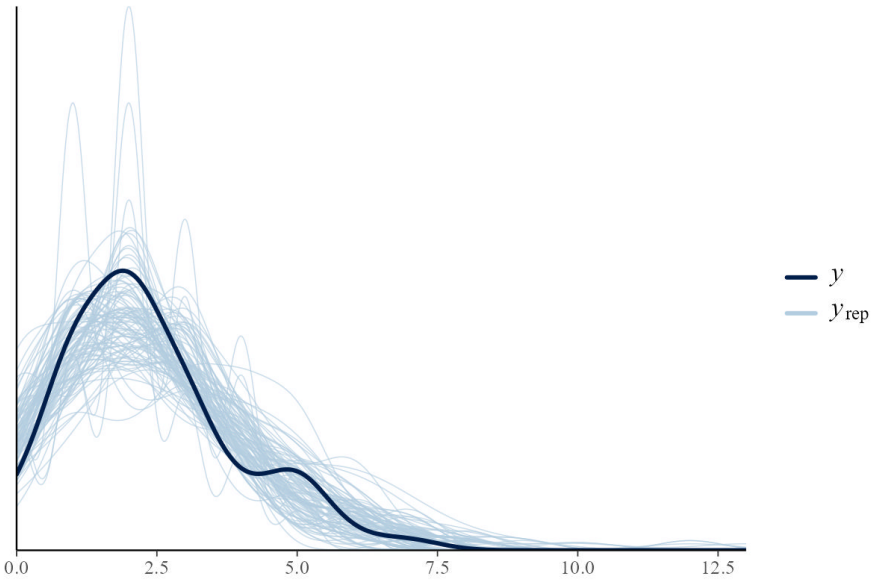

Figure G.9: Posterior predictive checks for the event size model for sex combination

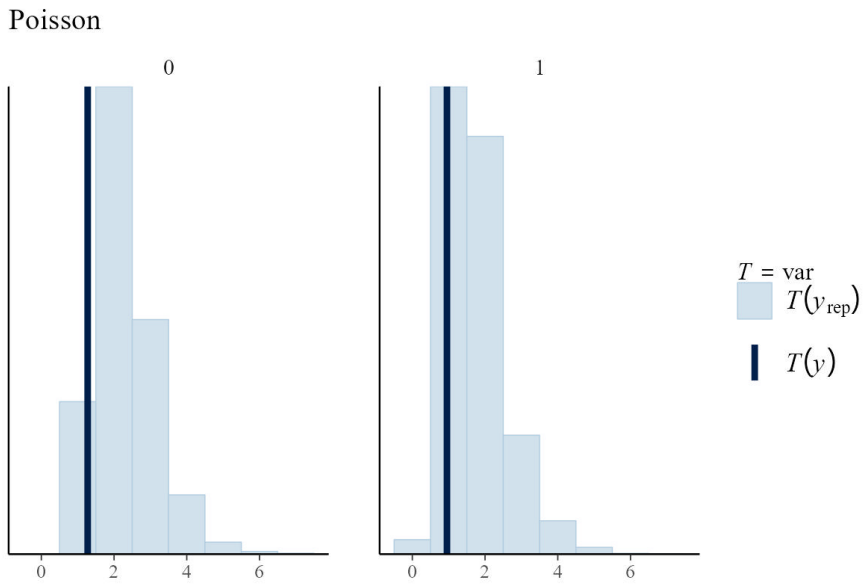

Figure G.10: Variance check for Poisson model for event size by infant presence

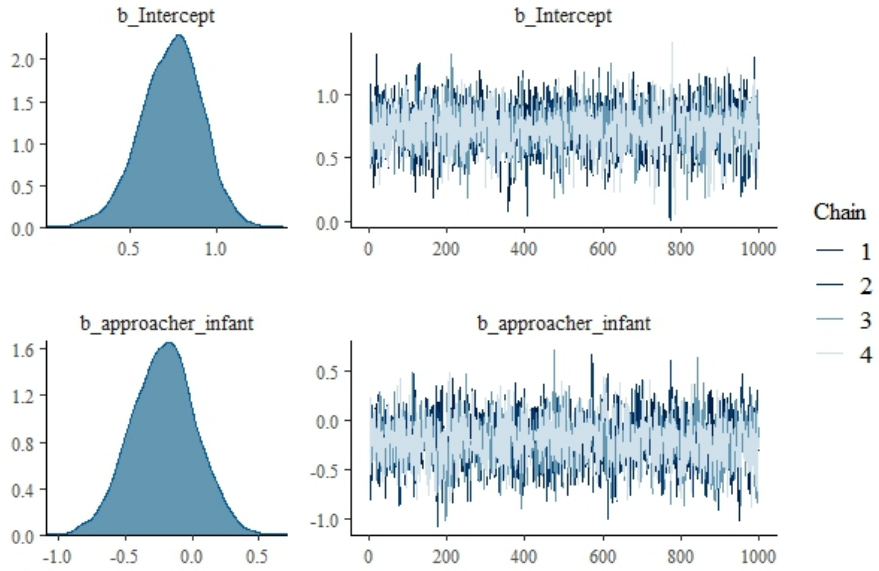

Figure G.11: Model diagnostics showing chain mixing for event size model for infant presence

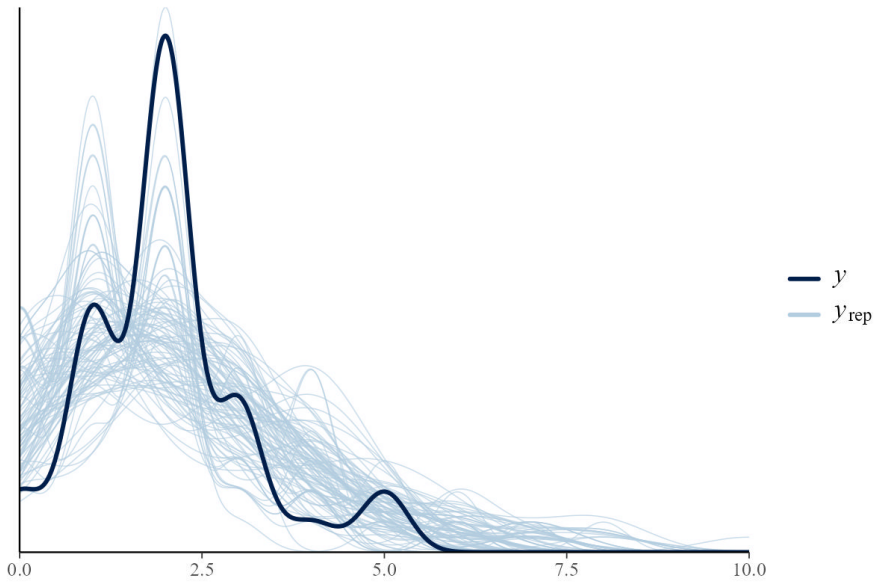

Figure G.12: Posterior predictive checks for the event size model for infant presence

H

Male greeting by species table

Table H.1: Comparison of male tolerance and male greeting form, context, and function across species

Species	Greeting behaviours	Sexes involved	Context	Function	Species attributes	Citations
Black-horned capuchin monkeys	Scream-embrace	Mostly between males; females embrace without the scream	Usually during reunions or sometimes during inter-group encounters	Potentially reinforcing affiliative bonds, unlikely to be for tension reduction or reconciliation (no correlation with agonistic actions or presence of high quality food)	Multimale-multifemale groups, male dispersal, linear rank hierarchy, fission-fusion social organisation	Alfaro (2008)
Vervet monkeys	Grunting, sometimes with lip-smacking or posturing	Primarily males	When approaching a male partner, particularly near rivers	Signalling benign intent or possibly to recruit assistance in situations of danger	Multimale-multifemale groups, clear linear dominance hierarchy	Mercier et al. (2017)
Spider monkeys	Pectoral sniffs and embraces	Both sexes	During fusion events and initial approach	Signalling benign intent in potentially tense interactions	Multimale-multifemale groups with fission-fusion	Schaffner & Aureli (2005)
Black-and-white colobus	Overhead mounting, mounting, and embracing	Males and females	nonagonistic situations and after aggressive encounters	Tension reduction	one dominant male, dominance based on age; females egalitarian	Kutsukake et al. (2006)

Table H.1: Comparison of male tolerance and male greeting form, context, and function across species

Species	Greeting behaviours	Sexes involved	Context	Function	Species attributes	Citations
Mantled howler monkeys	Vocalisations (throat rumbling and clucking), mutual shoulder grabbing, armpit sniffing, and genital sniffing while in a rump-to-face position	Males	Agaltepec, Mexico: Most often during joining of sub-groups or during moving; more greeting between individuals with close dominance ranks	Agaltepec, Mexico: Tension reduction to signifiy when there will not be a challenge to rank	Single- or multimale-multifemale groups, both sexes disperse, and males usually have clear, linear dominance hierarchies; Agaltepec, Mexico: Very high population density of males	Dias et al. (2008)
Mantled howler monkeys	Vocalisations (throat rumbling and clucking), mutual shoulder grabbing, armpit sniffing, and genital sniffing while in a rump-to-face position	Males	La Pacifica, Costa Rica: Most greetings during social disruptions (e.g., competition or intergroup encounter) than during neutral contexts (e.g., traveling or resting)	La Pacifica, Costa Rica: Possibly functions to moderate or reduce tension	Single- or multimale-multifemale groups, both sexes disperse, and males usually have clear, linear dominance hierarchies	Corewyn & Setchell (2019)

Table H.1: Comparison of male tolerance and male greeting form, context, and function across species

Species	Greeting behaviours	Sexes involved	Context	Function	Species attributes	Citations
Tonkean macaques	Lip-smacking, silent-bared-teeth display, touching, mounting, presenting, hip holding, genital touching, and/or expressive runs	Males	Primarily a netural context	Reinforcing social bonds	Multimale-multifemale groups, female philopatric, male disperal, high rates of grooming between adult males, relaxed dominance hiearchies, high social tolerance	De Marco et al. (2014)
Moor macaques	Lip-smacking, silent-bared-teeth display, averting face, presenting, touching, mounting, and/or genital touching	Males	Primarily a neutral context; most common between males with uncertain dominance relationships and low-quality relationships	Easing tension and assessing willingness to build social bonds	Multimale-multifemale groups, female philopatric, male disperal, relatively clear and linear dominance hiearchy in males, lower rate of male-male aggression than in several other macaque species, and also some social tolerance and male-male grooming	Riley et al. (2014)

Table H.1: Comparison of male tolerance and male greeting form, context, and function across species

Species	Greeting behaviours	Sexes involved	Context	Function	Species attributes	Citations
Bonnet macaques	Embrace, rump clasp, touch, muzzle, present, mount, and/or insepct	Males	Greetings often between males similar in rank according to Silk, 1994 (captive), but Sugiyama, 1971 (wild) observed mountings, embracing, and genital touching both up and down the hierarchy, often with multiple steps in rank between	To test rank stability or reduce tension; males were less likely to form coalitions against males they greeted (Silk, 1994)	Multimale-multifemale groups, female philopatric, male disperal, high level of affiliative behaviour between males, form coalitions between most dyads at various timepoints, male-male grooming, male/female sex ratio in troops more even than in other macaques (e.g., Japanese macaques)	Silk (1994), Sugiyama (1971)
Crested black macaques	Mounting and penis-grabbing	Males	Not reported	Limited greeting behaviour; unclear function - possibly tension reduction	Multimale-multifemale groups, clear linear dominance hierarchy in males, highly skewed sex ratio, male dispersal, little affiliative behaviour between males	Reed et al. (1997)

Table H.1: Comparison of male tolerance and male greeting form, context, and function across species

Species	Greeting behaviours	Sexes involved	Context	Function	Species attributes	Citations
Pig-tailed macaques	Eye-brow and scalp retraction, often accompanied by approach-retreat interactions, hip-touch, and sometimes short play bouts	Both sexes	Usually a neutral context, but sometimes in times of group disruption	Possibly tension reduction, but sometimes also lead to an affiliative interaction	Multimale-multifemale groups, male dispersal, steep sex imbalance, strong dominance hierarchies, relatively despotic but less so than rhesus macaques	Maestripieri (1997)
Tibetan macaques	Presenting, mounting, penis-sucking, embracing, and/or genital touching	Males	Primarily neutral contexts	Tension reduction and increasing social bond strength	Multimale-multifemale groups with high socionomic sex ratios, male-male tolerance and grooming, male dispersal	Ogawa (1995)
Chacma baboon	Lip-smacking, ear-flattening, hind-quarter touching, hip-grasping, presenting, mounting, genital touching	Males	TBA	Unknown	Multimale-multifemale groups, male dispersal, highly sexual dimorphic, high male competition and strong dominance hierarchy	Chapter 4, Saayman (1971), Kalbitzer et al. (2015)

Table H.1: Comparison of male tolerance and male greeting form, context, and function across species

Species	Greeting behaviours	Sexes involved	Context	Function	Species attributes	Citations
Yellow baboon	Lip-smacking, ear-flattening, hind-quarter touching, hip-grasping, presenting, mounting, genital touching, sometimes resulting in grabbing, slapping, and holding or pressing down approacher	Males	Neutral context, tense interactions	Signal status	Multimale-multifemale groups, male dispersal, strong dominance hierarchy, male competition, some coalition behaviour	Hausfater & Takacs (1987), Pelaez (1982)
Olive baboon	Lip-smacking, ear-flattening, hind-quarter touching, hip-grasping, presenting, mounting, genital touching	Males	Neutral context, tense interactions	Potentially variable function: In younger individuals it may be used to negotiate status/rank, while it may be a marker of relationship quality and cooperative potential in older males	Multimale-multifemale groups, male dispersal, strong dominance hierarchy, male competition, some coalition behaviour	Smuts & Watanabe (1990), Watanabe & Smuts (2004)

Table H.1: Comparison of male tolerance and male greeting form, context, and function across species

Species	Greeting behaviours	Sexes involved	Context	Function	Species attributes	Citations
Hamadryas baboon	Circular approach with swaggering gait, lip-smacking, ear-flattening, hind-quarter touching, hip-grasping, presenting, mounting, genital touching	Males	Often during tense circumstances (e.g., competition over a female), most often between individuals close in rank	Tension reduction, signalling submission, or rank negotiation	Male philopatric, multi-level society, one-male units maintained through coercion, some grooming between leader male and follower or between solitary males, occasional male-male alliances in between-group conflicts	Colmenares (1990), Colmenares (1991b), Colmenares (1991a), Fraser & Plowman (2007)
Guinea baboon	Lip-smacking, ear-flattening, hind-quarter touching, hip-grasping, presenting, mounting, genital touching, prancing, polonaise. Generally more intense and frequent than other baboons	Males	Neutral/not tied to any specific context	Signal party membership, assess relationship quality and cooperative potential	Male philopatric, multi-level society, strong affiliative relationships between males and high male-male tolerance	Whitham & Maestripieri (2003),Dal Pesco & Fischer (2018)

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