Regulation of inter-sexual relationships within the microcosm of Guinea baboon units

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Hereby I declare that I have written this thesis independently and with no other aids or sources than quoted.

Göttingen, 14th of November 2022 Dominique Treschnak

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Summary

Male reproductive success is linked in most animals to their access to fertile females. Resulting competition among males presents a strong selective pressure on male reproductive strategies. In species with female choice males show behaviours aimed at attracting the opposite sex. Displays of quality in various modalities allow females to assess and choose a potential partner. Alternatively, male social investment and support for females, but also into current offspring, can inform females about potential future parental investment. Males compete not only for access to females; they are also under selection to monitor the state and behaviour of females to assess suited mating partners or seize mating opportunities. While in many species, females become the centre of male attention when they reproductively active, in species where males and females form long-lasting bonds males might be permanently incentivised to monitor and control associated females. The extent to which animals monitor their conspecifics and their interactions varies, and the drivers behind the evolution of abilities to gather and process social information are still debated.

Non-human primates provide the opportunity to study the link between sociality and mechanisms underlying reproductive strategies and social cognition since they are highly social animals with differentiated relationships and often advanced social skills and knowledge. Further, they present a wide range of social systems, with a remarkable variety of grouping and mating patterns.

The general aim of this PhD thesis was to investigate the relationship between Guinea baboon primary males and their associated females. My main focus was hereby, firstly, on testing whether the relaxed social environment of the Guinea baboon society affects males' attention to social information, and secondly, how primary males distribute social investment among their associated females.

Guinea baboons (*Papio papio*) live in a nested multi-level society. At the core are 'units' consisting of one primary male, one to seven associated females, and their offspring. Several units and bachelor males form a 'party', which in turn aggregate into 'gangs'. Females associate with one primary male and show mate fidelity but enjoy relatively high spatial freedom. Male Guinea baboons form strong bonds with other males, support each other in conflicts and show low aggression rates.

For my two studies, I collected behavioural data and conducted playback experiments on a wild population of Guinea baboons that ranges close to the Centre de Recherche de Primatologie (CRP) Simenti, a field station of the German Primate Center (DPZ) located in the Niokolo Koba National Park in Senegal. The population comprised approximately 400 individually identified Guinea baboons that belonged to three main parties.

In my first study, we investigated whether Guinea baboon primary males keep track of their females' whereabouts. First, I tested experimentally whether male Guinea baboons respond to play back vocalisation from associated and non-associated females differently. In the main experiment I tested if males keep track of their females' position. I presented vocalisation of associated females from locations that were either consistent or inconsistent (i.e., violating their expectation) with the actual position of the female. While males seem to be able to recognize their female by voice, as evidenced by stronger responses to calls from unit females than non-unit females, they apparently lack the ability or motivation to track their females' movements. In the second study we investigate the allocation of social investment in primary males. I analysed proximity and rates of socio-positive interactions for unit-females in relation to their age and reproductive state. Males were closer to and interacted more frequently with females that were reproductively active, and were also more likely to be found in close proximity to lactating females. Males further showed a preference for mature and young adult females over subadult and old females.

In summary, the results of my first study fall in line with existing evidence which suggests that the level of competition affects the value of social information and, as a consequence, the motivation to attend to social signals. I further was able to show that Guinea baboon primary males maintain social relationships with all of their associated females but allocate their social investment depending on female short- and long-term reproductive value. Thus, the current reproductive value of a female partner is an influential characteristic even for species living in a relative tolerant and low competitive social system.

Zusammenfassung

Der Fortpflanzungserfolg von Männchen ist bei den meisten Tieren an den Zugang zu fruchtbaren Weibchen gebunden. Der daraus resultierende Wettbewerb zwischen Männchen übt einen starken Selektionsdruck auf männliches Fortpflanzungsverhalten aus. Bei Arten, mit weiblicher Partnerwahl, zeigen Männchen Verhaltensweisen, die darauf abzielen, das andere Geschlecht anzuziehen. Männliche Indikatoren von Qualität und Kondition in verschiedenster Modalität können Weibchen das Beurteilen und Auswählen eines potentiellen Partners erleichtern.

Alternativ dazu können soziale Investitionen und die Unterstützung von Männchen für Weibchen, aber auch für den aktuellen Nachwuchs, Weibchen über potentielle zukünftige elterliche Investitionen informieren. Männchen konkurrieren nicht nur um den Zugang zu Weibchen, sondern stehen auch unter Selektionsdruck, den Zustand und das Verhalten von Weibchen zu beobachten, um geeignete Paarungspartner zu beurteilen oder Paarungsgelegenheiten wahrzunehmen. Während bei vielen Arten Weibchen in den Mittelpunkt der männlichen Aufmerksamkeit rücken, wenn sie fortpflanzungsaktiv sind, könnten Männchen bei Arten, bei denen Männchen und Weibchen eine dauerhafte Bindung eingehen, einen ständigen Anreiz haben, assoziierte Weibchen zu überwachen und zu kontrollieren. Das Ausmaß, in dem Tiere ihre Artgenossen und deren Interaktionen beobachten, ist unterschiedlich, und welche Mechanismen die Entwicklung von Fähigkeiten, soziale Informationen zu sammeln und zu verarbeiten, antreiben sind noch umstritten. Nicht-menschliche Primaten bieten die Möglichkeit, die Verbindung zwischen Sozialität und den Mechanismen, die den Fortpflanzungsstrategien und der sozialen Kognition zugrunde liegen, zu untersuchen, da sie hochgradig soziale Tiere mit differenzierten Beziehungen und oft fortgeschrittenen sozialen Fähigkeiten und Kenntnissen sind. Darüber hinaus weisen sie ein breites Spektrum an Sozialsystemen mit einer bemerkenswerten Vielfalt in ihrer sozialen Organisation, Paarungssystemen und Sozialstruktur auf.

Das allgemeine Ziel dieser Doktorarbeit war es, die Beziehung zwischen adulten Guineapavian-Männchen und ihrer Weibchen zu untersuchen. Mein Hauptaugenmerk lag dabei zum einen darauf, zu prüfen, ob das entspannte soziale Umfeld der Guineapavian-Gesellschaft die Aufmerksamkeit der Männchen für soziale Informationen beeinflusst, und zum anderen, wie männliche soziale Investitionen auf ihre Weibchen verteilt sind.

Guineapaviane (*Papio papio*) leben in einer mehrstufigen Gesellschaft. Den Kern bilden polygyne *Units*, die aus einem adulten Männchen, einem bis sieben Weibchen und deren Nachwuchs bestehen. Mehrere *Units* und Junggesellenmännchen bilden eine *Party*, die sich wiederum zu *Gangs*

zusammenschließen. Die Weibchen sind mit einem adulten Männchen verpaart und zeigen Paartreue, genießen aber eine relativ große räumliche Freiheit. Männliche Guineapaviane gehen starke Bindungen mit anderen Männchen ein, unterstützen sich gegenseitig bei Konflikten und zeigen geringe Aggressionsraten.

Für meine beiden Studien sammelte ich Verhaltensdaten und führte Playback-Experimente an einer wilden Population von Guinea-Pavianen durch, die in der Nähe des Centre de Recherche de Primatologie (CRP) Simenti, einer Feldstation des Deutschen Primatenzentrums (DPZ) im Niokolo-Koba-Nationalpark in Senegal, lebt. Die Population bestand aus etwa 400 individuell identifizierten Guinea-Pavianen, die zu drei *Parties* gehören.

In meiner ersten Studie untersuchten wir, ob adulte Guineapavian-Männchen den Aufenthaltsort ihrer Weibchen verfolgen. Zunächst testete ich experimentell, ob männliche Guineapaviane auf das Abspielen von Vokalisationen von *Unit*-Weibchen und nicht-*Unit*-Weibchen unterschiedlich reagieren. Im Hauptexperiment testete ich, ob Männchen die Position ihrer Weibchen verfolgen. Ich präsentierte ihnen Vokalisation von *Unit*-Weibchen von Orten, die entweder mit der tatsächlichen Position des Weibchens übereinstimmten (Testbedingung) oder nicht übereinstimmten (d. h. ihre Erwartung verletzten, Kontrolle). Obwohl die Männchen in der Lage zu sein scheinen, ihre Weibchen an der Stimme zu erkennen, wie die stärkeren Reaktionen auf Rufe von *Unit*-Weibchen im Vergleich zu nicht-*Unit*-Weibchen zeigen, fehlt ihnen offenbar die Fähigkeit oder Motivation, die Bewegungen ihrer Weibchen zu verfolgen. In der zweiten Studie untersuchten wir die Verteilung der sozialen Investitionen bei adulten Männchen. Ich analysierte die Nähe und die Häufigkeit sozio-positiver Interaktionen mit Weibchen in Abhängigkeit von deren Alter und Reproduktionsstadiums. Männchen interagierten häufiger und hielten sich in der Nähe von Weibchen auf, die reproduktiv aktiv waren, und waren häufiger in der Nähe von laktierenden Weibchen zu finden. Darüber hinaus zeigten die Männchen eine Vorliebe für junge und reife Weibchen gegenüber subadulten und alten Weibchen.

Zusammenfassend lässt sich sagen, dass die Ergebnisse meiner ersten Studie mit bereits vorhandenen Erkenntnissen übereinstimmen, die darauf hindeuten, dass das Ausmaß des Wettbewerbs den Wert sozialer Informationen und folglich die Motivation, auf soziale Signale zu achten, beeinflusst. Außerdem konnte ich zeigen, dass primäre Guineapavian-Männchen soziale Beziehungen zu allen *Unit*-Weibchen unterhalten, aber ihre sozialen Investitionen in Abhängigkeit vom kurz- und langfristigen Reproduktionswert der Weibchen aufteilen. Der aktuelle Reproduktionswert einer Partnerin ein einflussreiches Merkmal selbst für Arten, die in einem relativ toleranten und konkurrenzarmen sozialen System leben.

Résumé

Chez la plupart des animaux, le succès reproducteur des mâles est lié à leur accès aux femelles fertiles. La concurrence entre les mâles qui en résulte exerce une forte pression sélective sur les stratégies de reproduction des mâles. Chez les espèces où les femelles ont le choix, les mâles présentent des comportements visant à attirer le sexe opposé. Des démonstrations de qualité sous diverses formes permettent aux femelles d'évaluer et de choisir un partenaire potentiel. Par ailleurs, l'investissement social des mâles et le soutien qu'ils apportent aux femelles, mais aussi à leur progéniture actuelle, peuvent informer les femelles sur leur investissement parental potentiel. Les mâles ne sont pas seulement en compétition pour l'accès aux femelles ; ils sont également sélectionnés pour surveiller l'état et le comportement des femelles afin d'évaluer les partenaires reproducteurs appropriés ou de saisir les opportunités d'accouplement. Alors que chez de nombreuses espèces, les femelles deviennent le centre d'attention des mâles lorsqu'elles sont actives sur le plan reproductif, chez les espèces où les mâles et les femelles forment des liens durables, les mâles peuvent être incités à surveiller et à contrôler en permanence les femelles qui leur sont associées. La mesure dans laquelle les animaux surveillent leurs congénères et leurs interactions varie, et les moteurs de l'évolution des capacités de collecte et de traitement des informations sociales sont encore débattus.

Les primates non humains offrent la possibilité d'étudier le lien entre la socialité et les mécanismes sous-jacents aux stratégies de reproduction et à la cognition sociale, car ce sont des animaux hautement sociaux, qui entretiennent des relations différenciées et possèdent souvent des compétences et des connaissances sociales avancées. De plus, ils présentent un large éventail de systèmes sociaux, avec une variété remarquable de modèles de regroupement et d'accouplement.

L'objectif général de cette thèse de doctorat était d'étudier la relation entre les mâles primaires de babouins de Guinée et les femelles qui leur sont associées. Mon objectif principal était donc, premièrement, de vérifier si l'environnement social tolérant des sociétés de babouins de Guinée affecte l'attention des mâles aux informations sociales, et deuxièmement, comment les mâles primaires distribuent l'investissement social parmi les femelles qui leur sont associées.

Les babouins de Guinée (*Papio papio*) vivent dans une société imbriquée à plusieurs niveaux. Au cœur de la société se trouvent des "unités" composées d'un mâle primaire, d’une à sept femelles associées et de leur progéniture. Plusieurs unités regroupées avec les mâles célibataires forment un "parti", qui à plusieurs se regroupent à leur tour en "gangs". Les femelles s'associent à un seul mâle primaire et font preuve de fidélité envers leur partenaire, mais jouissent d'une liberté spatiale relativement grande. Les babouins de Guinée mâles forment des liens forts avec d'autres mâles, se soutiennent mutuellement dans les conflits et présentent un faible taux d'agression.

Pour mes deux études, j'ai recueilli des données comportementales et mené des expériences de playback sur une population sauvage de babouins de Guinée vivant à proximité du Centre de Recherche de Primatologie (CRP) Simenti, une station de terrain du German Primate Center (DPZ) située dans le Parc National du Niokolo Koba au Sénégal. La population comprenait environ 400 babouins de Guinée identifiés individuellement et appartenant à trois groupes principaux.

Dans ma première étude, nous avons cherché à savoir si les mâles primaires de babouins de Guinée suivent les allées et venues de leurs femelles. Tout d'abord, j'ai testé expérimentalement si les babouins de Guinée mâles répondent différemment aux vocalisations de retour des femelles associées et non associées. Dans l'expérience principale, j'ai testé si les mâles suivent la position de leurs femelles. J'ai présenté des vocalisations de femelles associées provenant d'endroits qui étaient soit cohérents, soit inconsistants (c'est-à-dire qui violaient leurs attentes) avec la position réelle de la femelle. Alors que les mâles semblent être capables de reconnaître leur femelle par la voix, comme en témoignent les réponses plus fortes aux appels des femelles unitaires que des femelles non unitaires, ils n'ont apparemment pas la capacité ou la motivation de suivre les mouvements de leurs femelles. Dans la deuxième étude, nous avons examiné l'allocation de l'investissement social chez les mâles primaires. J'ai analysé la proximité et les taux d'interactions socio-positives des femelles unitaires en fonction de leur âge et de leur état reproducteur. Les mâles étaient plus proches et interagissaient plus fréquemment avec les femelles actives sur le plan reproductif, et étaient également plus susceptibles de se trouver à proximité des femelles allaitantes. Les mâles ont également montré une préférence pour les femelles matures et les jeunes adultes par rapport aux femelles subadultes et âgées.

En résumé, les résultats de ma première étude sont en accord avec les preuves existantes qui suggèrent que le niveau de compétition affecte la valeur des informations sociales et, par conséquent, la motivation à prêter attention aux signaux sociaux. De plus, j'ai pu montrer que les mâles primaires de babouins de Guinée entretiennent des relations sociales avec toutes les femelles qui leur sont associées, mais qu'ils répartissent leur investissement social en fonction de la valeur reproductive des femelles à court et à long terme. Ainsi, la valeur reproductive actuelle d'une partenaire féminine est une caractéristique influente même pour les espèces vivant dans un système social relativement tolérant et peu compétitif.

Chapter 1

General Introduction

As male reproductive success is linked in most animals to their access to fertile females, competition among males presents a strong selective pressure (Darwin, 1871). In order to maximise their reproductive success, males show a great variety of morphological adaptation and behavioural strategies (West-Eberhard, 1979). Non-human primates function as a valuable model to study variation in reproductive strategies and how these relate to differences in their ecological and social environment. Guinea baboons (*Papio papio*) live in a multi-level society with male philopatry and female-biased dispersal. The core of their society is formed by ‘units’ composed of one primary male and its associated females. Males are tolerant i.e., they show low levels of aggression and high spatial tolerance, form strong bonds and support each other in conflicts. Females play an essential role in intersexual relationship maintenance and mate choice (Fischer et al., 2017). The comparatively low level of competition in Guinea baboons compared to other baboon species, has been linked to the peculiarities of male-female associations (discussed in more detail in chapters 2, 3 and 4; Dal Pesco et al., 2022) and male attention to social information (Faraut & Fischer, 2019; Maciej et al., 2013). In this thesis I follow up on previous studies and I continue to investigate the relationship of Guinea baboon primary males and their females. Firstly, I experimentally test the social knowledge of primary males with regards to the acoustic recognition of their associated females and, secondly, in their ability to monitor the spatial position of their females. Further, I investigate the allocation of social investment of primary males among females of their unit with the goal of identifying female characteristics that influence males’ behaviour.

In the following paragraphs I will provide information about the variety of social systems of non-human primates (chapter 1.1), briefly recapitulate the evolutionary drivers that lead animals to aggregate into groups (section 1.2) and describe the diverse relationships that group-living animals form with their group members (section 1.3.1). I, hereby, put special emphasise on the relationships between males and females (section 1.3.2). Next, I discuss the cognitive demands of group living and existing theories that link aspects of group living with the evolution of higher cognitive capacities (section 1.4). Finally, I present the unique aspects of my study species, the Guinea baboon (*Papio papio*) and outline the main goals that I investigated within this PhD thesis (section 1.5).

1.1 Social system

Primates present a great variety of social systems. For example, in nocturnal lesser galagos (*Galago senegalensis*), males are solitary and defend territories, mating is polygynous, and occurs often with multiple females with which they share overlapping territories (reviewed in Bearder, 1987)). Many gibbons (Hylobatidae) are known for their pair-bonded social systems, where male and female form strong relationships and defend territories together (Leighton, 1987). Further, in gibbon pairs mating is mainly monogamous, and males show infant care (Palombit, 1999). However, there are also records of extra pair copulation in gibbons, for instance, in wild siamangs (*Hylobates syndactylus*, Palombit, 1994)). In many macaques and baboon species, animals aggregate into large mixed-sex groups, in which the mating system is mainly polygynandrous (Petersdorf & Higham, 2016) and individuals of these groups form diverse and complex relationships with their group mates. Of particular interest are multi-level social systems, which are societies that are based on one-male multi-female units, which are nested within one or more levels of organisation that differ in their social and ecological function, such as in snub-nosed monkeys (*Rhinopithicus* sp.) (Kirkpatrick & Grueter, 2010).

To study and understand the diversity in primate social systems, it has shown to be advantageous to split the social system into three main components (Kappeler & van Schaik, 2002). First, the *social organisation* describes the distribution of individuals in space and time, the size, composition (e.g., age and sex) and genetic structure of animal aggregations. Second, the *mating system* describes mating patterns, i.e. who mates with whom, in which ratio do both sexes reproduce (e.g. monogamy, polyandry, polygyny, polygynandry), and what are the morphologic (Leutenegger, 1978, Plavcan, 2001) and genetic consequences (Johnstone, 2000) of such mating patterns. Finally, the *social structure* describes the tenor, frequency, and distribution of interactions among conspecifics (Silk, 2002), and encompasses the analyses of function and emergence of kin relationships (Kapsalis, 2004; Silk, 2001), dominance hierarchies (Hausfater et al., 1982; Shively, 1985), strong bonds (Kalbitz et al., 2016; Silk et al., 2010a), and coalitionary support (Deag, 1977; Meikle & Vessey, 1981; Walters, 1980).

1.2 Group living

Group living can be found in a large variety of vertebrates (Krause et al., 2013). Many studies have shown evidence of the benefits and costs of group living. First, group living provides benefits in terms of reduced predation risks. Associating with many conspecifics reduces, under constant predation pressure, the individual risk to become the target of an attack (‘dilution-effect’, Hamilton, 1971; Vine, 1971). Additionally, higher group densities make predator detection (Beauchamp, 2015; Boland, 2003), confusion (Jeschke & Tollrian, 2007; Neill & Cullen, 1974; Schradin, 2000) and defense (Caro, 2005; Jungwirth et al., 2015) more likely, which further reduces individual predation risks.

Group living can further increase individual foraging efficiency. Information about food resources can actively or passively spread among the group (Clay et al., 2012; Gillam, 2007; Ward & Zahavi, 1973), collective foraging can improve exploitation efficiency (Alexander, 1974), larger groups are better in defending territories and displacing competitors (Cassidy et al., 2015; Mosser & Packer, 2009; R. W. Wrangham, 1980), and collective hunting has shown to be more successful than solitary attempts (Bailey et al., 2013; Holekamp et al., 1997; Kruuk, 1972). Individuals aggregating in close proximity allows further for better heat retention and thermoregulation (Terrien et al., 2011), for example in deer mice (*Peromyscus maniculatus*) (Andrews & Belknap, 1986), macaques (*Macaca sylvanus)* (McFarland & Majolo, 2013) or in hibernating barbastelle bats (*Barbastella barbastellus*) (Russo et al., 2017) and alpine marmots (*Marmota marmota*) (Arnold, 1990).

On the other hand, group living also entails costs, including increased competition over resources, such as food competition (Isbell, 1991; van Schaik & Janson, 1988) or reproductive competition (Bray et al., 1975; Burger & Gochfeld, 1988), increased energy and time expenditure due to greater home-ranges and daily travel time (Chapman, 2000; Clutton-Brock, 1977; Korstjens et al., 2006; Pollard & Blumstein, 2008), higher likelihood for pathogen transmission (Cote & Poulinb, 1995; Rifkin et al., 2012), and higher overall detection risks by predators (Lindström, 1989). Negative aspects of group living can further be aggravated when competition affects kin, as individual and inclusive fitness are affected (West et al., 2001). The stability and size of a group in which animals live represents the interplay between benefits and costs of gregariousness (Davies et al., 2012).

1.3 Social relationships

The majority of social interactions between individuals within a group can be seen as the result of competition or cooperation processes (Kappeler, 2012). Nevertheless, independent of whether it is due to competition or cooperation, a contingent series of interaction between two individuals leads to unique dyadic relationships (Hinde, 1976, p. 19). The social structure of group living primates is shaped by the relationships that individuals establish throughout their lifespan. Most relationships are hereby based on relatedness, dominance dynamics, or friendships (Gouzoules, 1984; Preuschoft & van Schaik, 2000; Silk et al., 2006).

Kinship plays an important role in shaping social relationships, for instance among female philopatric species (e.g., Japanese macaques, *Macaca fuscata* Kurland, 1977, rhesus macaques, *Macaca mulatta* Miller *et al*., 1973), vervet monkeys, *Chlorocebus pygerythrus* Cheney, 1983, and some baboon species (e.g., yellow baboons, *Papio cynocephalus* Altmann, 1980), in which societies are built around matrilines. Females that are kin related spend most of their time together, groom frequently, and support each other in conflicts (Silk, 2002). Kin relationships not only influence affiliative relationships but also affect individuals’ dominance relationships and position within the group (Chapais & Berman, 2004).

When individuals compete over resources, fighting, aggression, and dominance hierarchies might arise (Taborsky et al., 2021). The establishment of hierarchies reduces the need for repeated costly fights. High social rank brings often priority of access to resources and reproductive opportunities (Maynard Smith, 1974). When hierarchies are pronounced, competitive encounter among group member are often very predictable and individuals can be ranked accordingly (Walters & Seyfarth, 1987). Females’ ranks are often directly linked to their mothers’ ranks, and it is usually inherited (Cheney, 1977; Walters & Seyfarth, 1987). As for males, dominance ranks are often strongly influenced by their physical capabilities, such as fighting ability, strength, but also their group tenure, age, and connectedness, i.e., available partners for coalitionary support. While female rank remains mostly unchanged during their lives, male rank tenure is comparably more variable (Walters & Seyfarth, 1987).

Reoccurring socio-positive interaction between individuals forming a dyad lead to the formation of bonds. Strong bonds are defined as frequent, enduring, and equitable socio-positive interactions (Silk, 2002). Many studies have provided evidence of the benefits and adaptive value of social bonds. For instance, in yellow baboons, infants of mothers that are more socially integrated have higher survival (Silk et al., 2003). Female chacma baboons (*Papio ursinus*) that form strong and stable relationships experience enhanced longevity compared to females with weaker relationships (Silk et al., 2010b). In Assamese macaque (*Macaca assamensis*), strong bonds among males are linked to coalition formation, which in turn predicts dominance status, and promotes paternity success (Schülke et al., 2010). Additionally, several other studies present alternative positive aspects of high numbers of social bonds. For instance, in Barbary macaques (*Macaca sylvanus*) thermoregulation plays an important role as they live in cold habitats. Survival of barbary macaques, in this context, has shown to be positively related to a high numbers of social bonds (McFarland & Majolo, 2013).

1.3.1 Male-female relationships

Apart from pair-living species, strong relationships between males and females are relatively rare. Since reproductive success of males is mainly limited through their access to mating opportunities, i.e., fertile females, strong investment and frequent interaction with a single female might not be deemed an optimal strategy (Trivers, 1972). The majority of interactions between males and females in group-living species are linked to reproduction and are driven in frequency and quality by the reproductive state of females. Several studies have shown how female receptiveness increases males' socio-positive interaction frequencies, proximity and general attention to females (chimpanzees: Deschner et al., 2004; Nishida, 1997; Proctor et al., 2011); baboons: (Byrne et al., 1990); howler monkeys: (van Belle et al., 2009)). Further, in many species males and females form sexual consortships, defined by Bercovitch as: "…a continuous, close spatial association between a male and a sexually receptive female, with evidence of sexual activity by the male." (Bercovitch, 1991, p.438), throughout female reproductive phases (DeVore & Hall, 1965; Hausfater, 1975; Hill, 1987).

In some species, especially in the cercopithecine subfamily, such as macaques and baboons, bonds between male and female take an unusual importance. Some adults may form close associations in the absence of an immediate sexual relationship (olive baboons: (Smuts, 1985); yellow baboons: (Altmann, 1980; Collins, 1986); chacma baboons: (Palombit et al., 1997; Silk, 2002), Assamese macaques: (Ostner et al., 2013)). These 'friendships' (Smuts, 1985) are characterised by increased proximity, higher rates of bidirectional allogrooming, and infant handling (Palombit et al., 1997). Males are also more likely to support their female "friends" in aggressive encounters (Palombit et al., 2000). In chacma and olive baboons, males responded more strongly to distress calls of their female "friends" (Lemasson et al., 2008, p. 200; Palombit et al., 1997). These special relationships are suggested to provide females protection from harassment and infanticide (Smuts, 1985; van Schaik & Dunbar, 1990; Wrangham, 1979), and/or for males higher chances for future mating (Smuts, 1985; van Schaik & Paul, 1996). Alternatively, paternal care might lead to higher association rates with mothers only as a by-product (Charpentier et al., 2008; Kummer et al., 1973).

In the genera *Rhinopithecus, Theropithecus,* and *Papio* we find several species living in multi-level societies. A commonality in these species is the presence of reproductive core units consisting of one male and one to several females, which are nested within a large and stratified community. The most common core units are hereby one-male multi-female units (Grueter et al., 2012; Stammbach, 1986). While superficially similarly organised, the relationships among male and the females within a unit show appreciable species-specific differences.

In hamadryas baboons (*Papio hamadryas*), for instance, units were classically described as having a star-shaped sociogram. Most interactions, e.g. grooming, were observed between individual females and their unit male, with little interaction among females (Kummer, 1968). This was later shown to not be necessarily the case for all hamadryas baboons, since in some units, females were equally likely to interact with other females as with their leader male (Swedell, 2002). Further, hamadryas baboon unit males use coercion to maintain control over female movements and associations (Schreier & Swedell, 2009). In geladas (*Theropithecus gelada*), males do not interact necessarily with all females of their unit but have a preferred main partner. Females are philopatric and form strong intrasexual bonds (Kawai et al., 1983). The main partner for male geladas are often females that lack available relatives and opt instead to interact with the male; while the male's interactions with his main partner are similar to those that characterize close female-female relationships, interactions with non-partner females are less frequent and often not reciprocated by the female (Dunbar, 1983). Interestingly, the quality of male-female relationships in geladas is suggested to affect the likelihood for evictions as unit-holders by other males (Dunbar, 1983). While living in superficially similar organised multi-level society, in snub nosed monkeys (*Rhinopithecus* sp.), males and females seem to show no tendency to develop strong relationships (Wang et al., 2013). Alternatively, it is suggested that socio-positive interaction from female snub-nosed monkeys are exchanged for copulations with males (Qi et al., 2017).

1.4 Social knowledge

Life in permanent and complex social groups entails the emergence of various social relationships among group members, which differ in their characteristics on a multitude of dimensions (Silk et al., 2013). Navigating such complex social environments can be a cognitively challenging task and likely favours individuals that have skill sets and the cognitive capacities to make use of social knowledge, i.e., gather and process social information about conspecifics and pay attention to and classify their relationships with others.

The potential interplay between sociality and the evolution of brain size and cognition in group-living animals has in the past motivated several theories attempting to explain its underlying mechanisms. In one of the earlier publications of Alison Jolly (1966) in which she was working on the behaviour and intelligence of lemurs, Jolly argued that interspecific competition within groups favoured the evolution of primate intelligence. Byrne and Whiten, later in 1988, formulated the 'Machiavellian Intelligence' hypothesis, emphasising that the cognitive abilities of primates have evolved in an arms race of increasingly sophisticated 'Machiavellian' strategies to deal with their social competitors. Even later, in 1998, Dunbar's 'Social Brain Hypothesis' shifted the focus on the general cognitive demands that living in complex societies with numerous and variable relationships in great numbers includes.

As a matter of fact, evidence suggesting the existence and use of such social knowledge is documented for a large number of species (Brown & Laland, 2003; Carazo et al., 2008; McComb et al., 2000; Tibbetts, 2002). While we find the bases for all higher social skills, namely the recognition of individuals, in simple and more complex forms in a variety of species (Wiley, 2013), especially the primate literature offers experimental evidence for a broad range of social knowledge and skills which vary in social context and complexity (Cheney & Seyfarth, 2008).

Several primate species have shown their ability to assess and monitor attributes of their group members, from more stable attributes like kin relations, or more specifically, close associate relations, e.g., vervet monkeys (Cheney & Seyfarth, 1980), crab-eating macaques (*Macaca fascicularis*) (Dasser, 1988), Japanese macaques (Schino et al., 2006), to rank positions within the group, e.g., chacma baboons (Cheney, 1995; Kitchen et al., 2005), ring-tailed lemurs (*Lemur catta*), (MacLean et al., 2008), sooty manabeys (*Cercocebus torquatus atys*) (Range & Noë, 2005), but also more transient attributes, like temporary friendships between female and male baboons (Smuts, 1985) or temporary sexual spatial associations, i.e. consortships (Crockford et al., 2007). Further, Bergman et al. (2003) presented interesting insight in the ability of chacma baboons to classify individuals simultaneously along two social dimensions, which were in this case matrilineal kinship and rank hierarchy, when testing the response of females to simulated rank reversals. Such knowledge hereby does not only extend to an individual's direct associations but also to third-party relationships (Bergman et al., 2003; Silk et al., 1999; Silk, 1993).

When navigating the social environment, the knowledge about previous interactions with group members, the capabilities of potential partners or competitors, and the nature and quality of relationships between others, can aid in predicting the outcomes of future interactions and allows therefore to act more strategically. For example, Tonkean macaques (*Macaca tonkeana*) respond more strongly to conflicts between strongly bonded individuals ('friends') compared to non-friends (Whitehouse & Meunier, 2020), lower-ranking chacma baboons use acoustic information, here playbacks of female calls, to deduce mating opportunities (Crockford et al., 2007), and hamadryas baboon "bachelor" males assess the bond strength of unit-males and their associated females before selecting targets for take-over attempts (Bachmann & Kummer, 1980).

In contrast, it is also important to point out that life in seemingly complex systems might not necessarily reflect the actual cognitive demands that individual animals are confronted with (Barrett et al., 2007). For instance, Bergman (2010) showed that gelada males only possess limited capabilities or motivation to recognise other males individually. This “missing social knowledge”, as Bergman explains, reflects how a species extent of social knowledge is not necessarily directly linked to life in a complex social system *per* se, but that it depends on individual demands that the social environment presents.

1.5 The genus *Papio* and the Guinea baboons

The genus *Papio* includes six recognised species: olive (*Papio anubis*), chacma (*P. ursinus*), Kinda (*P. kindae*), yellow (*P. cynocephalus*), hamadryas (*P. hamadryas*) and Guinea baboons (*P. papio*). Baboons are distributed across large parts of Subsaharan Africa and the south-west Arabian Peninsula in different ecological conditions (e.g., Chala et al. 2019). Among the six members, we find substantial variation in their social structure, organisation and mating systems (Fischer et al., 2019). Chacma, olive, Kinda, and yellow baboons live in multi-male-multi-female groups with female philopatry and male-biased dispersal. Male dominance hierarchies are often clearly distinguishable, and a high rank strongly correlates with reproductive success (Altmann et al., 1988; Henzi & Barrett, 2005). In contrast, hamadryas and Guinea baboons live in complex multi-level societies with philopatric males and female-biased dispersal. At the base of the society are the reproductive one-male units, which aggregate into higher-order levels, serving different social and ecological functions (Kummer, 1968; Patzelt et al., 2014; Schreier & Swedell, 2009; Stammbach, 1986). The variation in ecological and social components between species but also within population of the same species makes them a good model to study effects of environmental conditions on social evolution.

The multi-level society of Guinea baboons (Patzelt et al., 2014) is based on ‘units’, which consist of a “primary” male, one to seven associated females and their offspring, as well as associated ‘bachelor’ males (Fischer et al., 2017; Goffe et al., 2016). Several units and bachelor males form ‘parties’, which in turn aggregate into ‘gangs’. Females socially and spatially associate mainly with their primary male and show mate fidelity (offspring within a unit are sired to 91.7 % by the primary male; Dal Pesco et al., 2022). Female tenures range from several weeks to years, and transfers to other males occur individually and are possible between all levels of the society, i.e. within parties but also among parties or gangs (Goffe et al., 2016). Females enjoy high spatial freedom, may move independently and interact with other group members, including other adult males. Further, females have considerable leverage in maintaining the relationship and are suggested to play a decisive role in mate selection (Goffe et al., 2016). Male Guinea baboons form strong bonds with other males, and bachelor males play an essential role in the cohesion of the party (Dal Pesco et al., 2022). Males support each other in conflicts and show low aggression rates, preventing researchers from discerning a clear dominance hierarchy (Dal Pesco et al., 2021). Moreover, overt attempts to take-over females from other primary males are extremely rare. Furthermore, male bonding appears to be promoted by higher genetic relatedness within parties than between parties (Dal Pesco et al., 2021). In previous playback experiments in the same study population, Guinea baboon males showed surprising response patterns that deviated from similar experiments in other baboon species: primary males paid greater attention to vocalisations from familiar males compared to neighbour or stranger males (Maciej et al., 2013), and also paid more attention to sequences of male and female vocalisation that confirmed current male-female association patterns compared to information that presented new and unusual information (Faraut & Fischer, 2019).

1.6 Study aims

The general aim of this PhD thesis was to characterise the relationship between Guinea baboon primary males and their associated females. My main focus was hereby, firstly, on testing whether the relaxed social environment of the Guinea baboon society affects males' attention to social information, and secondly, how primary males distribute social investment among their associated females.

In my first study (**chapter 2**) I use playback experiments to test male Guinea baboons' knowledge of their females. In a first experiment I tested if males can recognise their female by voice. In two occasions, I either presented the vocalisation of an associated females or of a non-associated female. In the main experiment I tested whether males keep track of the whereabouts of associated females shortly after the female left the proximity of the male. I presented vocalisations of associated females from locations that were either consistent or inconsistent with the actual spatial position of the female, and I analyse whether males show signs of surprise when tested in the physically impossible, inconsistent condition.

The aim of my second study (**chapter 3**) was to identify female characteristics that might affect male interaction with the female. Under time budgetary constraints, primary male might be forced to distribute their time for social interaction among their females. In this study, I tested whether female characteristics reflecting their current and long-term reproductive value, namely reproductive state and age, affect male interaction rates and spatial proximity.

In a general discussion (**chapter 4**), I summarised the main results of both studies and discuss the findings in a broader context. Finally, I suggest potential future avenues of research.

Chapter 2

Male Guinea baboons are oblivious to their females' whereabouts

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Author Contributions:

Dominique Treschnak, **Dietmar Zinner** and **Julia Fischer** designed the study. **Dominique Treschnak** collected the data. **Dominique Treschnak** prepared the data for analyses. **Dominique Treschnak** analysed the data and prepared the figures. **Dominique Treschnak** drafted the manuscript. **Dominique Treschnak**, **Dietmar Zinner**, and **Julia Fischer** discussed the results and edited the manuscript.

2.1 Abstract

In group-living species, evolution puts a premium on the ability of individuals to track the state, whereabouts, and interactions of others. The value of social information might vary with the degree of competition within and between groups, however. We investigated male monitoring of female location in wild Guinea baboons (*Papio papio*). Guinea baboons live in socially tolerant multi-level societies with one-male-units comprising 1-6 females and young at the core. Using field playback experiments, we first tested whether male Guinea baboons (N=14) responded more strongly to playbacks of associated vs. non-associated females, which was the case. In the second and core experiment, we tested whether males (N=22 males, N=62 trials) keep track of the whereabouts of associated females by playing back unit females' calls from locations that were either consistent or inconsistent with the actual position of the female. Contrary to predictions, males responded equally strongly in both conditions. While males seem to recognize their females by voice, they might lack the attention or motivation to track their females' movement patterns. These results reinforce the view that the value of social information may vary substantially with the distribution of power in a society. While highly competitive regimes necessitate high attention to deviations from expected patterns, egalitarian societies allow for a certain degree of obliviousness.

2.2 Introduction

Knowledge about conspecifics and their relationships guides social decision-making in many group-living animals. The use of such social knowledge is documented for a large number of species, ranging from simple and more complex forms of individual recognition (Wiley, 2013) to the assessment and monitoring of stable or transient social attributes of group members, like kinship, rank, or bond strengths. Such knowledge extends not only to an individual's direct associations but also to third-party relationships (Seyfarth & Cheney, 2015). When navigating the social environment, knowledge about previous interactions with group members, the capabilities of potential partners or competitors, and the nature and quality of relationships between others, aids in predicting the outcomes of future interactions and allows to act strategically. For example, spotted hyenas (*Crocuta crocuta*) joining into dyadic fights mainly support the dominant individual and are subsequently also more likely to attack relatives of the subordinate (Engh et al., 2005). Pinyon jays (*Gymnorhinus cyanocephalus*) assess their relative rank difference to strangers by observing them in encounters with known individuals (Paz-y-Miño C et al., 2004). Tonkean macaques (*Macaca tonkeana*) respond more strongly to conflicts between strongly bonded individuals ('friends') compared to non-friends (Whitehouse & Meunier, 2020).

Besides kin and allies, mating partners are of particular value to an individual. Males compete not only for access to females (Clutton-Brock & Parker, 1992; Clutton-Brock & Vincent, 1991); they are also under selection to monitor the state and behaviour of females. Males may increase their reproductive success by assessing suited mating partners (A. D. Davies et al., 2020) or mating opportunities (Balsby & Dabelsteen, 2005; Crockford et al., 2007). In many species, females become the centre of male attention when they approach the fertile phase of their reproductive cycle. In contrast, in species where males and females form long-lasting bonds as in monogamous (Birkhead & Møller, 1995) or polygynandrous species (e.g., plains zebras (*Equus burchellii*) (Rubenstein & Hack, 2004), hamadryas baboons (*Papio hamadryas*) (Swedell & Plummer, 2012)), males are permanently incentivised to monitor and control associated females' whereabouts and interactions with other group members.

We tested male knowledge of female whereabouts in wild Guinea baboons (*Papio papio*). The species lives in multi-level societies. At the core are one-male units consisting of one primary male, one to six associated females, and their offspring. Bachelor males may be associated with several such units (Dal Pesco et al., 2021). Several units form a party, which in turn aggregate into gangs (Patzelt et al., 2014a). Females associate with one primary male and show mate fidelity (Goffe et al., 2016). Still, in contrast to hamadryas baboons, they also enjoy spatial freedom, i.e., they may spend considerable time away from their male (Goffe et al., 2016). Females may transfer to other males between all levels of the baboon society. Transfers have even been observed for females while pregnant or with a dependent infant. We hypothesized that primary males keep track of the movement patterns of their associated females, as proximity or interactions between associated females and other males could indicate potential transfer intentions of their females to primary males. To test this hypothesis, we conducted a playback experiment (Fischer et al., 2013), in which we presented female grunts from a location that was either consistent or inconsistent with the actual position of the female. We made use of the violation-of-expectation paradigm and presented the animals with a physically impossible scenario, similar to Townsend et al. (2012). We tested a male immediately after the female had left him and assumed that he would have noticed the direction in which she disappeared. We predicted that males would show 'signs of surprise', meaning a stronger response, when they were confronted with information that the female was in an unexpected – indeed physically impossible – location compared to their response when the female's vocalisation came from the direction into which she had recently disappeared. In a preparatory experiment, we tested the prerequisite that males can recognise their associated females by voice. We tested if males respond more strongly to the vocalizations of females from their unit compared to the vocalizations of females from another unit but the same party. We predicted that males would show stronger responses when presented with vocalisation from unit females.

2.3 Methods

The experiments took place between January 2019 and August 2021 at the Centre de Recherche de Primatologie Simenti in the Niokolo-Koba National Park in Senegal, a field station maintained by the German Primate Center (see Fischer et al., 2017 for details). The study population comprised ~ 200 individually identified Guinea baboons that belonged to three parties, with a varying number of reproductive units (between 15 and 25 per year across three parties) suitable for the experiments. The baboons are habituated to the presence of researchers and allow approaches within a few meters without signs of disturbance.

For the experimental stimuli, we recorded 'grunt' vocalisations of sub-adult and adult females during their non-receptive phase, i.e., the females did not show any swelling of their anogenital skin as a sign of high ovulation probability. Individual females were chosen opportunistically based on the availability of high quality recordings. Grunts are the most frequently occurring vocalisation in Guinea baboons (47.8 ± 30.1 call elements/h/individual) and are mainly produced in affiliative contexts (Maciej, Ndao, et al., 2013). To produce high-quality experimental stimuli, we selected only recordings with a high signal-to-noise ratio, i.e., a large difference between signal amplitude and the amplitude of other background sound sources and no other sounds overlaying the individual grunts. We inserted silent segments between individual grunt elements and normalised call amplitudes to a percentage of their dynamic range (65 - 90%). Female grunt vocalisations show individual differences in structural characteristics, such as the length and number of elements within a grunting bout. While we wanted to maintain these inter-individual differences, we also wanted to use stimuli that did not vary too much in their structure, potentially influencing the responses of males independently of the test condition. We, therefore, set limitations for the total length of a grunt sequence (duration from the start of the first grunt to the end of the last grunt), number of grunts per sequence, and the total grunt duration within a sequence (sum of the length of all individual grunts within a sequence). The final stimuli had an average total length of 2.23 s (2.12 –2.49 s), an average number of six grunt elements per sequence (4 –7), and an average total grunt duration per sequence of 0.58 s (0.48 – 0.74 s). We measured the sound pressure level for each stimulus at a distance of 10 m (comparable to experimental conditions). We also controlled whether the stimuli sounded subjectively similar to actual vocalisations of female baboons (figure 2.1).

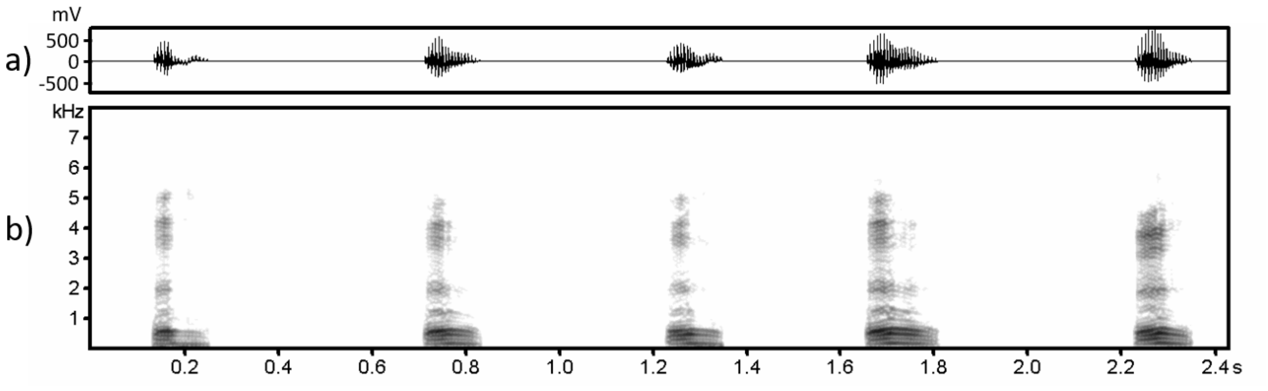

Figure 2.1: Example of experimental stimulus. a) Waveform (envelope) of the call amplitude changing over time. b) Spectrogram depicting the distribution of different amplitudes (shades of grey) over the frequency spectrum and over time. FFT length = 512, Hamming window, overlap 93.75 %, sampling frequency = 16 kHz, time resolution = 2 msec.

For the recordings, we used a solid-state recorder (Marantz PMD661 MKII, Marantz, Kanagawa, Japan) with Sennheiser directional microphones (K6 power module with ME66 recording head, Sennheiser Electronic KG, Barleben, Germany) and Rycote windshields (Rycote, Gloucestershire, UK) with a sampling frequency of 44.1 kHz and 16-bit resolution. We only used recordings taken from a distance < 5 m to the animal to avoid effects of signal attenuation (Maciej et al., 2011)). We used

Avisoft-SASLab Pro 5.2 (Avisoft Bioacoustic, Glienicke, Germany) and Audacity 3.1 (Audacity Team, https://audacityteam.org) to analyse and prepare the playback files.
In Experiment 1 (individual recognition), we presented males with calls from a female from their unit (*unit-female* condition) and a female from another unit (*non-unit-female* condition). Trials were separated by at least five days and conducted only when females were non-receptive. Once the female whose call was to be played back was not visible to the subject, a loudspeaker was positioned at a 90° angle to the left or right of the male depending on the actual position of the female, and the stimulus presented. Male responses were video recorded for three minutes after the onset of the stimulus. We conducted 28 playback trials testing 14 primary males.

In Experiment 2 (spatial monitoring), we tested males in a within-subject design and presented grunts from a unit-female on two occasions separated by at least seven days. As above, trials were conducted only when females were non-receptive. In the *consistent* condition, the loudspeaker was hidden in a location matching the actual direction of the departed female. In contrast, in the *inconsistent* condition the loudspeaker was hidden in the opposite direction (i.e., the angle in direction between the positions of loudspeaker and female was ~180°), presenting an impossible scenario (figure 2.2). A male was tested after he had been near a unit-female, she had then walked away and was no longer in sight. We aimed to conduct trials within 180 s of the female being out-of-sight to ensure that the female would not be able to reach the location of the loudspeaker (median time out-of-sight: 70 s, range 8 s – 273 s). A loudspeaker was then hidden in vegetation, at a 90° angle to the left or right of the male and a distance of approximately 10 m. Male responses were video recorded for 10 min. after the onset of the stimulus. Throughout the experimental trials, only the researcher who video-recorded the response of the male from a distance of 3 to 7 m was visible to the male. We only conducted experimental trials in generally calm periods, i.e., not during aggressive episodes among group members and not on days where groups encountered predators or other disturbances occurred. Males were only tested when they were resting or feeding, not being in direct contact or interacting with other adult baboons and if no other baboon was between the loudspeaker and the male. We conducted 62 playback trials with 22 primary males. Nine of these males were tested twice with the call of a different female (average time between first and second run: 43 weeks (min: 3, max: 100)).

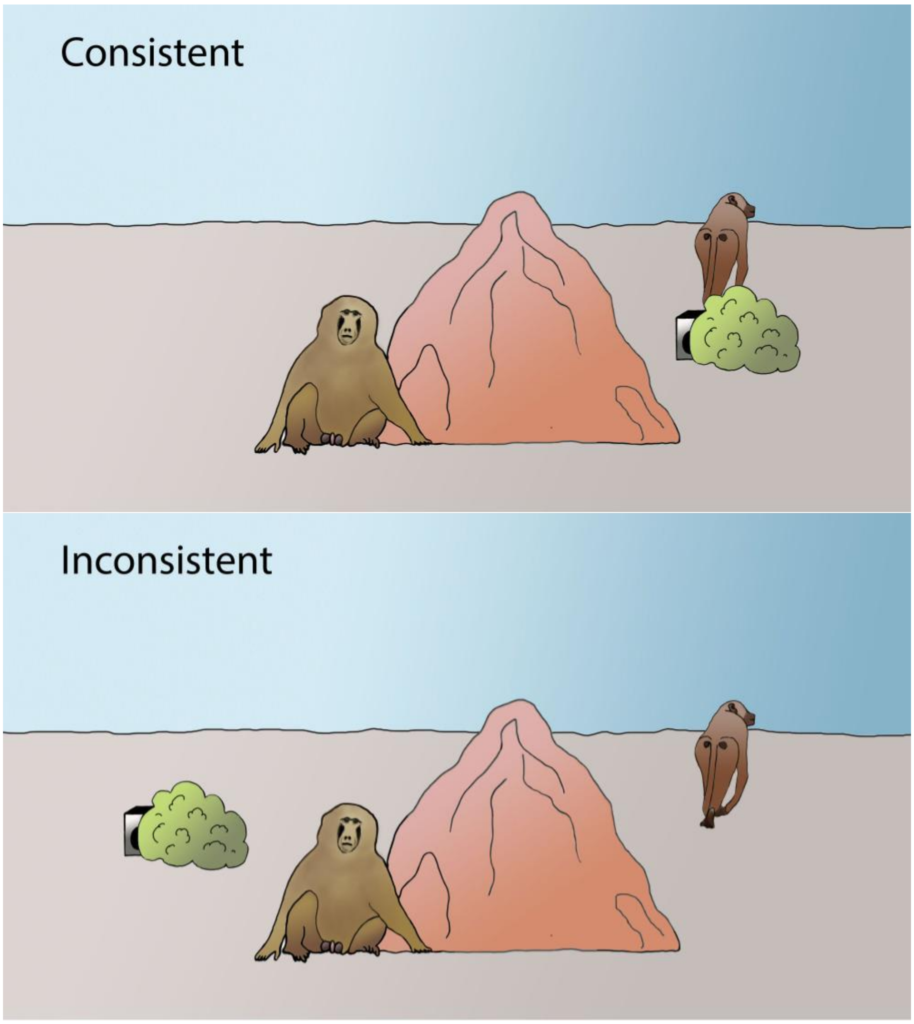

Figure 2.2: Set-up experiment 2 (spatial monitoring). In the consistent condition, a loudspeaker is positioned close to the location where the female has been before leaving, in the inconsistent condition, the loudspeaker is placed in the opposite direction in respect to the male's position.

The sequence in which experimental conditions were presented was counterbalanced and then randomly assigned to individuals. Males that were tested with a second female in experiment 2 were exposed to the experimental conditions in the opposite order in their second run. We could not control the direction from which stimuli were presented to males as the positions of male, female and the trial condition dictated the experimental setup. We only used recordings from females that were non-receptive at the time of the recording to avoid a potential influence of female reproductive state. Also, we only conducted the trials when females were non-receptive.

For the playback, we first used a DAVIDactive loudspeaker with an integrated battery (VISONIK, Berlin, Germany) connected to a handheld solid-state recorder (Marantz PMD661 MKII, Marantz, Kanagawa, Japan) by cable. In 2021, we switched to a wireless loudspeaker (Sonos Move, Sonos, Santa Barbara CA, US) connected to a Gigaset GX290 smartphone (Gigaset, Bocholt, Germany) via a portable Wifi

Network from a second Gigaset GX290 smartphone. With the new wireless set-up, experimental trials could be conducted more efficiently. Old and new loudspeakers were accordingly adjusted to produce qualitatively comparable stimuli. We conducted 22 trials with the first set-up and 68 with the second. Videos were recorded using a Panasonic HC-X909 video camera (Panasonic Corporation, Kadoma, Japan). Sound pressure levels were, measured using a sound level meter (Voltcraft SL-400, Voltcraft, Germany).

Video recordings were coded using Solomon coder beta (András Péter, solomon.andraspeter.com) on a frame-by-frame basis (25 frames/s). We examined male responses by coding changes in their head orientation; i.e., changes between the neutral position: male faces the camera or in the opposite direction to the loudspeaker, and subsequent looks exceeding an angle of 45° towards the direction of the loudspeaker or away from it. We measured the duration of the first-look and the latency to respond. We measured the onset of the first responses for all trials and examined the histogram of latencies blind to the experimental condition searching for a latency which separates putative actual responses with a short latency from later responses which might have happened for reasons other than the playback. We settled on a cut-off criterion for responses to be counted as valid if they occurred within the first 2.5 s of presenting the stimulus (figure 2.3). Responses that occurred after the cut-off criterion of 2.5 s were counted as non-response, with a duration of 0 s and censored latency. As the first look in the inconsistent condition could be truncated because the male may turn his attention to look into the direction where the female was last seen, we additionally measured the total time vigilant (all looks toward the loudspeaker or actual position of the female) within 30 s after stimulus onset in the social monitoring experiment, (appendix, figure A2.1 (classification of responses)).

For twenty randomly selected trials (representing 22% of all trials), the video recordings were coded by a second observer blind to the general experimental setup and research question and compared to the coding results of the first author (DT). We compared the amount of correctly coded changes in head orientation (according to the 45° rule; see Methods) and the looking durations and latencies for each trial. Both coders correctly agreed on the occurrence of the first response in 19 out of 20 trials. Consecutive head orientation changes after the first response were correctly coded in 43 out of 55 instances (78%). The few head orientation changes that were not coded by both observers correctly were either relatively short glances or head movements where it was difficult to determine whether or not the 45° rule was fulfilled. As first responses could be clearly and reliably detected in almost all trials by both observers, our main criterion for reliability was the exact quantitative coding of the response. A Spearman's rank correlation for looking duration and latency revealed high inter-observer reliability for both measures (duration: rho = 0.99, $P < 0.001$; latency: rho = 0.95, $P < 0.001$). After the reliability of the coding procedure was ascertained, DT coded and analysed the full data set.

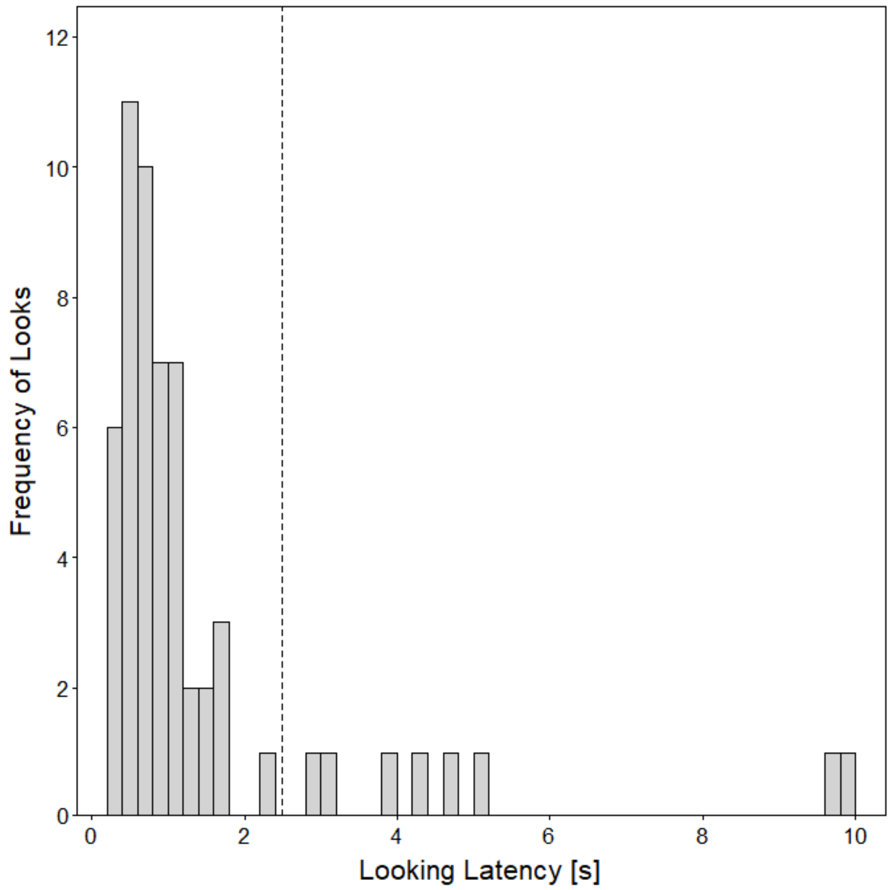

Figure 2.3: Histogram of the latency to the first response after presentation of the experimental stimulus. In 49 out of 62 trials a response occurred within the first 2.5 s. The vertical dashed line shows the selected cut-off point for valid responses at 2.5 s.

We used a Linear Mixed model (Baayen et al., 2008) for first-look duration (experiment 1) and vigilance time, a Generalized Linear Mixed Model with gamma error structure and log link function (Baayen et al., 2008) for the duration of the first-look (experiment 2), and a survival analysis (Jahn-Eimermacher et al., 2011) for latencies. In addition to the main predictor ‘experimental condition’, we included total unit size for each male as a fixed effect to control for the influence of the number of unit-females and male identity as random intercept. To investigate the effect of the main predictor we compared full models to null models lacking the main predictor of interest (experimental condition) in the fixed effect part, using a likelihood ratio test (Dobson & Barnett, 2008). Confidence intervals of estimates and fitted values were determined using a parametric (LMM & GLMM) and non-parametric (survival analysis) bootstrap (*N*=1000 bootstraps). Responses that occurred after the cut-off criterion of 2.5 s were considered censored for survival models and entered the duration models with a length of zero. Model stability was assessed by comparing model estimates for the complete data set with estimates for data sets with levels of the random effect (subject) excluded one at a time.

Experiment 1 (individual recognition): Model validity checks for the first-look duration model revealed no obvious deviations from assumptions of normality or homoscedasticity, which allowed for the use of a Linear Mixed Model. For the first-look latencies, we used a survival analysis (Cox proportional hazard model), as this method allows for the inclusion of trials without a response and has fewer distributional assumptions. Prior to the analysis, we log-transformed (base e) first-look durations to achieve an approximately symmetrical distribution. The assessment revealed acceptable stability for the survival model (see table A2.2). We found instability in the range for the estimated effect of the main predictor 'experimental condition' in the Linear Mixed Model for first-look duration (see table A2.1 – A2.2), which could be traced back to the influence of one single trial, that, when being removed, led to a dysfunctional model with essentially zero residual variance and hence unrealistic model estimates. The observed instability can therefore be seen as an artefact and not as the effect of removing an influential case. As the same call (stimulus) could be used for different males in Experiment 1, and some calls were from the same female, we included female ID and stimulus ID as additional random intercept effects. No random slopes were included, as none were theoretically identifiable.

Experiment 2 (spatial monitoring): We used Generalised Mixed Models for the first-look duration as model validity checks revealed deviations from assumptions of homoscedasticity. We found no deviations for vigilance durations and used a Linear Mixed Model. For first-look latencies, we again calculated a survival analysis (Cox proportional hazard model). In the GLMM, 'first-look' durations of 0 were changed to 0.01 s to allow the use of the gamma error distribution. Vigilance durations were squared to achieve a more symmetrical distribution. The assessment revealed acceptable stability (see table A2.3 – A2.5). The GLMM showed slight underdispersion (dispersion parameter = 0.93; dispersion parameter <1 reveals underdispersion). Underdispersion can lead to over-conservative model estimates, which would, in this case, unlikely change the general interpretation of the model results. We did not calculate confidence intervals for the estimated effects in the survival model, as to our knowledge, there is no methodological approach available that allows calculating confidence intervals for Cox proportional hazard models with more than one random effect included.

After conducting the data analyses for the spatial monitoring experiment, we discussed the potential influence on male attention of the presence of other baboon parties when conducting the trials. We, therefore, formulated new models for all three outcome variables including a binary indicator indicating whether other parties were overlapping in space with the party of the tested male (other parties in proximity (mingled) = Y; no parties in proximity = N) (model estimates for all three alternative models, table A2.6). Information about the presence of other parties was recorded directly after the conduction of successful trials.

Analyses were carried out in R (version 4.1.1; R Core Team, 2021). GLMMs and LMMs were fitted using the function *glmer* of the R package *lme4* (version 1.1- 27.1; Bates, 2015). For the Cox proportional hazard model, we used the packages *survival* (3.2- 13) and *coxme* (2.2- 16). Model stability and overdispersion were assessed using a function provided by Roger Mundry (see details just below). The bootstrapped confidence intervals were obtained using the function *bootMer* of the package *lme4*. We calculated test statistics and *P*-values for LMMS using the *lmer* function of the *lmerTest* package (3.1-3).

This research adhered to the ASAB/ABS Guidelines for the Use of Animals in Research ('Guidelines for the Treatment of Animals in Behavioural Research and Teaching', 2020). Approval and research permission were granted by the Direction des Parcs Nationaux and the Ministère de l'Environnement et de la Protection de la Nauture de la République du Sénégal (date: 22/04/2019). Research was conducted within the regulations set by Senegalese agencies as well as by the Animal Care Committee at the German Primate Center (Göttingen).

2.4 Results

In experiment 1 (individual recognition), males responded to the playback of calls in 24 out of 28 trials. The average duration of the first response was 3.2 s ± 2.5 s (median ± IQR). Males looked longer when presented with calls from unit-females (3.4 s ± 4.6 s) compared to non-unit females (2.3 s ± 3.8 s) (figure 2.4a; full-null model comparison: χ^2_1=8110, *P*=0.004, table A2.1a). The average latency of responses was 1.0 s ± 0.9 s for the unit-female and 1.3 s ±3.2 s for non-unit-females (median ± IQR). Unit size had no obvious effect on response duration or latency (Duration: *P*=0.48; Latency: *P*=0.37, table A2.1a, A2.2).

In experiment 2 (spatial monitoring), males responded to the playback in 49 out of 62 trials (consistent condition: *N*=22, inconsistent: *N*=27). There was no obvious difference in the duration of first-looks in the consistent (2.8 s ± 4.4 s, median ± IQR) compared to the inconsistent (2.9 s ± 2.6 s) condition (figure 2.4b; full-null model comparison: χ^2_1=0.0002, *P*=0.99, table A2.3). There were no obvious differences in response latencies between the two conditions (consistent: 0.7 s ± 0.5 s; inconsistent: 0.8 ± 0.6 s (median ± IQR); full-null model comparison: χ^2_1 =1.10, *P*=0.29, table A2.4). There were also no obvious differences in the overall time vigilant (consistent: 7.8 s ± 7.2 s (median ± IQR); inconsistent: 8.1 s ± 6.4 s; full-null model comparison: χ^2_1 =0.04, *P*=0.84, table A2.5). We found no evidence that unit size influenced any of the response variables (Duration: *P*=0.38; Latency: *P*=0.63, Vigilance: *P*=0.15, tables A2.3, A2.4, A2.5). The presence of other parties during the trial did not affect the responses of the males (Duration: *P*=0.94; Latency: *P*=0.73, Vigilance: *P*=0.89, tables A2.7, A2.8, A2.9).

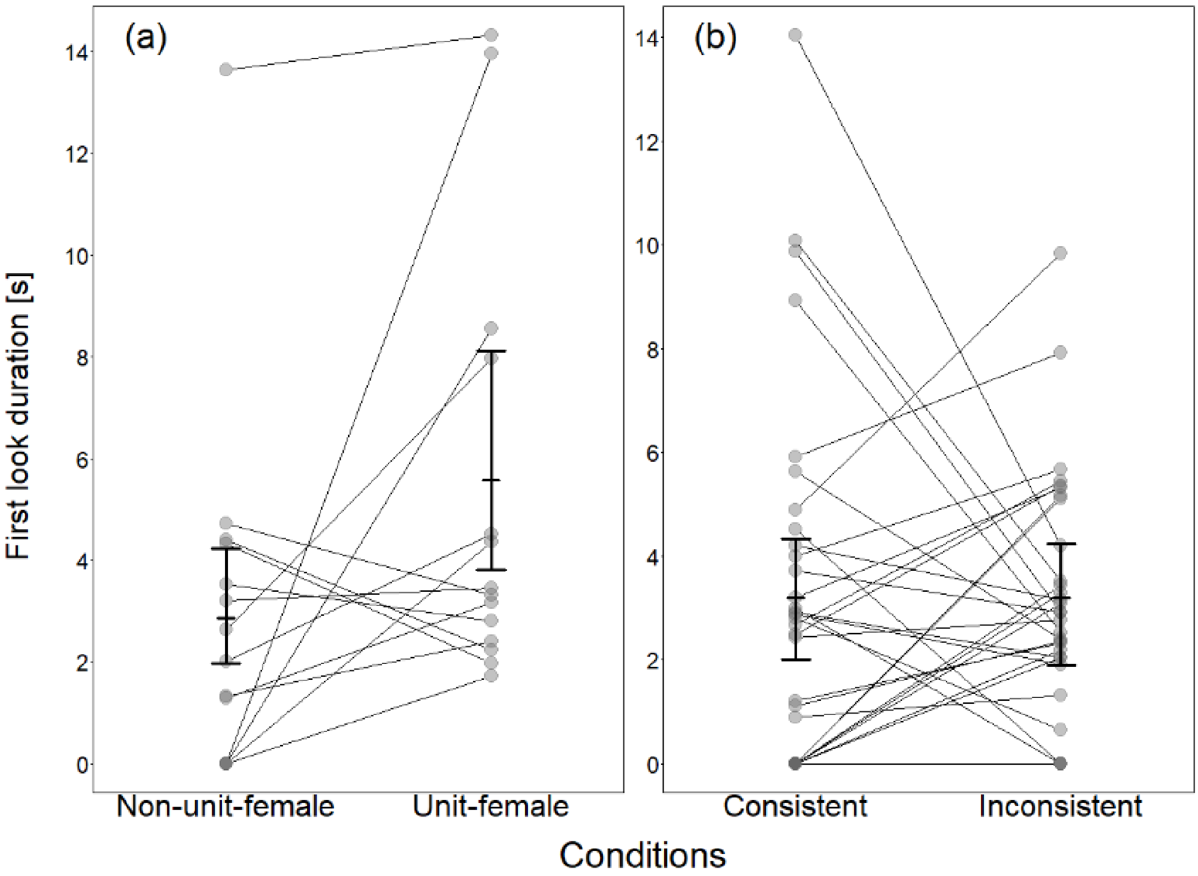

Figure 2.4: First-look duration for males in the a) individual recognition experiment and b) spatial monitoring experiment. Connected points represent data from the same individual (a: *N*=14; b: *N*=22). Thick black lines depict bootstrapped mean and 95% confidence intervals for males with average unit size.

2.5 Discussion

Male Guinea baboons showed no signs of surprise when calls from associated females were played back from an impossible location. Instead, they responded equally strongly to playbacks of calls from an impossible or a possible location. Further, males responded more strongly to the playback of vocalizations from unit-females compared to non-unit-females. While males seemed to be able to recognise their unit's females by voice, they lacked either the ability or the motivation to track their females' positions.

These findings were not in line with our initial prediction that primary males monitor the whereabouts of their females. Guinea baboons form one-male units similar to hamadryas baboons or mountain gorillas (*Gorilla b. beringei*). In both of these species, sexual coercion (Smuts & Smuts, 1993) is used by leader males to control female movement and interactions and to prevent transfers to other males (Schreier & Swedell, 2009b; Sicotte, 1993). In Guinea baboons, we did not observe such overt aggression towards females, except for some occasional chasing of females. Indeed, female Guinea baboons can roam relatively unimpeded and interact socially with other group members, including other adult males (Goffe et al., 2016).

The lack of differentiated response fits with the relatively laid-back stance of Guinea baboon males. Males form strong bonds with other males (Dal Pesco et al., 2021, 2022; Patzelt et al., 2014a). They also show low levels of overt aggression, preventing us from discerning a clear dominance hierarchy (Dal Pesco et al., 2021). At the same time, female Guinea baboons have considerable leverage in mate choice and intersexual bond maintenance (Goffe et al., 2016). Male strategies mainly seem to consist of investing their social time into female grooming and support. Interestingly, males appear to face a trade-off in the allocation of social time, as male investment into socio-positive interactions with other male declines with increasing unit size (Dal Pesco et al., 2022). Social investment into females thus might be important for intersexual bond maintenance and potentially female mate choice in the first place.

Since we tested males when the female whose calls were played was not receptive, we do not know whether males would be more attentive if the female would be able to conceive. We conducted the trials only while females were non-receptive because, during females' oestrus, primary males and females are less likely to separate (Goffe, 2016), leaving very few opportunities for conducting the experimental trials. Thus, we cannot exclude the possibility that males would respond differentially in conditions where they should be more motivated to track their female's whereabouts. It is important to note that we do not make any claims about the males' ability to track female whereabouts – it might well be that they are aware of their_females' locations but simply do not care to attend to apparent violations of their expectations. This inability to distinguish between what the animals 'can do' and 'do do' is, unfortunately, one of the limitations of such kinds of field experiments (Fischer, 2022).

Our study adds to the accumulating evidence that the need to monitor the social environment varies between species with the degree of competition among individuals. For instance, the highly competitive chacma baboons (*Papio ursinus*), which live in female-philopatric groups, show strong responses to the playback of vocalisation from unfamiliar males (Kitchen et al., 2005, 2013), while Guinea baboons showed greater attention to vocalisations from familiar males compared to neighbours or strangers (Maciej, Patzelt, et al., 2013). In geladas (*Theropithecus gelada*), which live in a multi-level society in aggregations of up to several hundred individuals, vocal recognition seems to be limited to individuals with a high degree of social overlap (Bergman, 2010). Additionally, when presenting individuals with information about changes in association patterns, chacma baboons responded strongly to simulated separations of consortships (Crockford et al., 2007), while Guinea baboons paid more attention to information consistent with current male-female association patterns (Faraut & Fischer, 2019). Similarly, Geladas did not differentiate between consistent or inconsistent information about male-female relationships at all (le Roux & Bergman, 2012).

While the link between group-living and sophisticated social knowledge is well documented (Seyfarth & Cheney, 2015), it is still unclear whether life in a socially complex environment per se (Holekamp, 2007) or rather the degree of competition within and between groups selects for advanced socio-cognitive skills ("Machiavellian intelligence"; Whiten & Byrne, 1988). Deciding on this issue is further complicated by the question of how to operationalize social complexity.

Kappeler (2019) provided a qualitative framework for social complexity, which encompassed Social organization, Social structure, the Mating system, and the Care system. Lukas and Clutton-Brock, 2018 distinguished between organisational complexity in animal societies, referring to the division of labour, and relational complexity, referring to the differentiation of social relationships among group members. They reject the idea of a unitary concept of social complexity (and we agree). Other authors have proposed to hone in on the differentiation of social relationships. Bergman & Beehner (2015) conceived social complexity in terms of the number of differentiated relationships a given individual maintains. Building on this idea, Fischer et al. (2017) proposed a method to quantify social complexity by assessing the diversity of individuals' relationships. Despite the variety of approaches to operationalising social complexity, the concept, unfortunately, remains elusive. Therefore, the present results cannot more specifically inform the debate between the link between social complexity and social cognition.

With regards to the link between the degree of competition between individuals and the allocation of social attention, more progress has been made. Bergman (2010, p. 2050) argued that "missing social knowledge" might be a consequence of the absence of a competitive environment that offers no benefits for the ability to assess and use of specific social information of conspecifics. Our results, as well as results from previous studies on the same population (Faraut & Fischer, 2019; Maciej, Patzelt, et al., 2013), suggest that a reduced competitive environment affects the value of social information, and as a consequence, the motivation or ability of an individual to attend to them. At the same time, both Guinea baboons and geladas live in highly structured multi-level groups, suggesting that a complex social organisation does not per se select for a high motivation to monitor the social environment. We contend that a skewed distribution of power influences the value of social information and therefore the motivation to attend to events in the social environment.

2.6 Acknowledgements

We thank the Diréction des Parcs Nationaux and Ministère de l'Environnement et de la Protection de la Nature du Sénégal for permission to work in the Niokolo-Koba National Park. We are grateful to all research assistants for their help in collecting data.

2.7 Funding

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2.8 Appendix

Figures

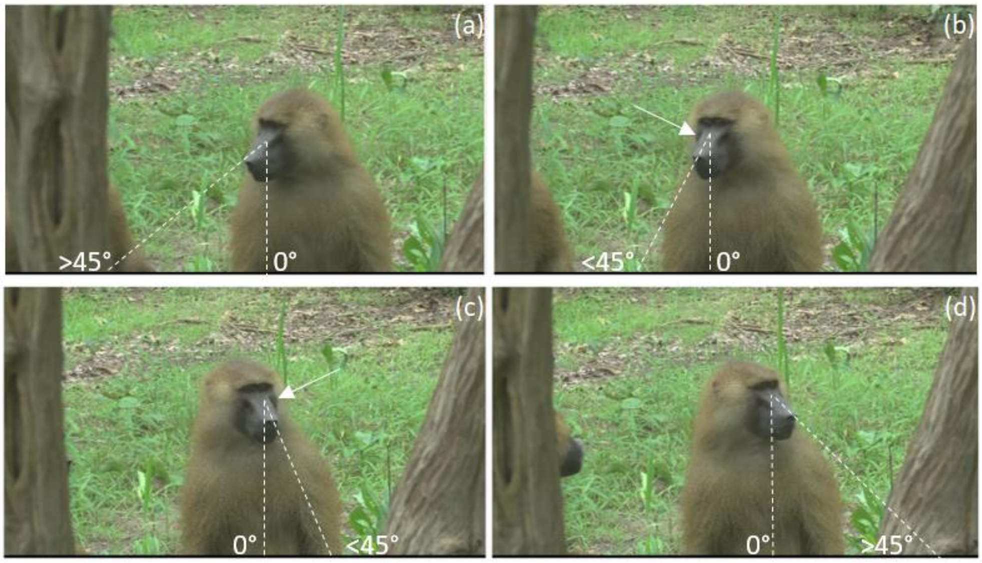

Figure A2.1 First look duration for males in the a) individual recognition experiment and b) spatial monitoring experiment. Connected points represent data from the same individual (a: *N*=14; b: *N*=22).

Tables

Table A2.1 Results of linear mixed model analysing the influence of the main predictor experimental condition (unit-female vs. non-unit-female) and unit size (number of females) on looking duration for experiment 1 (individual recognition).

Term	Estimate	SE	lower CI	upper CI	t	df	*P*	min	max
Intercept	1.269	0.289	0.637	1.898	(1)	(1)	(1)	0.576	1.653
Condition	0.664	0.181	0.248	1.108	3.275	1	0.008	-0.111(2)	1.198
Nr_Females	-0.075	0.081	-0.258	0.109	-0.669	1	0.521	-0.192	0.080

SE: standard error, CI: confidence interval, min/max: minimum and maximum estimate from model stability analyses. (1) Not presented due to very limited interpretability. (2) Model stability test without dysfunctional model (table A2.2) leads to different range of estimates (min: 0.478, max: 1.198). Model formula: lmer(log(First_Look_Dur) ~ Condition + Nr_Females + (1|MaleID) + (1|FemaleIID) + (1|CallID)).

Table A2.2 Reduced linear mixed model analysing the influence of the main predictor experimental condition (unit-female vs. non-unit-female) and unit size (number of females) on looking duration for experiment 1 (individual recognition).

Term	Estimate	SE	t	df	*P*
Intercept	1.567	0.149	(1)	(1)	(1)
Condition	-0.111	<0.001	-227 237.570	1	<0.001
Nr_Females	-0.017	<0.001	-146 467.080	1	<0.001

When assessing model stability, removal of a single level ("FFE") of the random intercept effect MaleID led to a dysfunctional model with unrealistic model estimates. Instability in the range for the estimated effects of the main predictor in table A2.1 can therefore be seen as an artefact and not as the effect of the removal of an influential case and does not reflect the actual range of estimated values.

Table A2.3 Results of Cox proportional hazard model analysing the influence of the main predictor experimental condition (unit-female vs. non-unit-female) and unit size (number of females) on looking latency for experiment 1 (individual recognition).

Term	Estimate	SE	lower CI	upper CI	Chi²	df	*P*	min	max
Condition	0.738	2.091	(1)	(1)	2.459	1	0.117	0.468	0.963
Nr_Females	0.247	1.280	(1)	(1)	0.809	1	0.369	0.123	0.495

SE: standard error, CI: confidence interval, min/max: minimum and maximum estimate from model stability analyses. (1) Confidence interval could not be calculated for Cox proportional hazard model with more than one random effect included. Model formula: coxme(Surv(First_Look_Lat) ~ Condition + Nr_Females + (1|MaleID) + (1|FemaleIID) + (1|CallID)).

Table A2.4 Results of generalised linear mixed model analysing the influence of the main predictor experimental condition (consistent vs. inconsistent) and unit size (number of females) on looking duration for experiment 2 (spatial monitoring).

Term	Estimate	SE	lower CI	upper CI	t	df	*P*	min	max
Intercept	1.529	0.469	0.739	2.068	(1)	(1)	(1)	1.212	1.661
Condition	-0.005	0.341	-0.538	0.517	<0.001	1	0.989	-0.079	0.142
Nr_Females	-0.145	0.165	-0.348	0.086	-0.669	1	0.381	-0.259	0.018

SE: standard error, CI: confidence interval, min/max: minimum and maximum estimate from model stability analyses. (1) Not presented due to very limited interpretability. Model formula: glmer(tr.First_Look_Dur ~ Condition + Nr_Females + (1|MaleID), family = Gamma(link = "log").

Table A2.5 Results of Cox proportional hazard model analysing the influence of the main predictor experimental condition (consistent vs. inconsistent) and unit size (number of females) on looking latency for experiment 2 (spatial monitoring).

Term	Estimate	SE	lower CI	upper CI	Chi²	df	*P*	min	max
Condition	0.318	1.374	-0.246	1.039	1.104	1	0.293	0.150	1.466
Nr_Females	-0.097	0.908	-0.556	0.563	0.232	1	0.630	-0.178	0.109

SE: standard error, CI: confidence interval, min/max: minimum and maximum estimate from model stability analyses. Model formula: coxme(Surv(First_Look_Lat) ~ Condition + Nr_Females + (1|MaleID)).

Table A2.6: Results of linear mixed model analysing the influence of the main predictor experimental condition (consistent vs. inconsistent) and unit size (number of females) on vigilance time for experiment 2 (spatial monitoring).

Term	Estimate	SE	lower CI	upper CI	t	df	*P*	min	max
Intercept	3.335	0.380	2.600	4.120	(1)	(1)	(1)	2.986	3.634
Condition	0.061	0.299	-0.530	0.660	0.202	1	0.841	-0.123	0.167
Nr_Females	-0.207	0.125	-0.460	0.050	-1.509	1	0.148	-0.284	-0.047

SE: standard error, CI: confidence interval, min/max: minimum and maximum estimate from model stability analyses. (1) Not presented due to very limited interpretability. Model formula:
lmer(Vigilance² ~ Condition + Nr_Females + (1|MaleID)).

Table A2.7 Model estimates for control predictor Mingled of alternative generalized linear mixed model (compare table A2.3; First-Look Duration) for experiment 2 (spatial monitoring) including the predictor Mingled (Y/N) to indicate the presence of another baboon party during the trial.

Term	Estimate	SE	lower CI	upper CI	t	df	*P*	min	max
Intercept	1.505	0.569	0.540	2.251	(1)	(1)	(1)	1.220	1.621
Condition	0.002	0.354	-0.545	0.551	0.007	1	0.994	-0.079	0.224
Nr_Females	-0.143	0.167	-0.362	0.072	-0.852	1	0.394	-0.256	0.017
Mingled	0.028	0.361	-0.555	0.641	0.077	1	0.939	-0.065	0.216

SE: standard error, CI: confidence interval, min/max: minimum and maximum estimate from model stability analyses. (1) Not presented due to very limited interpretability. Model formula:
glmer(tr.First_Look_Dur~Condition + Nr_Females + Mingled + (1|MaleID), family = Gamma(link = ”log”).

Table A2.8 Model estimates for control predictor *Mingled* of alternative Cox proportional hazard model (compare table A2.4, First-Look Latency) for experiment 2 (spatial monitoring) including the predictor *Mingled* (Y/N) to indicate the presence of another baboon party during the trial.

Term	Estimate	SE	lower CI	upper CI	T	df	*P*	min	max
Condition	0.347	1.415	-0.271	1.173	1.223	1	0.269	0.186	0.491
Nr_Females	-0.093	0.911	-0.556	0.555	0.223	1	0.637	-0.182	0.110
Mingled	0.127	1.135	-0.565	0.856	0.120	1	0.729	-0.101	0.259

SE: standard error, CI: confidence interval, min/max: minimum and maximum estimate from model stability analyses. Model formula: coxme(Surv(First_Look_Lat) ~ Condition + Nr_Females + Mingled + (1|MaleID)).

Table A2.9: Model estimates for control predictor *Mingled* of alternative linear mixed model (compare table A2.5, Vigilance Time) for experiment 2 (spatial monitoring) including the predictor *Mingled* (Y/N) to indicate the presence of another baboon party during the trial.

Term	Estimate	SE	lower CI	upper CI	t	df	*P*	min	max
Intercept	3.372	0.470	2.394	4.331	(1)	(1)	(1)	2.991	3.914
Condition	0.047	0.318	-0.532	0.663	0.142	1	0.888	-0.139	0.195
Nr_Females	-0.209	0.127	-0.469	0.039	-1.498	1	0.150	-0.308	-0.047
Mingled	-0.045	0.329	-0.671	0.605	-0.138	1	0.891	-0.301	0.124

SE: standard error, CI: confidence interval, min/max: minimum and maximum estimate from model stability analyses. (1) Not presented due to very limited interpretability. Model formula: lmer(Vigilance^2 ~ Condition + Nr_Females + Mingled + (1|MaleID)).

Chapter 3

Allocation of social investment of Guinea baboon males

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Dominique Treschnak, **Dietmar Zinner** and **Julia Fischer** designed the study. **Dominique Treschnak** and **Federica Dal Pesco** collected the data. **Dominique Treschnak** and **Federica Dal Pesco** prepared the data for analyses. **Dominique Treschnak** and **Roger Mundry** analysed the data and prepared the figures. **Dominique Treschnak** drafted the manuscript. **Dominique Treschnak**, **Dietmar Zinner**, **Federica Dal Pesco** and **Julia Fischer** discussed the results and edited the manuscript.

3.1 Abstract

In species with female choice, male social investment and support can serve as initial selection criteria and a male strategy to maintain access to females. Male aiming to maximise their reproductive success under time budgetary constraints should allocate their social investment strategically. when aiming to maximise their reproductive success. In this study, we investigated the allocation of social investment of wild Guinea baboon (*Papio papio*) primary males. Guinea baboons live in socially tolerant multi-level societies with ‘units’ at the core, which are comprised of a primary male, 1-7 associated females and their young. Using behavioural data of 51 individual primary males and 93 associated females over a period of eight years (2014 to 2021), we compared rates of socio-positive interactions and proximity between females of different reproductive state and age. Males interacted more frequently and were close to females that were showing signs of receptivity, and were more likely found in close proximity to lactating females. Males further showed a preference for young adult and mature females over subadult and old females. While Guinea baboon primary males maintain social relationships with all of their associated females, males’ social investment varies with female short- and long-term reproductive value.

3.2 Introduction

In most mammals, females are the limiting resource for reproduction of males (Trivers, 1972). The resulting competition among males for mating opportunities and control over potential reproductive partners constitutes an intense selection pressure shaping male mating behaviour in many ways (Clutton-Brock & Vincent, 1991; West-Eberhard, 1979). In multi-male multi-female groups, this competition among males results in dominance by the individual with the highest resource-holding potential. Males with the appropriate physical capabilities (e.g., body size, condition, weaponry) can dominate other males and claim the priority of access to receptive females (Altmann, 1962; Clutton-Brock et al., 1982; Ellis, 1995). In addition to indicators of male fighting ability, a male's social integration has shown to be a good predictor of reproductive success (Chowdhury et al., 2015; Gilby, 2012; Schülke et al., 2010).

The potential to monopolise females depends not only on male quality but also on female spatial distribution and reproductive synchrony (Taborsky et al., 2021). If females are easily defendable, reproductive success in a group might be completely skewed in favour of the dominant male. Dominant males are able to exclude competitors from reproducing through control over receptive females (Bercovitch, 1983, 1986; DeVore & Hall, 1965; Packer & Pusey, 1979, p. 19; Sherman, 1989) or directly through physical interferences into the mating attempts of subordinates (Clutton-Brock & Parker, 1995). Males that are unlikely to reach dominance status within a group are not fully excluded from reproduction, though, as alternative mating strategies, for example, sneaky copulations (Clutton-Brock et al., 1979), still allow for some reproductive success (Alberts, 2012; Taborsky et al., 2008). Further, sexual coercion by males, including harassment, intimidation, and forced copulations, are common strategies to gain access to females and control the reproduction of females (Muller & Wrangham, 2009).

In species with female choice, males show behaviours and morphological features aimed at attracting females. True displays of male quality in various modalities (Ryan & Keddy-Hector, 1992; Setchell, 2005) and exaggerated male traits (e.g. large canine, wide manes or elongated tails) are classical features affecting females' partner choice (Fisher, 1999; Kokko et al., 2002). Further, male social investment and support for females, but also into current offspring, can inform females about potential future parental investment and general behavioural tendencies (Ferrari, 1992; Lemasson et al., 2008; Price, 1990). Non-human primates provide the opportunity to study the link between differences in a species' social system and mechanisms underlying their reproductive strategies, since they are highly social animals with differentiated relationships and often advanced social skills and knowledge (Cheney & Seyfarth, 2008, 2018; Seyfarth & Cheney, 2003). Further, they present a wide range of social systems, with a remarkable variety of grouping and mating patterns (Mitani et al., 2012; Seyfarth & Cheney, 2012).

The members of the genus *Papio* show substantial variation in their social organisation and mating systems (Fischer et al., 2019). Chacma (*P. ursinus*), olive (*P. anubis*), Kinda (*P. kindae*) and yellow baboons (*P. cynocephalus*) live in multi-male-multi-female groups with female philopatry and male-biased dispersal. Male dominance hierarchies are often clearly distinguishable, and a high rank strongly correlates with reproductive success (Altmann et al., 1988; Henzi & Barrett, 2005). Interactions between males and females are mainly restricted to phases in which females are receptive, but some females and males maintain lasting relationships independent of their reproductive state (Paciência et al., 2019; Smuts, 1985). In contrast, hamadryas (*P. hamadryas*) and Guinea baboons (*P. papio*) live in complex multi-level societies with philopatric males and female-biased dispersal. At the base of the society are the reproductive one-male units, which aggregate into higher-order levels, serving different social and ecological functions (Kummer, 1968; Patzelt et al., 2011; Schreier & Swedell, 2009; Stammbach, 1986). Females form lasting associations, independent of their reproductive state, with the unit male. While hamadryas baboon leader males enforce female proximity often through aggression (Schreier & Swedell, 2009), Guinea baboon females enjoy comparably high spatial tolerance from their primary male (Goffe et al., 2016). Guinea baboon females may spend time away from their males and even interact with other party and even gang members unimpeded (chapter 2). Female tenures range from several weeks to years, and transfers to other males occur individually and are possible between all levels of the society (Goffe et al., 2016).

Previous studies have shown various reproductive strategies for baboon males of different species. For example, lower-ranking chacma baboons use acoustic information to deduce mating opportunities (Crockford et al., 2007), hamadryas baboon “bachelor” males assess the bond strength of unit-males and their associated females before selecting targets for take-over attempts (Bachmann & Kummer, 1980), while lower-ranking yellow baboons form coalitions to fight over access to receptive females with high-ranking males (Ronald & Sluijter, 1990).

In our study population, almost all males reached at some point the status of primary male, i.e., they acquired associated females. Due to the high paternity certainty in this species (offspring within a unit are sired to 91.7 % by the primary male; Dal Pesco et al., 2022), male reproductive success largely depends on the number of females they can acquire and the length of female tenure i.e. the time a female stays part of the unit. While most males that have established themselves as reproductively active males are associated with two or three females, we also observed units with just one or up to seven females.

Little is known about factors driving the observed variation in unit size and tenure lengths. Still, it appears that females have considerable leverage in maintaining the relationship with a particular unit male and are suggested to play a decisive role in mate selection (Goffe et al., 2016). Male Guinea baboons form strong bonds with other males, and bachelor males play an essential role in the cohesion of the party (Dal Pesco et al., 2022). Males support each other in conflicts, show low aggression rates, and overt attempts to take-over females from other primary males are extremely rare. Furthermore, male bonding appears to be promoted by higher genetic relatedness within parties than between parties (Dal Pesco et al., 2021). Dal Pesco and colleagues tested whether reproductive success is linked to strong male-male bonds but could not find supporting evidence. On the contrary, the larger the unit size, and the higher the number of offspring, the less time males spent with other males (Dal Pesco et al., 2022).

Males also engage in socio-positive interactions with females and their offspring. Such behaviours might also be under consideration for females when choosing a partner. However, as noted above, males with a higher number of females in their unit spent less time socialising with other males. Under time budget constraints, increasing demand to socialise with and invest time into associated females requires reducing time with males (Dal Pesco et al., 2022).

In the present study, we ask how males regulate their investment into their relationships with females within their units. We assume that males also operate on a time-budget constraint regarding their social time with females. Thus, if male social investment affects their reproductive output, males need to decide how they allocate their available time and in which females to invest preferentially to maximise their reproductive success (Proctor et al., 2011).

In this study, we investigate which female characteristics affect males’ decision-making in light of their aim to maximise reproductive success. Female age has commonly been shown affecting female reproductive value and thus should affect male mate choice. Parous females may represent a safer investment, as they already have proven to be able to reproduce successfully (Anderson, 1986). Mature females might therefore be selected as targets for social time more frequently than very young or very old females. At the same time, males should preferentially invest in females that present the currently highest reproductive potential, i.e., that are sexually receptive. Suppose males are under budgetary constraints and have to allocate social investment strategically, we predict that males prefer parous females over subadult or old females. Secondly, we expect males to favour females that are currently ready to conceive. An increasing number of females in the unit might result in more time spent socialising with females. Alternatively, primary males may keep the overall socialising time similar but devote less time to each of their females.

3.3 Methods

3.3.1 Field site and study animals

Data collection took place at the Centre de Recherche de Primatologie (CRP) Simenti, a field station of the German Primate Center (DPZ) located in the Niokolo Koba National Park in Senegal (13°01´34´´N, 13°17´41´´W). The data collection was part of a long-term research project on the life history of wild Guinea baboons (see Fischer et al., 2017 for details). Between April 2014 and December 2021, we collected data on a study population of Guinea baboons, which comprised approximately 400 identified and habituated individuals. We studied units that were part of three main parties (party [5]: 4-8 primary males (males with at least one associated female), 9-15 associated females, party [6]: 6-8 primary males, 9-17 associated females, party [9]: 5-12 primary males, 8-17 associated females). These parties belonged to two gangs (Mare gang, Simenti gang). Party [6] and [9] were studied continuously from 2014 to 2021, and party [5] from 2015 to 2021. Due to the COVID-19 pandemic, researchers had to leave the field site from April 2020 to November 2020. When returning in December 2020, party [6] had split into two parties, [6I]: 1-3 primary males, 3-5 associated females and [6W]: 4-6 primary males, 10-13 associated females. Additionally, only a subset of party [9] was still present, named [9B]. It comprised 6 primary males and 9 associated females. Further, we collected data for some peripheral units not associated directly with our main parties but regularly nearby and well-habituated. Some of these baboons were previously members of the main parties but had transferred to other parties or where sub-groups that had split from the main parties. These parties ([13]: 3 primary males, 11 associated females, study period: since 2021; [14]: 2 primary males, four associated females, study period: 2019; [15]: 1 primary male, four associated females, study period: since 2021) contained just a few units and were studied for shorter periods but could still be used to address our study aims. Overall, we collected data on 51 individual primary males and 93 associated unit-females, over changing unit constellations (average unit size: 2.34 females, range: 1 - 6).

3.3.2 Data collection

We collected behavioural data of primary males using 20-minute focal follows (Altmann, 1974). Daily data collection followed a systematic schedule aiming to balance between parties and individuals. Fieldwork was conducted between 06:30 to 13:00, with three evenly spaced time categories, allowing us to balance the daytime of focal protocol collection. We collected, on average, 4.6 focal protocols per male per month and a total of 5495 focal observation protocols, equivalent to 1930 h (average total observation hours per male: median 32h (0.8 h – 381 h); for party [5]: 411 h, party [6] 758 h, party [9]: 699, party [13] 39 h, party [14] 5 h, and party [15] 20 h).

We recorded all occurrences and durations of grooming and greeting events in which a primary male and one of his associated females were involved (see supplement A3.1). We focussed on those interactions where the male was the active partner, i.e., the male was actively grooming, or the male initiated the greeting. Further, we recorded all male approaches and leaves towards/from females within a distance of 1 m of the female. The duration males spent within 1m to a female was later calculated based on the time difference between such approaches and leaves. We recorded the observational data using electronic forms created with the software Pendragon version 7.2.21 (Pendragon Software Corporation, Chicago, IL, USA) and the Pendragon Forms Android application running on smartphones (Samsung Galaxy Note II GT-7100 and Gigaset GX290).

3.3.3 Female reproductive state

In addition to behavioural data, we collected daily census information about all individuals present. Apart from general information about the presence/absence and the health status of the individuals, these data also included the reproductive state of females. We distinguished between four mutually exclusive reproductive states: pregnant (P), which included all females, where a reddening of the anogenital area was detectable, indicating conception (Gauthier, 1999). At later stages, pregnancy was confirmed by the absence of reproductive swellings and changes in the physical appearance; lactating (L): we categorised females as lactating from the day of birth of the offspring until she resumed swelling; cycling detumescent (CD): cycling females (not lactating or pregnant) but at the time without any sexual swelling; cycling tumescent (CS), cycling females (not lactating or pregnant) that show an enlargement of their anogenital and paracallosal skin. Depending on the size of the sexual swelling, CS was subdivided into C1: minor swelling, C2: medium swelling, and C3: maximum swelling (Goffe 2016; see table A3.2; Dal Pesco & Fischer, 2022).

3.3.4 Female age

As complete demographic information (specifically birth dates) was not available for all of the females, due to the female dispersal in this species, we assessed female age using several developmental and reproductive characteristics. Subadult females (SAF) had not yet reached the adult body size and had started swelling but were still nulliparous. Young adult females (YAF) had not reached adult body size but were sexually mature with regular swellings. They had already given birth once (primiparous). Mature adult females (MAF) had reached their full body size and had given birth to more than one infant (multiparous). Finally, we established the category of old adult females (OAF), mainly identified by their declining body condition, such as thinning of the fur, severe wear and discolouration of their teeth (see table A3.2; Dal Pesco & Fischer, 2022).

3.3.5 Unit association

Male-female associations, i.e., unit compositions, were assessed daily throughout the data collection period. Female transfers could usually be detected directly by the researchers in the field based on the spatial association and interaction frequencies between the female and the new vs the old male. We nevertheless verified all suggested transfers by analysing all interactions between males and females (greetings, grooming, contact-sits, copulations, aggressions) in a given period (Goffe et al., 2016). Within this study, unit size refers to the number of individual females associated with the same primary male.

3.3.6 Data analyses

3.3.6.1 Data extraction

From the focal protocols, we created a data set that comprised information about male-female dyadic interactions for each focal protocol and each female that was part of a male's unit on that day. We extracted all occurrences and durations of grooming bouts, approaches, leaves, and greetings in which the primary male actively interacted with one of his associated females. If males did not interact with a particular female in a given focal protocol, zeros were entered for the individual behaviours. The final data set contained 12,916 dyadic observations.

3.3.6.2 R packages and general statistical procedures

Analyses were carried out in R (version 4,1,1; R Core Team, 2021). Generalised linear mixed models (GLMM) for all Poisson and binomial models were fitted using the function *glmer* of the R package *lme4* (version 1.1- 27.1; (Bates et al., 2015)) and the function *glmmTMB* of the R package *glmmTMB* (version 1.1.4, (Brooks et al., 2017)) for beta models. All GLMMs were fitted with the optimiser *bobyqa,* and maximum iterations were set to 100,000. To ease model convergence further, we z-transformed continuous predictor variables to a mean of zero and a standard deviation of one (Schielzeth & Forstmeier, 2009). To avoid overconfident estimation and to maintain type I error rates at the nominal level of 0.05, we formulated all models with a maximum random effect structure, including random intercepts, all theoretically identifiable random slopes, and interactions between intercepts and slopes (Barr et al., 2013; Schielzeth & Forstmeier, 2009)). However, due to convergence problems, we had to drop the parameters for the correlation between random intercepts and slopes.

We validated the absence of collinearity between all predictor variables (female age and reproductive status) by calculating variance inflation factors (VIF) for refitted standard linear models lacking random effects using the function *vif of the* car package (version 3.0-12). We tested for overdispersion using an R function developed by Roger Mundry. The model stability was verified by comparing model estimates for the complete data set with estimates for data sets with levels of the random effects excluded one at a time (R function also provided by Roger Mundry). To test for an overall effect of multiple predictor variables on any specific response variable, we compared the full model with a null model lacking the test predictor of interest using a likelihood ratio test (Dobson & Barnett, 2002). We calculated test statistics and p-values for individual predictors in GLMMs using the *drop1()* function implemented in base R (Chambers & Hastie, 1992) with the '*test'* argument set to '*Chisq*' using a likelihood ratio test. The bootstrapped confidence intervals were obtained using the function *bootMer* of the package *lme4* using 1000 parametric bootstraps over the random effects.

3.3.6.3 Proximity proportion/Grooming proportions

To examine whether the time males groom or stay close to associated females is affected by the females' reproductive state or age, we ran two GLMMs with beta error structure. As response variables, we calculated the proportion of observation time males were in proximity and were grooming individual females by dividing the total duration in proximity and of grooming bouts per focal protocol by the duration of the protocol in seconds. As beta models cannot be fitted with response values of precisely zero, we transformed the response values to avoid being exactly zero or one (Smithson & Verkuilen, 2006). In both models, we tested the effect of the two main predictor variables, 'female reproductive state' and 'female age', and added 'unit size' as a control predictor to control for the influence of the number of females in the unit. We included a random intercept effect for the ID of the male, the ID of the female, and the combination of male and female (the dyad). In addition, we included random slopes of the fixed effects of female reproductive state and unit size within all three random intercepts. We also added the random slope for female age in male ID. The unit size was z-transformed, female reproductive state and female age manually dummy coded and centred to a mean of zero.

Both models had convergence problems that could only be resolved when removing significant parts of the random effect structure, leaving only the random intercept effects in the model. As the resulting models were compromised severely in their inference, we opted to drop the analyses of grooming and proximity durations and instead focussed on the general probability of observing both behaviours within a focal protocol.

3.3.6.4 Grooming probability

To assess grooming probabilities, we re-coded the absence (0) or presence (1) of grooming bouts as a binary variable for each data entry per focal observation and male-female dyad. To analyse whether female characteristics affect the probability of males grooming a particular female, we fitted a GLMM with a binomial error structure. In addition to the main predictors female reproductive state and female age, we added the control predictor unit size. We include random intercept effect for male ID, female ID and dyad ID, and random slopes for female reproductive state and unit size within male ID, female ID and dyad ID. We further added the random slope for female age in male ID. No correlation between intercepts and slopes was included. Both categorical predictors were manually dummy coded and centred, and unit size was z-transformed. Test for model stability revealed good stability for all estimates (table 3.1). The model was not overdispersed (dispersion parameter: 0.898). Instead, it revealed a slight underdispersion. A dispersion parameter <1 reveals underdispersion, potentially leading to over-conservative model estimates. The model showed no problems of collinearity among predictors (maximum VIF: 1.02). The sample analysed comprised 12916 observations for 51 individual males, 93 individual females and 166 dyads; 827 observations contained ones and 12089 zeros.

3.3.6.5 Proximity probability

To examine the probability for males to be close to females, we re-coded the calculated proximity durations into a binary response, with each data entry per focal observation and male-female dyad receiving either a one if a male and female were in proximity or zero if not. To analyse the effect of female reproductive state, female age and the control predictor unit size on a male’s probability to be in proximity with a particular female, we fitted a GLMM with a binomial error structure. We included random intercept effect for male ID, female ID and dyad ID, random slopes for female reproductive state and unit size within male ID, female ID and dyad ID. Additionally, we added the random slope for female age in male ID. No correlation between intercepts and slopes was included. We dummy-coded and centred both categorical predictors and z-transformed unit size. Model stability checks revealed overall good stability for all model estimates (table 3.2). The test for overdispersion revealed that the model was not overdispersed (dispersion parameter: 0.966). Collinearity among predictors appeared to be no issue (maximum VIF: 1.03). The sample analysed comprised 12,916 observations for 51 individual males, 93 individual females and 166 dyads; 3988 observations contained ones and 8928 zeros.

3.3.6.6 Greeting rates

To estimate the effect of female reproductive state and female age on greeting rates, we used a GLMM with Poisson error structure and log link function (McCullagh & Nelder, 2019). We added unit size as an additional control predictor. To account for variation in observation time, we included the focal duration in seconds (divided by the average duration of a focal observation (1200 s) and consecutively log-transformed) as an offset term in the model (McCullagh & Nelder, 2019). To account for repeated observations, we included random intercept effects for male ID, female ID and dyad ID. We added random slopes for female reproductive state and unit size within male ID, female ID and dyad ID into the model. Further, we added the random slope for female age in male ID. For better model convergence, no correlation between intercepts and slopes was included.

Before the modelling, we dummy-coded and centred both categorical predictors and z-transformed unit size. Model stability checks revealed the model to be of good stability (table 3.3). A check for collinearity among the predictors revealed no issues (maximum VIF: 1.02). The calculated dispersion parameter 0f 0.942 showed no overdispersion in the response. The sample analysed comprised 12916 observations for 51 individual males, 93 individual females and 166 dyads.

3.3.6.7 Theoretical effect of unit size

To assess the effect of unit size on grooming, proximity probabilities, and greeting rates, we calculated the theoretically expected change for each response variable under the assumption that the total time invested into the respective behaviours would not change with increasing unit size. The expected values for different unit sizes were calculated by dividing the behavioural probability or rate for a unit of the size of one with the respective unit size.

3.4 Results

3.4.1 Male-female interactions

Males actively groomed one or more associated females in 14 % (*N*= 748/5495) of the focal protocols. The average grooming duration (median ± IQR) was 64 s ± 114 s; range: 2 s – 766 s. In the majority of protocols in which grooming events were observed (n= 748), the male groomed a single female (90 %), and in a few cases, two (9 %) or three (<1 %) females per focal protocol. In 52 % of focal protocols, males were close to an associated female (average time in proximity: median ± IQR: 38 s ± 73 s; range: 1s – 1177s). Males spent, on average, 1.26 min/h of the time in proximity to one or more of their associated females. In the subset of protocols in which males spent time in proximity with females (*N*= 2854), males were in proximity with one (68 %), two (26 %), three (6 %), four (1 %) or five (< 1 %) individual females per focal protocol. Greetings initiated by males occurred in 24 % of focal protocols with a rate of 0.43 greetings/h (average number of greetings: median ± IQR: 1 ± 1; range: 1 – 5 greetings). From focal protocols with greetings (*N*= 1330), males interacted with a single female (86 %), two (12 %), three (1 %) or four (<1 %) individual females per focal protocol.

3.4.2 Probability of grooming

We found a significant effect of the fixed effects of female reproductive state (FRS), female age and unit size on the male's probability to groom an associated female (full-null model comparison: χ^2= 47.413, *df* = 8, *P* = < 0.001). More specifically, the probability of being groomed was generally higher for females with a sexual swelling (FRS: C1, C2, C3), with the highest probability for females with a maximum swelling size (FRS: C3). Cycling but not swollen, pregnant or lactating females were less likely to be groomed (figure 3.1a, table 3.1). Further, male grooming probability varied with unit size. A male's probability to groom an individual female was highest in a small unit (number of females: 1) and decreased with an increasing number of females being part of the unit (figure 3.4a, table 3.1). The observed decrease in grooming probability mirrors the predicted change in probabilities under the assumption that overall time investment in grooming would not change with increasing unit size. (figure 3.4a, red line). There was no apparent effect of female age on male grooming probability (figure. 3.1b, table 3.1).

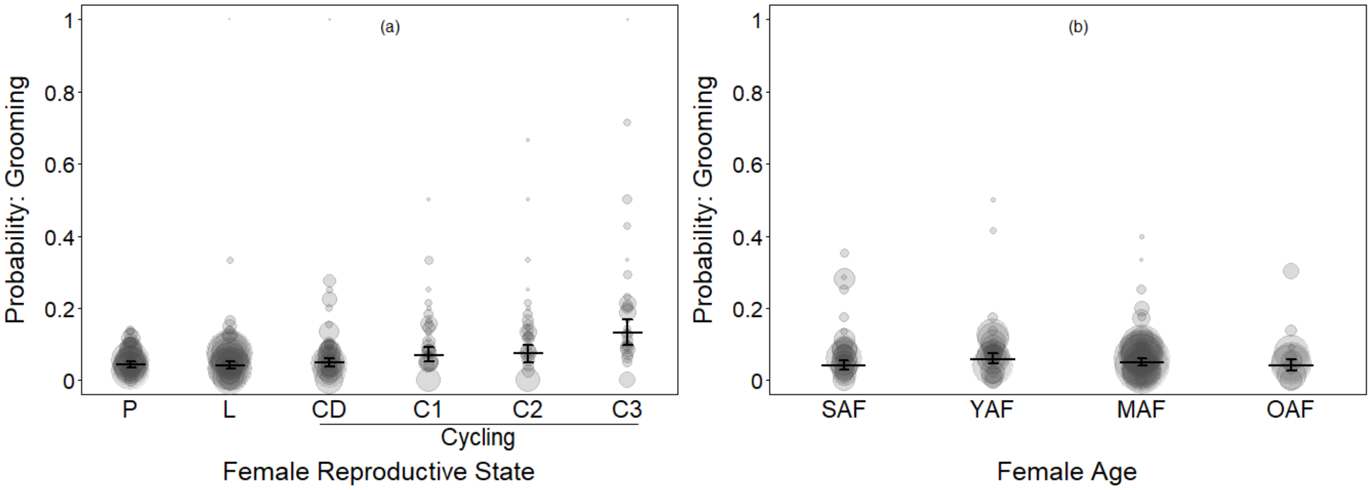

Figure 3.1: Probability of primary males grooming associated females. (a): grooming probability dependent on females' reproductive state (*P* pregnant, *L* lactating, *CD* cycling detumescent, *C1* cycling small size, *C2* cycling medium size, *C3* cycling maximum size). (b): grooming probability dependent on females' age (*SAF* subadult female, *YAF* young adult female, *MAF* mature adult female, *OAF* old adult female). The area of the circles represents the number of observations per data point (a: median = 40, range = 1 to 445; b: median = 89, range = 3 to 658). Horizontal black lines depict bootstrapped mean and 95% confidence intervals with all other predictors being at their average (female reproductive state and age dummy coded and centred, unit size z-transformed to a mean of 0 and standard deviation of 1).

3.4.3 Probability proximity:

The predictor female reproductive state, female age and the unit size influenced males' probability of being near associated females (full-null model comparison: $\chi^2_= 111.41$, *df* = 8, *P* = < 0.001). Female reproductive state affects males' probability of being nearby in two ways. Firstly, males generally were more like to be in proximity with females that show reproductive swellings (FRS: C1, C2, C3), reaching the highest probability with females showing a maximum swelling size (FRS: C3). Further, the probability of being in proximity was also higher for lactating females (figure 3.2a; table 3.2). Male proximity also varied with female age. Males were more likely to be near young-adult-female (YAF) and mature-adult-female (MAF), while the youngest and oldest females (SAF, OAF) were less likely to be found in proximity (figure 3.2b; table 3.2). Finally, male proximity varied with unit size, with male probability to be in proximity of a female being highest for the smallest units (number of females: 1) and decreasing with increasing unit size, reaching a minimum at the maximum unit size (number of females: 6) (figure 3.4b; table 3.2). The effect of unit size on the probability of being near associated females was less strong than expected from the calculated theoretical values (figure 3.4b; red line).

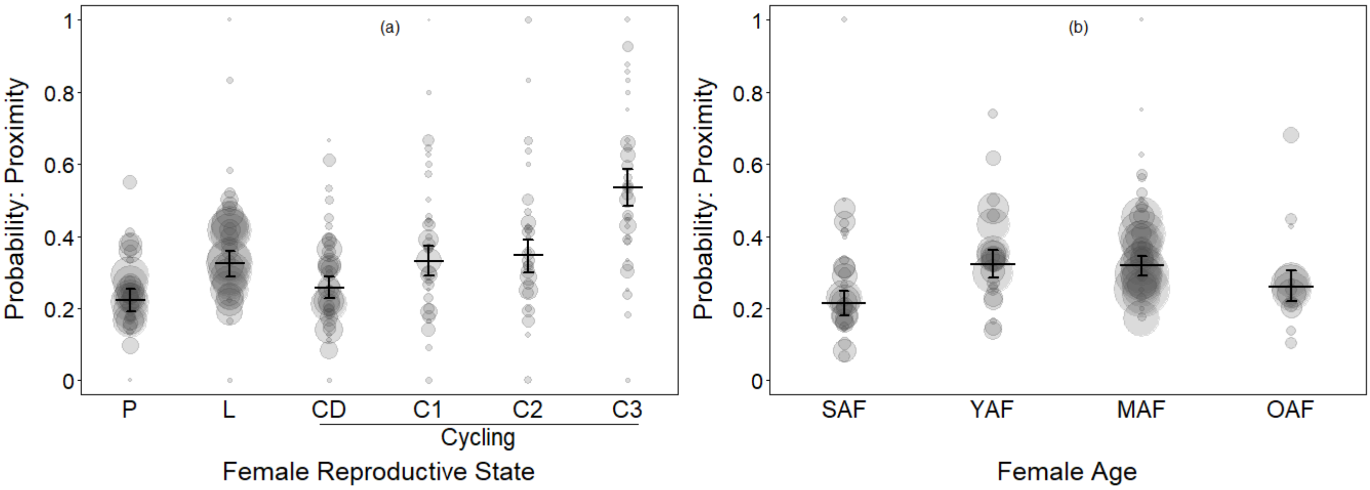

Figure 3.2: Probability of primary males being in proximity to an associated female. (a): probability of being in proximity-dependent on females' reproductive state (*P* pregnant, *L* lactating, *CD* cycling detumescent, *C1* cycling small size, *C2* cycling medium size, *C3* cycling maximum size). (b): probability of being in proximity-dependent on females' age (*SAF* subadult female, *YAF* young adult female, *MAF* mature adult female, *OAF* old adult female). The area of the circles represents the number of observations per data point (a: median = 29.5, range = 2 to 445; b: median = 62, range = 3 to 658). Horizontal black lines depict bootstrapped mean and 95% confidence intervals with all other predictors being at their average (female reproductive state and age dummy coded and centred, unit size z-transformed to a mean of 0 and standard deviation of 1).

3.4.4 Greeting rate

Overall, male greeting rate varied with female reproductive state and unit size (full-null model comparison: χ^2= 39.456, *df* = 8, *P* = < 0.001). Greeting rates were lowest for lactating females (figure 3.3a; table 3.3). Greeting rates per female slightly decreased with increasing unit size (figure 3.4c; table 3.3). The effect of unit size on greeting rates was smaller than expected based on the calculated theoretical values (figure 3.4c; red line). Greeting rates did not obviously vary with female age rates (figure 3.3c, table 3.3).

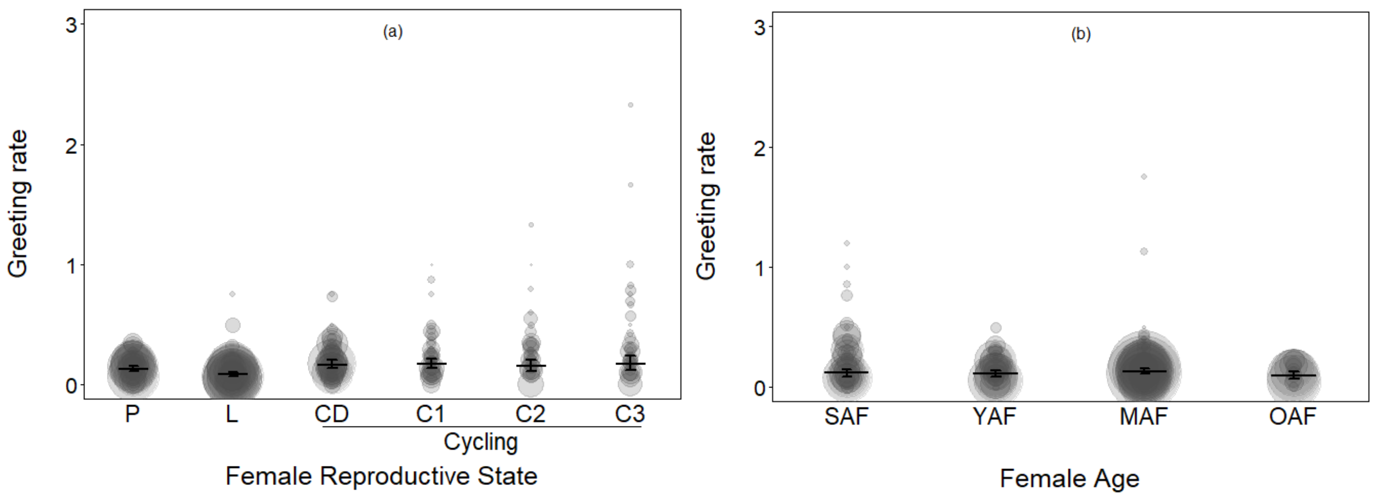

Figure 3.3: Rate of greetings per 20 minutes (average focal protocol duration) initiated by primary males and directed at associated females. a: greeting rates dependent on females' reproductive state (*P* pregnant, *L* lactating, *CD* cycling detumescent, *C1* cycling small size, *C2* cycling medium size, *C3* cycling maximum size). b: greeting rates dependent on females' age (*SAF* subadult female, *YAF* young adult female, *MAF* mature adult female, *OAF* old adult female). The area of the circles represents the number of observations per data point (a: median = 35, range = 1 to 445; b: median = 61, range = 2 to 658). Horizontal black lines depict bootstrapped mean and 95% confidence intervals with all other predictors being at their average (female reproductive state and age dummy coded and centred, unit size z-transformed to a mean of 0 and standard deviation of 1).

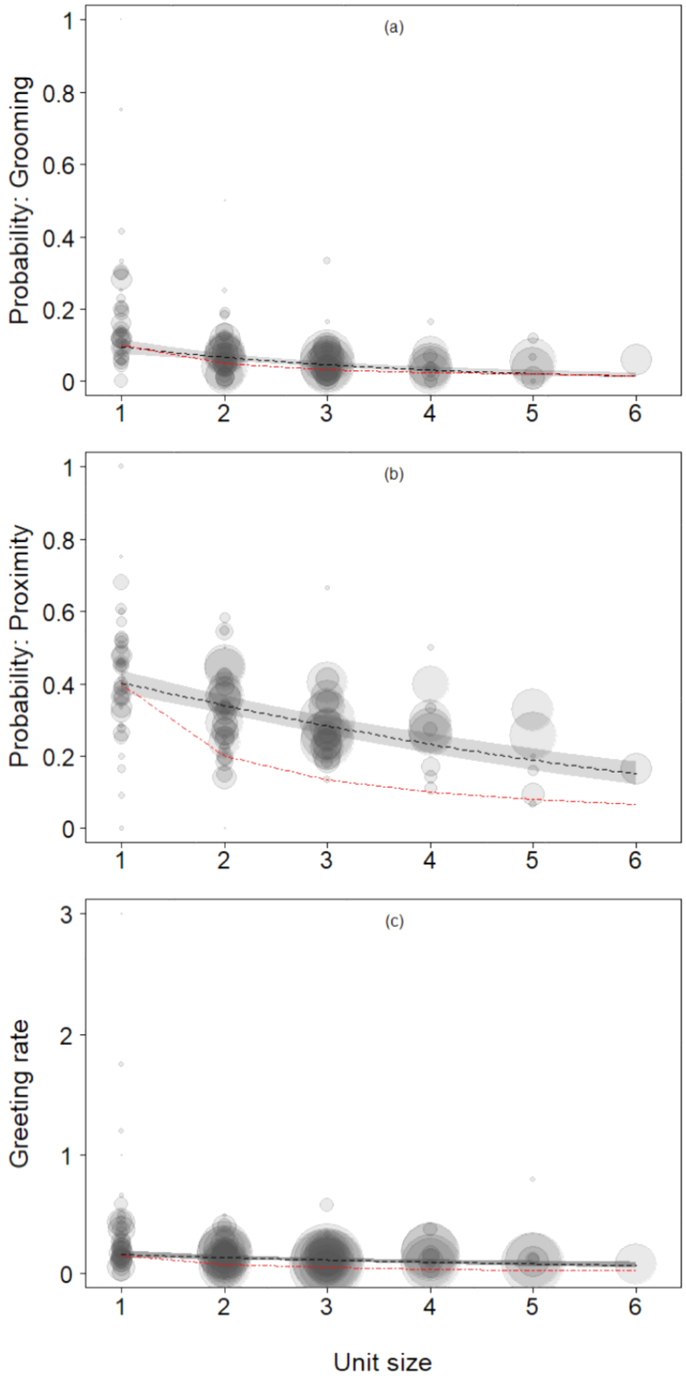

Figure 3.4: Relationship between unit size and (a) male probability to groom associated females, (b) male probability to be in proximity to associated females and (c) rate of greetings per 20 minutes (average focal protocol duration) initiated by males and directed at associated females. The area of the circles represents the number of observations per data point (a: median = 69.5, range = 1 to 654; b: median = 60, range = 2 to 654; c: median = 55, range = 1 to 654). The dashed line depicts the fitted model, and the shaded area depicts bootstrapped 95% confidence intervals with all other predictors being at their average (female reproductive state and age dummy coded and centred). The dash-dotted red lines depict the theoretically expected changes in probabilities and interaction rates if the total time invested into the respective behaviours would not change with increasing unit size.

Table 3.1: Results of generalised linear mixed model analysing the influence of female reproductive state, female age and unit size on males' probability to groom associated females. SE: standard error, CI: confidence interval, min/max: minimum and maximum estimate from model stability analyses. (1) Not presented due to very limited interpretability. (2) Female reproductive state is manually dummy coded with C1 (focal_FRS_C1) being the reference level. The indicated test results refer to the overall effect of female reproductive state based on a likelihood ratio test. (3) Female age is manually dummy coded with MAF (female_age_MAF) being the reference level. The indicated test results refer to the overall effect of female age based on a likelihood ratio test. (4) Unit size was z transformed to a mean of 0 and a standard deviation (sd) of 1. The mean and sd of the original variable were 2.836 and 1.128, respectively. The sample analysed comprised 12916 observations for 51 individual males, 93 individual females and 166 dyads.

Term	Estimate	SE	lower CI	upper CI	x^2	df	*P*	min	max
(Intercept)	-2.567	0.163	-2.894	-2.265	(1)	(1)	(1)	-2.678	-2.503
focal_FRS_C2[2]	0.083	0.201	-0.353	0.475	44.7	5	< 0.001	0.002	0.179
focal_FRS_C3	0.724	0.179	0.331	1.054				0.643	0.812
focal_FRS_CD	-0.341	0.152	-0.653	-0.059				-0.384	-0.280
focal_FRS_L	-0.530	0.150	-0.835	-0.238				-0.583	-0.438
focal_FRS_P	-0.511	0.162	-0.845	-0.200				-0.559	-0.396
female_age_OAF[3]	-0.193	0.173	-0.615	0.127	4.77	3	0.190	-0.304	-0.115
female_age_SAF	-0.236	0.185	-0.639	0.110				-0.335	-0.158
female_age_YAF	0.159	0.141	-0.120	0.421				0.098	0.254
z.unit_size[4]	-0.441	0.075	-0.583	-0.304	26.82	1	< 0.001	-0.483	-0.402

Model formula:

```
glmer(Groom.binom ~ focal_FRS + female_age + z.unit_size +
    (1 + focal_FRS.C2 + focal_FRS.C3 + focal_FRS.CD + focal_FRS.L + focal_FRS.P +
    z.n_females_in_unit || Dyad_ID) + (1 + focal_FRS.C2 + focal_FRS.C3 + focal_FRS.CD +
    focal_FRS.L + focal_FRS.P + z.unit_size || female_ID) + (1 + female_age.OAF +
    female_age.SAF + female_age.YAF + focal_FRS.C2 + focal_FRS.C3 + focal_FRS.CD + focal_FRS.L +
    focal_FRS.P + z.unit_size || male_ID), data = t.data.binom, family = "binomial",
    control = glmerControl(optimizer = "bobyqa",optCtrl = list(maxfun = 100000)))
```

Table 3.2: Results of generalised linear mixed model analysing the influence of female reproductive state, female age and unit size on males' probability to be in proximity of associated females. SE: standard error, CI: confidence interval, min/max: minimum and maximum estimate from model stability analyses. (1) Not presented due to very limited interpretability. (2) Female reproductive state is manually dummy coded with C1 (focal_FRS_C1) being the reference level. The indicated test results refer to the overall effect of female reproductive state based on a likelihood ratio test. (3) Female age is manually dummy coded with MAF (female_age_MAF) being the reference level. The indicated test results refer to the overall effect of female age based on a likelihood ratio test. (4) Unit size was z transformed to a mean of 0 and a standard deviation (sd) of 1. The mean and sd of the original variable were 2.836 and 1.128, respectively. The sample analysed comprised 12916 observations for 51 individual males, 93 individual females and 166 dyads; 3988 observations contained ones and 8928 zeros.

Term	Estimate	SE	lower CI	upper CI	x^2	df	*P*	min	max
(Intercept)	-0.584	0.106	-0.806	-0.366	(1)	(1)	(1)	-0.628	-0.529
focal_FRS_C2²	0.072	0.113	-0.160	0.293	89.05	5	< 0.001	0.010	0.105
focal_FRS_C3	0.844	0.119	0.609	1.089				0.808	0.876
focal_FRS_CD	-0.362	0.095	-0.542	-0.166				-0.407	-0.320
focal_FRS_L	-0.030	0.108	-0.235	0.193				-0.091	0.015
focal_FRS_P	-0.552	0.110	-0.765	-0.322				-0.601	-0.484
female_age_OAF³	-0.280	0.105	-0.507	-0.080	23.55	3	< 0.001	-0.329	-0.214
female_age_SAF	-0.535	0.106	-0.746	-0.335				-0.572	-0.493
female_age_YAF	0.014	0.086	-0.148	0.191				-0.033	0.047
z.unit_size ⁴	-0.300	0.033	-0.366	-0.236	39.16	1	< 0.001	-0.313	-0.286

Model formula:

```
glmer(Prox.binom ~ focal_FRS + female_age + z.unit_size +
        (1 + focal_FRS.C2 + focal_FRS.C3 + focal_FRS.CD + focal_FRS.L + focal_FRS.P +
        z.unit_size || Dyad_ID) + (1 + focal_FRS.C2 + focal_FRS.C3 + focal_FRS.CD +
        focal_FRS.L + focal_FRS.P + z.unit_size || female_ID) + (1 + female_age.OAF +
        female_age.SAF + female_age.YAF + focal_FRS.C2 + focal_FRS.C3 + focal_FRS.CD + focal_FRS.L +
        focal_FRS.P + z.unit_size || male_ID), data = t.data.binom, family = "binomial",
        control = glmerControl(optimizer = "bobyqa",optCtrl = list(maxfun = 100000)))
```

Table 3.3: Results of linear mixed model analysing the influence of female reproductive state, female age and unit size on hourly greeting rate initiated by males and directed at associated females. SE: standard error, CI: confidence interval, min/max: minimum and maximum estimate from model stability analyses. (1) Not presented due to very limited interpretability. (2) Female reproductive state is manually dummy coded with C1 (focal_FRS_C1) being the reference level. The indicated test results refer to the overall effect of female reproductive state based on a likelihood ratio test. (3) Female age is manually dummy coded with MAF (female_age_MAF) being the reference level. The indicated test results refer to the overall effect of female age based on a likelihood ratio test. (4) Unit size was z transformed to a mean of 0 and a standard deviation (sd) of 1. The mean and sd of the original variable were 2.836 and 1.128, respectively. The sample analysed comprised 12916 observations for 51 individual males, 93 individual females and 166 dyads.

Term	Estimate	SE	lower CI	upper CI	x^2	df	*P*	min	max
(Intercept)	-1.673	0.117	-1.906	-1.465	(1)	(1)	(1)	-1.744	-1.639
focal_FRS_C2[2]	-0.108	0.167	-0.452	0.204	34.08	5	< 0.001	-0.190	-0.035
focal_FRS_C3	0.021	0.166	-0.313	0.325				-0.032	0.098
focal_FRS_CD	-0.030	0.113	-0.226	0.183				-0.063	0.049
focal_FRS_L	-0.716	0.126	-0.948	-0.475				-0.758	-0.661
focal_FRS_P	-0.278	0.118	-0.490	-0.054				-0.324	-0.224
female_age_OAF[3]	-0.296	0.165	-0.628	-0.017	5.04	3	0.169	-0.450	-0.225
female_age_SAF	-0.080	0.154	-0.359	0.199				-0.154	-0.027
female_age_YAF	-0.160	0.115	-0.391	0.046				-0.198	-0.110
z.unit_size[4]	-0.186	0.057	-0.293	-0.088	10.96	1	0.001	-0.216	-0.157

Model formula:

```
glmer(greeting_given_freq ~ focal_FRS + female_age + z.unit_size +
    (1 + focal_FRS.C2 + focal_FRS.C3 + focal_FRS.CD + focal_FRS.L + focal_FRS.P +
    z.unit_size || Dyad_ID) + (1 + focal_FRS.C2 + focal_FRS.C3 + focal_FRS.CD + focal_FRS.L +
    focal_FRS.P + z.unit_size || female_ID) + (1 + female_age.OAF + female_age.SAF +
    female_age.YAF + focal_FRS.C2 + focal_FRS.C3 + focal_FRS.CD + focal_FRS.L +focal_FRS.P +
    z.unit_size || male_ID) + offset(log(focal_duration_sec / (20 * 60))), family = poisson,
    data = t.data.greet, control = glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 100000)))
```

3.5 Discussion

The aim of this study was to identify female characteristics that might affect male social decision-making within the reproductive units of Guinea baboons. The males' social investment and spatial preferences were affected by female reproductive state and age. Males were more likely to groom and to be close to females that were reproductively active. The highest likelihood was for females with maximally enlarged sexual swellings, indicating that they were probably close to ovulation (Gesquiere et al., 2007; Nunn, 1999; Wildt et al., 1977). Males were also more likely to spend time close to lactating females, and they preferred young and mature females over subadult and old females.

Initially, we had planned to analyse the durations of our main response variables, grooming and proximity. Yet, these models did not converge, and we, therefore, reverted to analysing the occurrences of grooming and proximity as binary response variables (occurrence yes/no per focal protocol). Of course, we may have lost some critical information in this way. For instance, observing that a male was briefly close to a female is not the same as sitting next to each other for several minutes. Despite this loss of information, the data revealed clear preferences in relation to female reproductive value.

The reproductive state of females often drives intersexual relationships. Attention to females often waxes and wanes with a female's reproductive cycle (Bercovitch et al., 2006; Klose et al., 2009; Proctor et al., 2011). We found a similar pattern in Guinea baboon males. Although their baseline association rate with females is likely higher than in female-philopatric baboon species (Palombit et al., 1997; Seyfarth, 1978), they still allocated their social time in relation to female reproductive value.

Several studies have shown how sexual swellings of females affect male sexual behaviour. For example, males show increased interaction rates and proximity, often forming consort pairs when females show enlarged swellings (Byrne et al., 1990; Nishida, 1997). An increased interest in a potentially receptive female and the motivation to mate can also explain the behavioural patterns we observed in Guinea baboon males. However, in Guinea baboons, males also interacted with females when they were not receptive (cycling detumescent, pregnant, lactating).

Male Guinea baboons showed preferential spatial association with young and mature adult females over subadult and old females, indicating a preference for females with higher fecundity (Muller et al., 2006; Setchell & Wickings, 2006). Subadult females, here by definition nulliparous, have not yet proven to be able to reproduce successfully and generally have a higher risk for miscarriage (Small & Rodman, 1981; Strum & Western, 1982; Turner et al., 1987). Very old females, in contrast, are less attractive due to their lower fecundity and decreased offspring quality due to their ageing germline (Monaghan et al., 2020; but see e.g., Muller et al., 2006). Under budgetary constraints, a preference for young adult and mature females is most likely the best strategy to maximize reproductive success for males. In addition, subadult females might not have established their position among the females within a unit. For example, dominance among females is often affected by their age (Archie et al., 2006; Clutton-Brock et al., 2006; Pusey et al., 1997). Younger females might, therefore, be spatially less central in the unit, which could explain why males would be less often in their proximity, if other older females are present.

Similar to the findings of Goffe and colleagues (2016), we observed reduced greeting rates with lactating females. At the same time, males were more likely to be in proximity to lactating females. Infants are highly attractive to conspecifics in many primate species (Gust et al., 1996; Maestripieri, 1999; Silk, 1999). Similarly, males frequently interact with and are protective of new offspring. Being more often close to lactating females can, therefore, likely be a side effect of the infants' attraction to males. Further, the presence of infants can also explain why greeting rates with their mothers decline, as males interact now preferably more often with the infant instead.

The unit size affected the allocation of grooming and proximity differentially. While males maintained a constant number of grooming interactions, irrespective of their unit size, the frequency they were in proximity to females and their greeting rates varied with unit size. Maintaining equal grooming relationships with an increasing number of associated females might be too time intensive for males to realise without reallocating time from other important activities (Borgeaud et al., 2021; Dunbar et al., 2009). Greeting interactions, in contrast, are not time intensive and, therefore, less costly to increase in frequency. Frequent greetings with all associated females could be a viable strategy to assess and maintain relationships with females under time budget limitations, similar to the regulation of relationships with other males (Dal Pesco & Fischer, 2018, 2020).

Further detailed analyses of male budgets, including both interactions with males and females, are needed to identify how precisely males allocate their social capital. Maintaining proximity to females might not seem too time demanding for Guinea baboons, as males can stay close to several females simultaneously. However, in 68% of our focal protocols in which proximity to a female was noted, males were in proximity to only one female. While female Guinea baboons are generally more likely to be close to members of their unit, they also move away independently of each other and out of sight of their males (Goffe et al., 2016; chapter 2). Maintaining proximity to up to seven independent associated females could be a challenging task.

Based on our observations, we cannot decide whether a male's social investment in resident females plays a role in attracting additional females. Interestingly, the male with the largest unit size groomed his females disproportionately long (figure 3.4a). While this observation is only anecdotal, it provides a direction for future investigation. Alternatively, females might simply select males with good quality. Male Guinea baboons possess various features that could be considered classical honest male signals, e.g., large manes and colouration of hind quarters, which might be more important drivers of female choice (Jolly, 2020; Kalbitzer, 2014).

In summary, while Guinea baboon primary males maintain social relationships with all of their associated females, males' social investment varies with female short- and long-term reproductive value. The interplay of the effects of females' age and reproductive state suggests a dynamically changing relationship among the primary male and females of their unit. While we now have an understanding of the allocation of social investment at the aggregate level, we still lack insights into the single choices that give rise to the observed pattern. Future studies should focus on the dynamics within single units to better understand male decision-making processes.

3.6 Acknowledgements

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3.8 Appendix

Supplementary text

Supplement A3.1: Ethogram:

The animals' behaviour was coded following the established definition and rules at the CRP Simenti (Dal Pesco & Fischer, 2022).

Grooming: "Movement of fingers or lips through the fur of another individual. A grooming bout ends when active manipulation is interrupted for more than 5 seconds. […] A grooming bout is considered finished only once the groomer stopped grooming his partner for more than 5 seconds."

Greeting: Ritualised behaviours exchanged in non-aggressive contexts. Greetings recorded in this study included: *Present*, *Touch general*, *Embrace*, *Genital manipulation* and *Mount*. See (Dal Pesco & Fischer, 2018) for detailed information.

Approach: "The focal individual walks directly towards the partner and decreases the distance between them to 1 m or less."

Leave: "The focal individual walks away and increases the distance to the partner to > 1 m."

Proximity: The duration a focal individual spends at a distance of 1 m or less from the partner, calculated as the time difference between consecutive approaches and leaves.

Supplementary tables

Table A3.2 Description and visual guide of reproductive states of cycling females

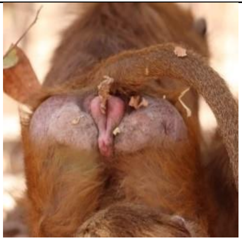
Swelling state		**Definition**	**Picture**
Cycling	S0	An absence of swelling in the anogenital area (AGA) and para-callosal skin (PCS). The skin around the anus and labia may be wrinkled and a bit loose immediately post swelling, or tight ca. a week after.	
	S1	A small swelling of the AGA. The swelling appears vertically, and broadens slightly.	
	S2	A medium-large swelling of the AGA and a small swelling of the PCS. The swollen area extends vertically and horizontally, and comes outward slightly.	
	S3	A large swelling of the AGA and full swelling of the PCS. The swollen area is three-dimensional, often forcing the tail to be carried elevated and causing the female to sit slightly sideways; some areas protrude outward more than others. The width at peak swelling does not extend beyond the outer extremities of the ischial callosities in *Papio papio* as it does in other baboon species.	

Table A.3.3 Subadult and adult female age category description

Age category	**Definition**
Subadult female	Females have not yet attained full body size, but have started swelling regularly or unregularly. These females are nulliparous (i.e., they never gave birth). The nipples are not elongated; as far as we can tell they had no (nursing) baby yet. The ischial callosities of the anogenital area (AGA) have a permanent gap between them.
Young adult female	Once females become pregnant and give birth, they are considered young adults. These females are primiparous (i.e., they gave birth once). They are sexually mature and undergo sexual swellings regularly. Females in this stage are still physically smaller and thinner than mature adult females (although the physical build of individuals may differ, and some females may keep a small build even when reaching maturity). The coat is shiny, and they typically have few scars. The teeth appear white and unchipped.
Mature adult female	Females that have reached full body size. These females are multiparous (i.e., they gave birth more than once). The teeth appear mostly white and unchipped, but some may appear slightly yellowing or present some chipping or wear.
Old adult female	The coat begins to thin out. Teeth present some discoloration on several teeth and evident breaks chipping or tooth wear.

Chapter 4

General Discussion

4.1 Summary of results

In study 1 (chapter 3), I used playback experiment to test the ability of male Guinea baboons to recognise individual females and their attention to spatial information about whereabouts of associated females. I presented evidence that males are able to differentiate associated females from non-associated females based on their vocalisations. However, contrary to predictions, males showed no signs to track the specific movement patterns of their females. While showing general attention to vocalisations of associated females, specific information about their location seemed to be less important. In study 2 (chapter 4), I presented evidence for preferential allocation of social investment and spatial preferences for specific associated females of male Guinea baboons. I showed that males interact and associate more frequently with females that have a high current reproductive value, i.e., were sexually receptive at the time. I further showed that males where more frequently close to lactating females, and presented a spatial preference for young and mature females over subadult and old females.

4.2 Attention to social information in context of social organisation

Differences in cognitive abilities between animal species are caused by differential selective pressures (Cheney & Seyfarth, 2008; Rowe & Healy, 2014). In the same way, differences in socio-cognitive skills and attention to information about conspecifics are likely shaped by the selective forces that the social environment exerts (Bond et al., 2003; Hick et al., 2014; MacLean et al., 2008). While there are plenty of studies linking group-living to advanced social cognition (Seyfarth & Cheney, 2015), there is still debate about the specific drivers affecting the evolution of abilities to gather and process social information.

Two of the more prominent theories about the evolution of social cognition are the ones of Dunbar, and Whiten and Byrne. Dunbar's 'Social Brain Hypothesis' (1998) suggests, life in a socially complex environment with a multitude of relationships that can quickly change as main selection pressure. In contrast, Whiten and Byrne (1988), suggest that the influence of varying competition among group members can lead to advanced ('Machiavellian') tactics, which fuels the evolution of social cognition.

When we compare the results of playback studies conducted on chacma baboons with my results on Guinea baboons presented in this thesis, and the results of two earlier studies conducted on the same Guinea baboon population, we see general differences in response patterns between both species of baboons. First, chacma baboons generally paid strong attention to information that might have indicated deviation from predicted patterns. For example, Kitchen et al. (2005) presented sequences of "wahoo" vocalisations produced by two males, which were either in adjacent or disparate ranks. "Wahoos" are a call type that is usually produced in male-male contest. When testing high ranking males, responses were stronger to playbacks of sequences containing males with disparate rank, suggesting they recognised the significance of those vocal interactions. Contest between very disparate males mainly occurs when either high value resources are involved, or when conditions of individual contestants have changed. Further, Crockford et al. (2007), tested if subordinate chacma baboon males keep track of consortships formed by dominant males and receptive females. They presented sequences of vocalisation that simulated temporary separation of the consort pairs, by presenting male and female vocalisation from different directions. Test subjects responded strongly in the test condition, i.e., were more attentive or even moved towards the direction of the female vocalisation.

On the contrary, Guinea baboons generally were more interested in information that match existing patterns. When tested for their ability to differentiate acoustically between subjects from their own vs. a neighbouring or a stranger social unit, Guinea baboon males responded strongly after playback calls of members of their own gang, while attending only briefly to neighbour or stranger calls (Maciej et al., 2013). Further, when testing whether males track the changes in male-female associations at the unit level by presenting call sequences of grunt exchanges that either simulate affiliative interactions between male and female of the same unit, or from individuals of different units, males responded strongly to the sequences that presented information that were consistent with the actual association patterns, while responding less to the inconsistent.

Based on the theories of Dunbar, and of Whiten and Byrne, we can make predictions about potential differences in the social knowledge of chacma and Guinea baboons. While chacma baboons live in a uni-level society with steep dominance hierarchies, Guinea baboons live in multi-level societies and with low competition among males. According to the 'Social Brain Hypothesis' (Dunbar, 1998), Guinea baboons should show more advanced socio-cognitive skills and high attention to their social environment, as they live in a more complex social environment with variation and fluidity in group compositions. Alternatively, following the 'Machiavellian Intelligence' hypothesis (Whiten & Byrne, 1988), we would expect the same results for chacma baboons, due to their highly competitive social environment.

The results obtained in study 1 (chapter 2), along with the results of the presented studies of Guinea and chacma baboons, suggest that differences in the competitive environment affect the value of social information, and as a consequence, the motivation or ability of an individual to attend to them. While both species share similarities in their abilities to recognise individuals based on grouping features, and can track associations between individuals, the target of their attention differs markedly.

4.3 Social investment in a tolerant multi-level society

Within the genus *Papio*, Guinea baboons are an interesting case when it comes to the relationship between male and females. On the one hand, in the majority of baboon species, including chacma, yellow, Kinda, and olive baboons, we observe multimale multi-female groups in which male attention and interaction with females is mainly limited to reproduction (but see section 1.3.1 for more information on male-female 'friendships') (Fischer et al., 2019). On the other hand, hamadryas baboon live in a multi-level society with 'one-male multi-female' units at the core (Kummer, 1968). Relationships between the male and the females are maintained through female-biased socio-positive interaction and, as a decisive feature of the hamadryas baboon unit, male coercive behaviours ('herding' (Kummer, 1968)) aimed at maintaining female proximity and to prevent interactions with other males and females outside their unit. Males serve as main protector but also as main aggressor of females (Swedell, 2015). What all these species share, is that exertion of dominance over competitors and females is an important factor for males to achieve reproductive success.

Alternatively, the Guinea baboon multi-level society presents a different social setting, as it is characterised through male philopatry with strong bonds among the tolerant males. Male bonding is hereby likely promoted by higher genetic relatedness within parties. Female are the dispersing sex, enjoy relatively high spatial freedom, and play a strong role in relationship maintenance and mate choice. Female unit tenures can last for several months, even years, but can also change seemingly spontaneously and last shortly (e.g., days or weeks). Eventually, almost all males in our population seem to establish themselves as reproductively active males and acquire females. While most males are associated with two or three females, we also observe units with just one female or up to seven. Male reproductive success in Guinea baboons seems to be strongly dependant on their ability to attract females and to maintain the exclusive reproductive relationships to them.

With my work I was able to show, contrary to an earlier study with a smaller sample size of Guinea baboons (Goffe et al., 2016), that male preferences for females are affected by females' current or theoretical long-term reproductive value. We could show that males preferentially interact with receptive females and with female of mature age, which could likely be related to their parity i.e. higher chance for successful reproduction. Guinea baboon males maintain also base-line interaction rates with their females independent of reproductive state and age, suggesting that regular interaction might be important for relationship maintenance, but, current mating opportunities seem to strongly influence their day-to-day decision making about in whom to invest social interactions and time.

4.4 Conclusion and future directions

Baboons haven proven to be an interesting and important test case to study the interplay between sociality and ecological factors (Barrett, 2009; Jolly, 2009). The results of study 1 (chapter 2) are in line with existing evidence showing that the level of competition affects the value of social information and, as a consequence, the motivation or ability to attend to social signals. With study 2 (chapter 3) I showed that Guinea baboon primary males maintain social relationships with all of their associated females but allocate their social investment to females in relation to female short- and long-term reproductive value. Irrespective of being a relative tolerant and low competitive species, the current reproductive value of a female partner is still an influential characteristic driving male Guinea baboon behaviour. While my studies presented new insight into the allocation of social attention and investment of Guinea baboon primary males, they also provided new questions and avenues for future research.

4.4.1 Attention to social information - future directions

To follow up with the findings obtained in study 1 (chapter 2), future research could further explore male social attention using the same experimental set up we used but alternatively, testing males with vocalisation of females when they are receptive. The results of chapter 3 have shown that males showed preferential interaction and association to females when they were receptive. We could therefore also expect an increase in attention to females and therefore more specific interest in the movement patterns of such receptive females. Doing so would also shed a light into whether males lacked motivation or the ability to track their females.

Further, a previous study on Guinea baboons suggested that males' weak responses to information that represents deviant interaction patterns might be explained because they regard it as 'social noise' (Faraut & Fischer, 2019). In an additional playback experiment, we could test responses that are more directly related to individual primary males. Mirroring Faraut and Fischer's experiment, we could now present affiliative sequences of grunting vocalisations from one of the primary males' females combined with vocalisations of a different male. Additionally, we could vary the selection of males that we include in the test condition, e.g., males that are part of the same or different party, to test if the simulated interactions lead to different responses based in primary males when the other male is a stranger or a known individual.

4.4.2 Male social investment - future directions

While study 2 (chapter 3) gave us insight into the relationship between male and female Guinea baboons, especially in regard to male preferences, we still lack insight into the specific decision-making process. In future studies we should look more specifically into individual units and try to describe and assess the inter-individual interaction patterns and temporal dynamics in interaction rates specifically in situations where males decide to interact with one specific female and not another.

Additionally, female unit tenure might present an interesting female characteristic that could influence male behaviour. In hamadryas baboons, interaction rates with females are especially high after females join the unit (Swedell & Schreier, 2009). If in Guinea baboons the social investment by males plays an important role for male-female relationship maintenance, we might also see differential investment based on a females' tenure. Newly acquired females might receive more attention as their relationship still needs to be established, while existing relationships with females of longer tenure might need less tending to. Furthermore, we might also find changing patterns based on male age-related strategies, with younger males focusing on acquiring and attracting new females, compared to old males who might have to focus on maintaining fewer, but important partner.

Further, as the study population and long-term data collection includes nowadays more males that have reached a high unit size (e.g., more than five females), analysing the potential link between male social investment and larger unit sizes might be an interesting avenue for future research.

An additional direction for future investigation could focus in elucidating the interest of males in lactating females. While we observed male spatial preferences for lactating females, we still need to disentangle whether these observed preferences are due to their interest in the female or in the potentially present female's infant. When looking at periods in which male and lactating females are in close proximity, we should be able to discern with whom the male is interacting, and compare situations in which lactating females have their offspring present or not.

References

Alberts, S. C. (2012). Magnitude and sources of variation in male reproductive performance In: Mitani J, Call J, Kappeler P, Palombit R, Silk JB, editors. The Evolution of Primate Societies. Chicago: University of Chicago Press.

Alexander, R. D. (1974). The evolution of social behavior. Annual Review of Ecology and Systematics, 325–383.

Altmann, J. (1974). Observational study of behavior: Sampling methods. Behaviour, 49(3–4), 227–266.

Altmann, J. (1980). Baboon mothers and infants. University of Chicago Press.

Altmann, J., Hausfater, G., & Altmann, S. A. (1988). Determinants of reproductive success in savannah baboons (Papio cynocephalus) Reproductive success. University of Chicago Press, Chicago.[Google Scholar].

Altmann, S. A. (1962). A field study of the sociobioligy of rhesus monkeys (Macaca mulatta). Annals of the New York Academy of Sciences, 102(2), 338–435. https://doi.org/10.1111/j.1749-6632.1962.tb13650.x

Anderson, C. M. (1986). Female age: Male preference and reproductive success in primates. International Journal of Primatology, 7(3), 305–326.

Andrews, R. V., & Belknap, R. W. (1986). Bioenergetic benefits of huddling by deer mice (Peromyscus maniculatus). Comparative Biochemistry and Physiology. A, Comparative Physiology, 85(4), 775–778.

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

Arnold, W. (1990). The evolution of marmot sociality: II. Costs and benefits of joint hibernation. Behavioral Ecology and Sociobiology.

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. Journal of Memory and Language, 59(4), 390–412. https://doi.org/10.1016/j.jml.2007.12.005

Bachmann, C., & Kummer, H. (1980). Male assessment of female choice in hamadryas baboons. Behavioral Ecology and Sociobiology, 6(4), 315–321. https://doi.org/10.1007/BF00292774

Bailey, I., Myatt, J. P., & Wilson, A. M. (2013). Group hunting within the Carnivora: Physiological, cognitive and environmental influences on strategy and cooperation. Behavioral Ecology and Sociobiology, 67(1), 1–17.

Balsby, T. J., & Dabelsteen, T. (2005). Simulated courtship interactions elicit neighbour intrusions in the whitethroat, Sylvia communis. Animal Behaviour, 69(1), 161–168. https://doi.org/10.1016/j.anbehav.2004.01.021

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. Journal of Memory and Language, 68(3), 255–278.

Barrett, L. (2009). A guide to practical babooning: Historical, social, and cognitive contingency. Evolutionary Anthropology: Issues, News, and Reviews, 18(3), 91–102. https://doi.org/10.1002/evan.20210

Barrett, L., Henzi, P., & Rendall, D. (2007). Social brains, simple minds: Does social complexity really require cognitive complexity? Philosophical Transactions of the Royal Society B: Biological Sciences, 362(1480), 561–575. https://doi.org/10.1098/rstb.2006.1995

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw, 67(1), 1–48.

Bearder, S. K. (1987). Lorises, Bushbabies, and Tarsiers: Diverse Societies in Solitary Foragers. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), Primate Societies (pp. 11–24). University of Chicago Press.

Beauchamp, G. (2015). Animal vigilance: Monitoring predators and competitors. Academic Press.

Bercovitch, F. B. (1983). Time budgets and consortships in olive baboons (Papio anubis). Folia Primatologica, 41(3–4), 180–190.

Bercovitch, F. B. (1986). Male rank and reproductive activity in savanna baboons. International Journal of Primatology, 7, 533–550.

Bercovitch, F. B. (1991). Mate selection, consortship formation, and reproductive tactics in adult female savanna baboons. Primates, 32(4), 437–452. https://doi.org/10.1007/BF02381935

Bercovitch, F. B., Bashaw, M. J., & del Castillo, S. M. (2006). Sociosexual behavior, male mating tactics, and the reproductive cycle of giraffe Giraffa camelopardalis. Hormones and Behavior, 50(2), 314–321.

Bergman, T. J. (2010). Experimental evidence for limited vocal recognition in a wild primate: Implications for the social complexity hypothesis. Proceedings of the Royal Society B: Biological Sciences, 277(1696), 3045–3053. https://doi.org/10.1098/rspb.2010.0580

Bergman, T. J., & Beehner, J. C. (2015). Measuring social complexity. Animal Behaviour, 103, 203–209. https://doi.org/10.1016/j.anbehav.2015.02.018

Bergman, T. J., Beehner, J. C., Cheney, D. L., & Seyfarth, R. M. (2003). Hierarchical Classification by Rank and Kinship in Baboons. Science, 302(5648), 1234–1236. https://doi.org/10.1126/science.1087513

Birkhead, T. R., & Møller, A. P. (1995). Extra-pair copulation and extra-pair paternity in birds. Animal Behaviour, 49(3), 843–848.

Boland, C. R. (2003). An experimental test of predator detection rates using groups of free-living emus. Ethology, 109(3), 209–222.

Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in corvids. Animal Behaviour, 65(3), 479–487.

Borgeaud, C., Jankowiak, B., Aellen, M., Dunbar, R. I. M., & Bshary, R. (2021). Vervet monkeys socialize more when time budget constraints are experimentally reduced. Ethology, 127(9), 682–696. https://doi.org/10.1111/eth.13205

Bray, O. E., Kennelly, J. J., & Guarino, J. L. (1975). Fertility of eggs produced on territories of vasectomized red-winged blackbirds. The Wilson Bulletin, 187–195.

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal, 9(2), 378–400.

Brown, C., & Laland, K. N. (2003). Social learning in fishes: A review. Fish and Fisheries, 4(3), 280–288.

Burger, J., & Gochfeld, M. (1988). Effects of group size and sex on vigilance in ostriches (Struthio camelus): Antipredator strategy or mate competition? Ostrich, 59(1), 14–20.

Byrne, R. W., Whiten, A., & Henzi, S. P. (1990). Social relationships of mountain baboons: Leadership and affiliation in a non-female-bonded monkey. American Journal of Primatology, 20(4), 313–329. https://doi.org/10.1002/ajp.1350200409

Carazo, P., Font, E., & Desfilis, E. (2008). Beyond 'nasty neighbours' and 'dear enemies'? Individual recognition by scent marks in a lizard (Podarcis hispanica). Animal Behaviour, 76(6), 1953–1963. https://doi.org/10.1016/j.anbehav.2008.08.018

Caro, T. (2005). Antipredator defenses in birds and mammals. University of Chicago Press.

Cassidy, K. A., MacNulty, D. R., Stahler, D. R., Smith, D. W., & Mech, L. D. (2015). Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park. Behavioral Ecology, 26(5), 1352–1360.

Chala, D., Roos, C., Svenning, J.-C., & Zinner, D. (2019). Species-specific effects of climate change on the distribution of suitable baboon habitats–Ecological niche modeling of current and Last Glacial Maximum conditions. Journal of Human Evolution, 132, 215–226.

Chambers, J. M., & Hastie, T. J. (1992). Linear models. Chapter 4 of statistical models in S. Wadsworth & Brooks/Cole, 1992.

Chapais, B., & Berman, C. M. (2004). Introduction: The Kinship Black box. In B. Chapais & C. M. Berman (Eds.), Kinship and Behavior in Primates (pp. 3-). Oxford University Press.

Chapman, C. A. (2000). Determinants of group size in primates: The importance of travel costs. On the Move: How and Why Animals Travel in Group.

Charpentier, M. J., Van Horn, R. C., Altmann, J., & Alberts, S. C. (2008). Paternal effects on offspring fitness in a multimale primate society. Proceedings of the National Academy of Sciences, 105(6), 1988–1992.

Cheney, D. L. (1995). The responses of female baboons to anomalous social interactions; evidence for causal reasoning.pdf.

Cheney, D. L. (1977). The acquisition of rank and the development of reciprocal alliances among free-ranging immature baboons. Behavioral Ecology and Sociobiology, 2(3), 303–318. https://doi.org/10.1007/BF00299742

Cheney, D. L. (1983). Extrafamilial alliances among vervet monkeys. Primate Social Relationships: An Integrated Approach.

Cheney, D. L., & Seyfarth, R. M. (1980). Vocal recognition in free-ranging vervet monkeys. Animal Behaviour, 28(2), 362–367. https://doi.org/10.1016/S0003-3472(80)80044-3

Cheney, D. L., & Seyfarth, R. M. (2008). Baboon metaphysics. In Baboon Metaphysics. University of Chicago Press.

Cheney, D. L., & Seyfarth, R. M. (2018). How monkeys see the world: Inside the mind of another species. University of Chicago Press.

Chowdhury, S., Pines, M., Saunders, J., & Swedell, L. (2015). The adaptive value of secondary males in the polygynous multi-level society of hamadryas baboons. American Journal of Physical Anthropology, 158(3), 501–513.

Clay, Z., Smith, C. L., & Blumstein, D. T. (2012). Food-associated vocalizations in mammals and birds: What do these calls really mean? Animal Behaviour, 83(2), 323–330.

Clutton-Brock, T. H. (1977). Species differences in feeding and ranging behaviour in primates. Primate Ecology: Studies of Feeding and Ranging Behaviour, 557–584.

Clutton-Brock, T. H., Albon, S. D., Gibson, R. M., & Guinness, F. E. (1979). The logical stag: Adaptive aspects of fighting in red deer (Cervus elaphus L.). Animal Behaviour, 27, 211–225.

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). Red deer: Behavior and ecology of two sexes. University of Chicago press.

Clutton-Brock, T. H., Hodge, S. J., Spong, G., Russell, A. F., Jordan, N. R., Bennett, N. C., Sharpe, L. L., & Manser, M. B. (2006). Intrasexual competition and sexual selection in cooperative mammals. Nature, 444(7122), 1065–1068.

Clutton-Brock, T. H., & Parker, G. A. (1992). Potential Reproductive Rates and the Operation of Sexual Selection. The Quarterly Review of Biology, 67(4), 437–456. https://doi.org/10.1086/417793

Clutton-Brock, T. H., & Parker, G. A. (1995). Punishment in animal societies. Nature, 373(6511), 209–216.

Clutton-Brock, T. H., & Vincent, A. C. J. (1991). Sexual selection and the potential reproductive rates of males and females. Nature, 351(6321), 58–60. https://doi.org/10.1038/351058a0

Collins, D. A. (1986). Interactions between adult male and infant yellow baboons (Papio c. Cynocephalus) in Tanzania. Animal Behaviour, 34(2), 430–443.

Cote, I. M., & Poulinb, R. (1995). Parasitism and group size in social animals: A meta-analysis. Behavioral Ecology, 6(2), 159–165. https://doi.org/10.1093/beheco/6.2.159

Crockford, C., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2007). Baboons eavesdrop to deduce mating opportunities. Animal Behaviour, 73(5), 885–890. https://doi.org/10.1016/j.anbehav.2006.10.016

Dal Pesco, F., & Fischer, J. (2018). Greetings in male Guinea baboons and the function of rituals in complex social groups. Journal of Human Evolution, 125, 87–98. https://doi.org/10.1016/j.jhevol.2018.10.007

Dal Pesco, F., & Fischer, J. (2020). On the evolution of baboon greeting rituals. Philosophical Transactions of the Royal Society B: Biological Sciences, 375(1805), 20190420. https://doi.org/10.1098/rstb.2019.0420

Dal Pesco, F., & Fischer, J. (2022). CRP Simenti work manual and guides. https://doi.org/10.17605/OSF.IO/AK3W4

Dal Pesco, F., Trede, F., Zinner, D., & Fischer, J. (2021). Kin bias and male pair-bond status shape male-male relationships in a multilevel primate society. Behavioral Ecology and Sociobiology, 75(1), 1–14. https://doi.org/10.1007/s00265-020-02960-8

Dal Pesco, F., Trede, F., Zinner, D., & Fischer, J. (2022). Male–male social bonding, coalitionary support and reproductive success in wild Guinea baboons. Proceedings of the Royal Society B, 289(1975), 20220347. https://doi.org/10.1098/rspb.2022.0347

Darwin, C. (1871). In C. Darwin. The Descent of Man, and Selection in Relation to Sex.

Dasser, V. (1988). A social concept in Java monkeys. Animal Behaviour, 36(1), 225–230.

Davies, A. D., Lewis, Z., & Dougherty, L. R. (2020). A meta-analysis of factors influencing the strength of mate-choice copying in animals. Behavioral Ecology, 31(6), 1279–1290. https://doi.org/10.1093/beheco/araa064

Davies, N. B., Krebs, J. R., & West, S. A. (2012). An introduction to behavioural ecology. John Wiley & Sons.

Deag, J. M. (1977). Aggression and submission in monkey societies. Animal Behaviour, 25, 465–474.

Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2004). Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees. Hormones and Behavior, 46(2), 204–215. https://doi.org/10.1016/j.yhbeh.2004.03.013

DeVore, I., & Hall, K. R. (1965). Baboon ecology. I. DeVore (Ed.), Primate Behavior. Field Studies of Monkeys and Apes, New York Etc.(Holt, Rinehart and Winston) 1965, Pp. 20-53.

Dobson, A. J., & Barnett, A. (2002). An Introduction to Generalized Linear Models (2008). CRC Pr I Llc. https://doi.org/10.1201/9781315182780

Dobson, A. J., & Barnett, A. G. (2018). An introduction to generalized linear models. Chapman and Hall/CRC.

Dunbar, R. I. M. (1998). The social brain hypothesis. Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, 6(5), 178–190.

Dunbar, R. I. M. (1983). Structure of gelada baboon reproductive units. III. The male’s relationship with his females. Animal Behaviour, 31(2), 565–575. https://doi.org/10.1016/S0003-3472(83)80080-3

Dunbar, R. I. M., Korstjens, A. H., Lehmann, J., & British Academy Centenary Research Project. (2009). Time as an ecological constraint. Biological Reviews, 84(3), 413–429. https://doi.org/10.1111/j.1469-185X.2009.00080.x

Ellis, L. (1995). Dominance and reproductive success among nonhuman animals: A cross-species comparison. Ethology and Sociobiology, 16(4), 257–333.

Engh, A. L., Siebert, E. R., Greenberg, D. A., & Holekamp, K. E. (2005). Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognize third-party relationships. Animal Behaviour, 69(1), 209–217. https://doi.org/10.1016/j.anbehav.2004.04.013

Faraut, L., & Fischer, J. (2019). How life in a tolerant society affects the attention to social information in baboons. Animal Behaviour, 152, 11–17. https://doi.org/10.1016/j.anbehav.2019.04.004

Ferrari, S. F. (1992). The care of infants in a wild marmoset (Callithrix flaviceps) group. American Journal of Primatology, 26(2), 109–118.

Fischer, J. (2022). Studying primate cognition: From the wild to captivity and back. Primate Cognitive Studies; Schwartz, B., Beran, M., Eds, 609–631.

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

Fischer, J., Higham, J. P., Alberts, S. C., Barrett, L., Beehner, J. C., Bergman, T. J., Carter, A. J., Collins, A., Elton, S., & Fagot, J. (2019). Insights into the evolution of social systems and species from baboon studies. Elife, 8.

Fischer, J., Kopp, G. H., Dal Pesco, F., Goffe, A., Hammerschmidt, K., Kalbitzer, U., Klapproth, M., Maciej, P., Ndao, I., Patzelt, A., & Zinner, D. (2017). Charting the neglected West: The social system of Guinea baboons. American Journal of Physical Anthropology, 162(S63), 15–31. https://doi.org/10.1002/ajpa.23144

Fischer, J., Noser, R., & Hammerschmidt, K. (2013). Bioacoustic Field Research: A Primer to Acoustic Analyses and Playback Experiments With Primates: Bioacoustic Field Methods. American Journal of Primatology, 75(7), 643–663. https://doi.org/10.1002/ajp.22153

Fisher, R. A. (1999). The genetical theory of natural selection: A complete variorum edition. Oxford University Press.

Gauthier, C.-A. (1999). Reproductive parameters and paracallosal skin color changes in captive female Guinea baboons, Papio papio. American Journal of Primatology: Official Journal of the American Society of Primatologists, 47(1), 67–74.

Gesquiere, L. R., Wango, E. O., Alberts, S. C., & Altmann, J. (2007). Mechanisms of sexual selection: Sexual swellings and estrogen concentrations as fertility indicators and cues for male consort decisions in wild baboons. Hormones and Behavior, 51(1), 114–125. https://doi.org/10.1016/j.yhbeh.2006.08.010

Gilby, I. C. (2012). Cooperation among non-kin: Reciprocity, markets and mutualism. The Evolution of Primate Societies, 514–530.

Gillam, E. H. (2007). Eavesdropping by bats on the feeding buzzes of conspecifics. Canadian Journal of Zoology, 85(7), 795–801.

Goffe, A. S. (2016). Social relationships of female Guinea baboons (Papio papio) in Senegal. Dissertation, Göttingen, Georg-August Universität, 2016.

Goffe, A. S., Zinner, D., & Fischer, J. (2016). Sex and friendship in a multilevel society: Behavioural patterns and associations between female and male Guinea baboons. Behavioral Ecology and Sociobiology, 70(3), 323–336. https://doi.org/10.1007/s00265-015-2050-6

Gouzoules, S. (1984). Primate mating systems, kin associations, and cooperative behavior: Evidence for kin recognition? American Journal of Physical Anthropology, 27(S5), 99–134.

Grueter, C. C., Chapais, B., & Zinner, D. (2012). Evolution of Multilevel Social Systems in Nonhuman Primates and Humans. International Journal of Primatology, 33(5), 1002–1037. https://doi.org/10.1007/s10764-012-9618-z

Guidelines for the treatment of animals in behavioural research and teaching. (2020). Animal Behaviour, 159, I–XI. https://doi.org/10.1016/j.anbehav.2019.11.002

Gust, D. A., Gordon, T. P., Gergits, W. F., Casna, N. J., Gould, K. G., & McClure, H. M. (1996). Male dominance rank and offspring-initiated affiliative behaviors were not predictors of paternity in a captive group of pigtail macaques (Macaca nemestrina). Primates, 37(3), 271–278.

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

Hausfater, G. (1975). Dominance and reproduction in Baboons (Papio cynocephalus). Contributions to Primatology, 7, 1–150.

Hausfater, G., Altmann, J., & Altmann, S. (1982). Long-term consistency of dominance relations among female baboons (Papio cynocephalus). Science, 217(4561), 752–755.

Henzi, S. P., & Barrett, L. (2005). The historical socioecology of savanna baboons (Papio hamadryas). Journal of Zoology, 265(3), 215–226.

Hick, K., Reddon, A. R., O'Connor, C. M., & Balshine, S. (2014). Strategic and tactical fighting decisions in cichlid fishes with divergent social systems. Behaviour, 151(1), 47–71.

Hill, D. A. (1987). Social relationships between adult male and female rhesus macaques: 1. Sexual consortships. Primates, 28(4), 439–456.

Hinde, R. A. (1976). Interactions, relationships and social structure. Man, 1–17.

Holekamp, K. E. (2007). Questioning the social intelligence hypothesis. Trends in Cognitive Sciences, 11(2), 65–69. https://doi.org/10.1016/j.tics.2006.11.003

Holekamp, K. E., Smale, L., Berg, R., & Cooper, S. M. (1997). Hunting rates and hunting success in the spotted hyena (Crocuta crocuta). Journal of Zoology, 242(1), 1–15.

Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. Behavioral Ecology, 2(2), 143–155.

Jahn-Eimermacher, A., Lasarzik, I., & Raber, J. (2011). Statistical analysis of latency outcomes in behavioral experiments. Behavioural Brain Research, 221(1), 271–275. https://doi.org/10.1016/j.bbr.2011.03.007

Jeanson, R., Dussutour, A., & Fourcassié, V. (2012). Key Factors for the Emergence of Collective Decision in Invertebrates. Frontiers in Neuroscience, 6. https://doi.org/10.3389/fnins.2012.00121

Jeschke, J. M., & Tollrian, R. (2007). Prey swarming: Which predators become confused and why? Animal Behaviour, 74(3), 387–393.

Johnstone, R. A. (2000). Models of reproductive skew: A review and synthesis (invited article). Ethology, 106(1), 5–26.

Jolly, A. (1966). Lemur Social Behavior and Primate Intelligence: The step from prosimian to monkey intelligence probably took place in a social context. Science, 153(3735), 501–506.

Jolly, C. J. (2009). Fifty years of looking at human evolution: Backward, forward, and sideways. Current Anthropology, 50(2), 187–199.

Jolly, C. J. (2020). Philopatry at the frontier: A demographically driven scenario for the evolution of multilevel societies in baboons (Papio). Journal of Human Evolution, 146, 102819. https://doi.org/10.1016/j.jhevol.2020.102819

Jungwirth, A., Josi, D., Walker, J., & Taborsky, M. (2015). Benefits of coloniality: Communal defence saves anti-predator effort in cooperative breeders. Functional Ecology, 29(9), 1218–1224.

Kalbitz, J., Ostner, J., & Schülke, O. (2016). Strong, equitable and long-term social bonds in the dispersing sex in Assamese macaques. Animal Behaviour, 113, 13–22. https://doi.org/10.1016/j.anbehav.2015.11.005

Kalbitzer, U. (2014). Foundations of variation in male aggressiveness and tolerance between chacma baboons (Papio ursinus) in Botswana and Guinea baboons (P. papio) in Senegal.

Kappeler, P. M. (2012). Verhaltensbiologie. Springer.

Kappeler, P. M., Clutton-Brock, T., Shultz, S., & Lukas, D. (2019). Social complexity: Patterns, processes, and evolution. Behavioral Ecology and Sociobiology, 73(1), 5, s00265-018-2613–2614. https://doi.org/10.1007/s00265-018-2613-4

Kappeler, P. M., & van Schaik, C. P. (2002). Evolution of primate social systems. International Journal of Primatology, 23(4), 707–740.

Kapsalis, E. (2004). Matrilineal kinship and primate behavior. Kinship and Behavior Inprimates, 153–176.

Kawai, M., Ohsawa, H., Mori, U., & Dunbar, R. (1983). Social organization of gelada baboons: Social units and definitions. Primates, 24(1), 13–24.

Kirkpatrick, R. C., & Grueter, C. C. (2010). Snub-nosed monkeys: Multilevel societies across varied environments. Evolutionary Anthropology: Issues, News, and Reviews, 19(3), 98–113. https://doi.org/10.1002/evan.20259

Kitchen, D. M., Cheney, D. L., Engh, A. L., Fischer, J., Moscovice, L. R., & Seyfarth, R. M. (2013). Male baboon responses to experimental manipulations of loud “wahoo calls”: Testing an honest signal of fighting ability. Behavioral Ecology and Sociobiology, 67(11), 1825–1835. https://doi.org/10.1007/s00265-013-1592-8

Kitchen, D. M., Cheney, D. L., & Seyfarth, R. M. (2005). Male chacma baboons (Papio hamadryas ursinus) discriminate loud call contests between rivals of different relative ranks. Animal Cognition, 8(1), 1–6. https://doi.org/10.1007/s10071-004-0222-2

Klose, S. M., Welbergen, J. A., Goldizen, A. W., & Kalko, E. K. (2009). Spatio-temporal vigilance architecture of an Australian flying-fox colony. Behavioral Ecology and Sociobiology, 63(3), 371–380.

Kokko, H., Brooks, R., McNamara, J. M., & Houston, A. I. (2002). The sexual selection continuum. Proceedings of the Royal Society of London. Series B: Biological Sciences, 269(1498), 1331–1340.

Korstjens, A. H., Verhoeckx, I. L., & Dunbar, R. I. (2006). Time as a constraint on group size in spider monkeys. Behavioral Ecology and Sociobiology, 60(5), 683–694.

Krause, J., Krause, S., Arlinghaus, R., Psorakis, I., Roberts, S., & Rutz, C. (2013). Reality mining of animal social systems. Trends in Ecology & Evolution, 28(9), 541–551. https://doi.org/10.1016/j.tree.2013.06.002

Kruuk, H. (1972). Surplus killing by carnivores. Journal of Zoology, 166(2), 233–244.

Kummer, H. (1968). Social organization of hamadryas baboons. Karger Publishers.

Kummer, H., Götz, W., & Angst, W. (1973). Pair bonds in baboons. 28.

Kurland, J. (1977). Kin selection in Japanese macaques. Contributions to Primatology. Vol, 12.

le Roux, A., & Bergman, T. J. (2012). Indirect rival assessment in a social primate, Theropithecus gelada. Animal Behaviour, 83(1), 249–255. https://doi.org/10.1016/j.anbehav.2011.10.034

Leighton, D. R. (1987). Gibbons: Territoriality and Monogamy. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), Primate Societies (pp. 135–145). University of Chicago Press.

Lemasson, A., Palombit, R. A., & Jubin, R. (2008). Friendships between males and lactating females in a free-ranging group of olive baboons (Papio hamadryas anubis): Evidence from playback experiments. Behavioral Ecology and Sociobiology, 62(6), 1027–1035. https://doi.org/10.1007/s00265-007-0530-z

Leutenegger, W. (1978). Scaling of sexual dimorphism in body size and breeding system in primates. Nature, 272(5654), 610–611.

Lindström, Å. (1989). Finch flock size and risk of hawk predation at a migratory stopover site. The Auk, 106(2), 225–232.

Lukas, D., & Clutton-Brock, T. (2018). Social complexity and kinship in animal societies. Ecology Letters, 21(8), 1129–1134. https://doi.org/10.1111/ele.13079

Maciej, P., Fischer, J., & Hammerschmidt, K. (2011). Transmission characteristics of primate vocalizations: Implications for acoustic analyses. PloS One, 6(8), e23015. https://doi.org/10.1371/journal.pone.0023015

Maciej, P., Ndao, I., Hammerschmidt, K., & Fischer, J. (2013). Vocal communication in a complex multi-level society: Constrained acoustic structure and flexible call usage in Guinea baboons. Frontiers in Zoology, 10(1), 58. https://doi.org/10.1186/1742-9994-10-58

Maciej, P., Patzelt, A., Ndao, I., Hammerschmidt, K., & Fischer, J. (2013). Social monitoring in a multilevel society: A playback study with male Guinea baboons. Behavioral Ecology and Sociobiology, 67(1), 61–68. https://doi.org/10.1007/s00265-012-1425-1

MacLean, E. L., Merritt, D. J., & Brannon, E. M. (2008). Social complexity predicts transitive reasoning in prosimian primates. Animal Behaviour, 76(2), 479–486. https://doi.org/10.1016/j.anbehav.2008.01.025

Maestripieri, D. (1999). Fatal attraction: Interest in infants and infant abuse in rhesus macaques. American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists, 110(1), 17–25.

Manser, M. B., Allen, C., & Townsend, S. W. (2011). A simple test of vocal individual recognition in wild meerkats. https://doi.org/10.1098/rsbl.2011.0844

Maynard Smith, J. (1974). The theory of games and the evolution of animal conflicts. Journal of Theoretical Biology, 47(1), 209–221.

McComb, K., Moss, C., Sayialel, S., & Baker, L. (2000). Unusually extensive networks of vocal recognition in African elephants. Animal Behaviour, 59(6), 1103–1109. https://doi.org/10.1006/anbe.2000.1406

McCullagh, P., & Nelder, J. A. (2019). Generalized linear models. Routledge.

McFarland, R., & Majolo, B. (2013). Coping with the cold: Predictors of survival in wild Barbary macaques, Macaca sylvanus. Biology Letters, 9(4), 20130428. https://doi.org/10.1098/rsbl.2013.0428

Meikle, D. B., & Vessey, S. H. (1981). Nepotism among rhesus monkey brothers. Nature, 294(5837), 160–161.

Miller, M. H., Kling, A., & Dicks, D. (1973). Familial interactions of male rhesus monkeys in a semi-free-ranging troop. American Journal of Physical Anthropology, 38(2), 605–611.

Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (2012). The evolution of primate societies. University of Chicago Press.

Monaghan, P., Maklakov, A. A., & Metcalfe, N. B. (2020). Intergenerational transfer of ageing: Parental age and offspring lifespan. Trends in Ecology & Evolution, 35(10), 927–937.

Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, Panthera leo. Animal Behaviour, 78(2), 359–370.

Muller, M. N., Thompson, M. E., & Wrangham, R. W. (2006). Male chimpanzees prefer mating with old females. Current Biology, 16(22), 2234–2238.

Muller, M. N., & Wrangham, R. W. (2009). Sexual coercion in primates and humans: An evolutionary perspective on male aggression against females. Harvard University Press.

Neill, Srs., & Cullen, J. M. (1974). Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. Journal of Zoology, 172(4), 549–569.

Nishida, T. (1997). Sexual behavior of adult male chimpanzees of the Mahale Mountains national park, Tanzania. Primates, 38(4), 379–398. https://doi.org/10.1007/BF02381879

Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. Animal Behaviour, 58(2), 229–246. https://doi.org/10.1006/anbe.1999.1159

Ostner, J., Vigilant, L., Bhagavatula, J., Franz, M., & Schülke, O. (2013). Stable heterosexual associations in a promiscuous primate. Animal Behaviour, 86(3), 623–631. https://doi.org/10.1016/j.anbehav.2013.07.004

Paciência, F. M. D., Rushmore, J., Chuma, I. S., Lipende, I. F., Caillaud, D., Knauf, S., & Zinner, D. (2019). Mating avoidance in female olive baboons (Papio anubis) infected by Treponema pallidum. Science Advances, 5(12), eaaw9724.

Packer, C., & Pusey, A. E. (1979). Female aggression and male membership in troops of Japanese macaques and olive baboons. Folia Primatologica, 31(3), 212–218.

Palombit, R. A. (1994). Dynamic Pair Bonds in Hylobatids: Implications Regarding Monogamous Social Systems. Behaviour, 128(1–2), 65–101. https://doi.org/10.1163/156853994X00055

Palombit, R. A. (1999). Infanticide and the evolution of pair bonds in nonhuman primates. Evolutionary Anthropology: Issues, News, and Reviews, 7(4), 117–129. https://doi.org/10.1002/(SICI)1520-6505(1999)7:4<117::AID-EVAN2>3.0.CO;2-O

Palombit, R. A., Seyfarth, R. M., & Cheney, D. L. (1997). The adaptive value of ‘friendships’ to female baboons: Experimental and observational evidence. Animal Behaviour, 54(3), 599–614.

Patzelt, A., Kopp, G. H., Ndao, I., Kalbitzer, U., Zinner, D., & Fischer, J. (2014). Male tolerance and male–male bonds in a multilevel primate society. Proceedings of the National Academy of Sciences, 111(41), 14740–14745. https://doi.org/10.1073/pnas.1405811111

Patzelt, A., Zinner, D., Fickenscher, G., Diedhiou, S., Camara, B., Stahl, D., & Fischer, J. (2011). Group composition of Guinea baboons (Papio papio) at a water place suggests a fluid social organization. International Journal of Primatology, 32(3), 652–668.

Paz-y-Miño C, G., Bond, A. B., Kamil, A. C., & Balda, R. P. (2004). Pinyon jays use transitive inference to predict social dominance. Nature, 430(7001), Article 7001. https://doi.org/10.1038/nature02723

Petersdorf, M., & Higham, J. P. (2016). Mating systems. The International Encyclopedia of Primatology, 1–5.

Plavcan, J. M. (2001). Sexual dimorphism in primate evolution. American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists, 116(S33), 25–53.

Pollard, K. A., & Blumstein, D. T. (2008). Time allocation and the evolution of group size. Animal Behaviour, 76(5), 1683–1699.

Preuschoft, S., & van Schaik, C. P. (2000). Dominance and communication. Natural Conflict Resolution, 77–105.

Price, E. C. (1990). Infant carrying as a courtship strategy of breeding male cotton-top tamarins. Animal Behaviour, 40(4), 784–786.

Proctor, D. P., Lambeth, S. P., Schapiro, S. J., & Brosnan, S. F. (2011). Male chimpanzees' grooming rates vary by female age, parity, and fertility status. American Journal of Primatology, 73(10), 989–996.

Pusey, A., Williams, J., & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. Science, 277(5327), 828–831.

Qi, X.-G., Huang, K., Fang, G., Grueter, C. C., Dunn, D. W., Li, Y.-L., Ji, W., Wang, X.-Y., Wang, R.-T., Garber, P. A., & Li, B.-G. (2017). Male cooperation for breeding opportunities contributes to the evolution of multilevel societies. Proceedings of the Royal Society B: Biological Sciences, 284(1863), 20171480. https://doi.org/10.1098/rspb.2017.1480

R Core Team. (2021). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. URL https://www.R-project.org/

Range, F., & Noë, R. (2005). Can simple rules account for the pattern of triadic interactions in juvenile and adult female sooty mangabeys? Animal Behaviour, 69(2), 445–452. https://doi.org/10.1016/j.anbehav.2004.02.025

Rifkin, J. L., Nunn, C. L., & Garamszegi, L. Z. (2012). Do animals living in larger groups experience greater parasitism? A meta-analysis. The American Naturalist, 180(1), 70–82.

Ronald, N., & Sluijter, A. A. (1990). Reproductive tactics of male savanna baboons. Behaviour, 113(1–2), 117–169.

Rowe, C., & Healy, S. D. (2014). Measuring variation in cognition. Behavioral Ecology, 25(6), 1287–1292.

Rubenstein, D. I., & Hack, M. (2004). Natural and sexual selection and the evolution of multi-level societies: Insights from zebras with comparisons to primates. In P. M. Kappeler & C. P. van Schaik (Eds.), Sexual Selection in Primates (1st ed., pp. 266–279). Cambridge University Press. https://doi.org/10.1017/CBO9780511542459.017

Russo, D., Cistrone, L., Budinski, I., Console, G., Della Corte, M., Milighetti, C., Di Salvo, I., Nardone, V., Brigham, R. M., & Ancillotto, L. (2017). Sociality influences thermoregulation and roost switching in a forest bat using ephemeral roosts. Ecology and Evolution, 7(14), 5310–5321.

Ryan, M. J., & Keddy-Hector, A. (1992). Directional patterns of female mate choice and the role of sensory biases. The American Naturalist, 139, S4–S35.

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. Behavioral Ecology, 20(2), 416–420.

Schino, G., Tiddi, B., & Di Sorrentino, E. P. (2006). Simultaneous classification by rank and kinship in Japanese macaques. Animal Behaviour, 71(5), 1069–1074.

Schradin, C. (2000). Confusion effect in a reptilian and a primate predator. Ethology, 106(8), 691–700.

Schreier, A. L., & Swedell, L. (2009). The fourth level of social structure in a multi-level society: Ecological and social functions of clans in hamadryas baboons. American Journal of Primatology: Official Journal of the American Society of Primatologists, 71(11), 948–955.

Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. Current Biology, 20(24), 2207–2210.

Setchell, J. M. (2005). Do female mandrills prefer brightly colored males? International Journal of Primatology, 26(4), 715–735.

Setchell, J. M., & Jean Wickings, E. (2006). Mate Choice in Male Mandrills (Mandrillus sphinx). Ethology, 112(1), 91–99. https://doi.org/10.1111/j.1439-0310.2006.01128.x

Seyfarth, R. M. (1978). Social relationships among adult male and female baboons. II. Behaviour throughout the female reproductive cycle. Behaviour, 64(3–4), 227–247.

Seyfarth, R. M., & Cheney, D. L. (2003). 8. The Structure of Social Knowledge in Monkeys. In F. B. M. de Waal & P. L. Tyack (Eds.), Animal Social Complexity (pp. 207–229). Harvard University Press. https://doi.org/10.4159/harvard.9780674419131.c16

Seyfarth, R. M., & Cheney, D. L. (2012). Knowledge of social relations. Evolution of Primate Societies.

Seyfarth, R. M., & Cheney, D. L. (2015). Social cognition. Animal Behaviour, 103, 191–202. https://doi.org/10.1016/j.anbehav.2015.01.030

Sherman, P. W. (1989). Mate guarding as paternity insurance in Idaho ground squirrels. Nature, 338(6214), 418–420.

Shively, C. (1985). The evolution of dominance hierarchies in nonhuman primate society. In Power, dominance, and nonverbal behavior (pp. 67–87). Springer.

Sicotte, P. (1993). Inter-group encounters and female transfer in mountain gorillas: Influence of group composition on male behavior. American Journal of Primatology, 30(1), 21–36. https://doi.org/10.1002/ajp.1350300103

Silk, J. B. (2001). Ties that bond: The role of kinship in primate societies. New Directions in Anthropological Kinship, 71.

Silk, J. B. (1993). Does participation in coalitions influence dominance relationships among male bonnet macaques? Behaviour, 126(3–4), 171–189.

Silk, J. B. (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. Animal Behaviour, 57(5), 1021–1032. https://doi.org/10.1006/anbe.1998.1065

Silk, J. B. (2002). Kin Selection in Primate Groups. International Journal of Primatology, 23(4), 849–875. https://doi.org/10.1023/A:1015581016205

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. Science, 302(5648), 1231–1234.

Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (Papio cynocephalus) I. Variation in the strength of social bonds. Behavioral Ecology and Sociobiology, 61(2), 183–195.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010a). Female chacma baboons form strong, equitable, and enduring social bonds. Behavioral Ecology and Sociobiology, 64(11), 1733–1747.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010b). Strong and consistent social bonds enhance the longevity of female baboons. Current Biology, 20(15), 1359–1361.

Silk, J. B., Cheney, D., & Seyfarth, R. (1999). The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. Behaviour, 136(6), 679–703. https://doi.org/10.1163/156853999501522

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

Small, M. F., & Rodman, P. S. (1981). Primigravidity and Infant Loss in Bonnet Macaques 1. Journal of Medical Primatology, 10(2–3), 164–169.

Smithson, M., & Verkuilen, J. (2006). A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychological Methods, 11(1), 54.

Smuts, B. B. (1985). Sex and friendship in baboons. Routledge.

Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: Evidence and theoretical implications. In Advances in the Study of Behavior (Vol. 22, pp. 1–63).

Stammbach, E. (1986). 10. Desert, Forest and Montane Baboons: Multilevel-Societies. In Primate societies (pp. 112–120). University of Chicago Press.

Strum, S. C., & Western, J. D. (1982). Variations in fecundity with age and environment in olive baboons (Papio anubis). American Journal of Primatology, 3(1-4), 61–76.

Swedell, L. (2002). Affiliation among females in wild hamadryas baboons (Papio hamadryas hamadryas). International Journal of Primatology, 23(6), 1205–1226.

Swedell, L. (2015). Strategies of sex and survival in female hamadryas baboons: Through a female lens. Routledge.

Swedell, L., & Plummer, T. (2012). A Papionin Multilevel Society as a Model for Hominin Social Evolution. International Journal of Primatology, 33(5), 1165–1193. https://doi.org/10.1007/s10764-012-9600-9

Swedell, L., & Schreier, A. (2009). Male Aggression toward Females in Hamadryas Baboons: Conditioning. In Sexual coercion in primates and humans: An evolutionary perspective on male aggression against females (p. 244). Harvard University Press.

Taborsky, M., Cant, M. A., & Komdeur, J. (2021). The evolution of social behaviour. Cambridge University Press.

Taborsky, M., Oliveira, R. F., & Brockmann, H. J. (2008). The evolution of alternative reproductive tactics: Concepts and questions. Alternative Reproductive Tactics: An Integrative Approach, 1, 21.

Terrien, J., Perret, M., & Aujard, F. (2011). Behavioral thermoregulation in mammals: A review. Frontiers in Bioscience-Landmark, 16(4), 1428–1444.

Tibbetts, E. A. (2002). Visual signals of individual identity in the wasp Polistes fuscatus. Proceedings of the Royal Society of London. Series B: Biological Sciences, 269(1499), 1423–1428. https://doi.org/10.1098/rspb.2002.2031

Trivers, R. L. (1972). Parental investment and sexual selection In: Campbell B, editor. Sexual selection and the descent of man, 1871–1971. Chicago: Aldine, 136–179.

Turner, T. R., Whitten, P. L., Jolly, C. J., & Else, J. G. (1987). Pregnancy outcome in free-ranging vervet monkeys (Cercopithecus aethiops). American Journal of Primatology, 12(2), 197–203.

van Belle, S., Estrada, A., Ziegler, T. E., & Strier, K. B. (2009). Sexual behavior across ovarian cycles in wild black howler monkeys (Alouatta pigra): Male mate guarding and female mate choice. American Journal of Primatology, 71(2), 153–164. https://doi.org/10.1002/ajp.20635

van Schaik, C. P., & Dunbar, R. I. (1990). The evolution of monogamy in large primates: A new hypothesis and some crucial tests. Behaviour, 115(1–2), 30–61.

van Schaik, C. P., & Janson, C. H. (1988). Recognizing the many faces of primate food competition: Methods. Behaviour, 105(1–2), 165–186.

van Schaik, C. P., & Paul, A. (1996). Male care in primates: Does it ever reflect paternity? Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, 5(5), 152–156.

Vine, I. (1971). Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. Journal of Theoretical Biology, 30(2), 405–422.

Walters, J. (1980). Interventions and the development of dominance relationships in female baboons. Folia Primatologica, 34(1–2), 61–89.

Walters, J. R., & Seyfarth, R. M. (1987). Conflict and cooperation. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), Primate societies (pp. 306–317). University of Chicago Press.

Wang, X., Wang, C., Qi, X., Guo, S., Zhao, H., & Li, B. (2013). A newly-found pattern of social relationships among adults within one-male units of golden snub-nosed monkeys (Rhinopithecus roxenalla) in the Qinling Mountains, China. Integrative Zoology, 8(4), 400–409.

Ward, P., & Zahavi, A. (1973). The importance of certain assemblages of birds as “information-centres” for food-finding. Ibis, 115(4), 517–534.

West, S. A., Murray, M. G., Machado, C. A., Griffin, A. S., & Herre, E. A. (2001). Testing Hamilton’s rule with competition between relatives. Nature, 409(6819), 510–513.

West-Eberhard, M. J. (1979). Sexual Selection, Social Competition, and Evolution. Proceedings of the American Philosophical Society, 123(4), 222–234.

Whitehouse, J., & Meunier, H. (2020). An understanding of third-party friendships in a tolerant macaque. Scientific Reports, 10(1), 9777. https://doi.org/10.1038/s41598-020-66407-w

Whiten, A., & Byrne, R. W. (1988). The Machiavellian intelligence hypotheses. Clarendon Press/Oxford University Press.

Wildt, D. E., Doyle, L. L., Stone, S. C., & Harrison, R. M. (1977). Correlation of perineal swelling with serum ovarian hormone levels, vaginal cytology, and ovarian follicular development during the baboon reproductive cycle. Primates, 18, 261–270.

Wiley, R. H. (2013). Specificity and multiplicity in the recognition of individuals: Implications for the evolution of social behaviour. Biological Reviews, 88(1), 179–195. https://doi.org/10.1111/j.1469-185X.2012.00246.x

Wrangham, R. (1979). On the evolution of ape social systems. Social Science Information, 18(3), 336–368.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. Behaviour, 75(3–4), 262–300.

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Curriculum Vitae

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Work experience

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2017	**Conduction of a statistical course** (work group) *Generalized Linear Models in R*
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