

Social relationships of female Guinea baboons
***(Papio papio)* in Senegal**

Dissertation

for the award of the degree

“Doctor of Philosophy”

Division of Mathematics and Natural Sciences

at the Georg-August-Universität Göttingen

in the doctoral programme of Behaviour and Cognition (BeCog)

at the Georg-August University School of Science (GAUSS)

submitted by

Adeelia S. Goffe

from St. Louis

Göttingen, August 2016

Thesis Committee

Prof. Dr. Julia Fischer, Cognitive Ethology Laboratory, German Primate Center GmbH

Prof. Dr. Julia Ostner, Department of Behavioral Ecology, University of Göttingen
Johann-Friedrich-Blumenbach Institute for Zoology and Anthropology

Dr. Michael Heistermann, Hormone Laboratory, German Primate Center GmbH

Members of the Examination Board

Referee:

Prof. Dr. Julia Fischer

Co-referee:

Prof. Dr. Julia Ostner

Further members of the Examination Board

Dr. Bernard Fink, Biological Personality Psychology, Georg-Elias-Müller-Institut for
Psychology, University of Göttingen

Prof. Dr. Martina Gerken, Ecology of Livestock Production, Faculty of Agricultural
Sciences, University of Göttingen

Dr. Cornelia Kraus, Department of Sociobiology/Anthropology, University of Göttingen

PD Dr. Christian Roos, Primate Genetics Laboratory, German Primate Center GmbH

Date of the oral examination:

17.10.2016

To those I lost along the way...

TABLE OF CONTENTS

SUMMARY	i
ZUSAMMENFASSUNG	iv
CHAPTER 1: General Introduction	1
Intersexual relationships	2
Anisogamy & Sexual Conflict	2
Sex differences in social and physical environments	3
Female Mate Choice	4
Female Intrasexual Relationships	4
Affiliation & Cooperation	4
Competition	6
Selection Theory	7
Dispersal and Philopatry in Social Animals	8
Multilevel Systems	10
Guinea baboons	12
Study Aims	13
CHAPTER 2: Sex and friendship in a multilevel society: behavioural patterns and associations between female and male Guinea baboons	15
CHAPTER 3: Meat sharing between male and female Guinea baboons (Papio papio)	41
CHAPTER 4: Weak Forces: determinants and consequences of female- female relationships in Guinea baboons	56

CHAPTER 5: General Discussion	80
The Guinea baboon system.....	80
Social System	81
Social Organisation.....	82
Mating System	83
Social Structure.....	86
Dispersal	89
Female-biased Dispersal in Guinea baboons	89
Do females choose or do males select?	89
Dispersal in a Multilevel Context.....	91
Conclusion and Future Work.....	91
 APPENDIX	 94
Supplementary information – Chapter 2.....	94
Supplementary information – Chapter 4.....	97
 REFERENCES	 106
 ACKNOWLEDGEMENTS	 134
 CURRICULUM VITAE	 136
 DECLARATION.....	 139

SUMMARY

Biologists and psychologists have held a long-term fascination for understanding sex-specific life history behaviours. Selection pressures occur via three main evolutionary mechanisms which may influence males and females differently: sexual selection, social selection and natural selection. In males, phenotypes are thought to be shaped more by processes of sexual selection, such as traits associated with competition for mates. However, by primarily focusing on the more sexy or conspicuous male traits, we are limiting our investigations of how evolutionary forces work to shape social organisations and social structures. This may cause us to overlook integral mechanisms operating at the intersection of female and male sexual and social strategies. There is convincing evidence that the “passive” females described by Darwin are not passive at all, but the evolutionary implications of active female strategies have often been overlooked. Females aren’t just along for the ride, but a part of the process of navigating through the evolutionary maze.

In this thesis, I investigate how female Guinea baboons (*Papio papio*), in an apparently male dominated society, are able to shape their social environments. Guinea baboons were already known to have a unique multilevel society which is characterised by female-biased dispersal, male spatial tolerance, male affiliation and low levels of male aggression. The nature of female-male and female-female relationships, however, were still unclear. Therefore, I addressed the question of female social relationships by investigating social and mating partner choice, the social effects of dispersal and potential elements of female competition in a group of Guinea baboons living in the Parc National de Niokolo-Koba, Senegal. My approach involved integrating a range of methods to thoroughly examine the behavioural, genetic and stress components of female social organisation in this species.

To investigate the role of intersexual relationships in Guinea baboon society I assessed spatial proximity using network analysis to explore intersexual spatial distances, and used those results to characterise spatial relationships into three status categories based on the comparative frequency within 2 m of focal females: “primary”, “secondary” and “other”. Using those status categories, I found that female Guinea baboons maintain a strong social and sexual relationship with a particular adult or subadult male (the “primary male”), but may also maintain social relationships with one or more male friends (the “secondary males”). The “one-male unit” (OMU) consisted of 1-4 harem females and their primary male. The occurrence and intensity of behaviours between the primary male and his females varied

marginally with female reproductive state as lactating females were found to have a lower probability of active or passive greeting than either cycling or pregnant females. Although social behaviour was consistent, females were often in close proximity (2-5 m) of males with whom they never interacted, indicating that spatial and social relationships do not always coincide. I also noted that females had a propensity to change primary males and tenure duration was highly variable. Although I did not perceive the exact moment of transfers, I was able to show that females' changes were unambiguous and preferences for the new male partners were immediate. This study further confirms the uniqueness of the Guinea baboon multilevel system and social organisation in comparison to other *Papionini*, allowing us to look further into the element of choice that females have in the intersexual social strategies they employ.

As I had found that primary males were important in all aspects of female-male relationships, I continued to explore intersexual relationships in Guinea baboons by looking into the occurrence and behavioural implications of killing and eating monopolisable vertebrate prey. I observed that males were the hunters, but that all hunting observed was opportunistic and did not involve group coordination. As such, males were always the first to have access to meat, but I found that in a number of cases harem females were able to acquire portions of the carcass from their primary males. I then went on to analyse the occurrences of passive meat sharing between males and females and found the one male unit membership, rather than female reproductive state, was influential. These analyses confirm results from studies in other primate species that social relationships are important in food sharing. Importantly, social relationships may allow for spatial tolerance between familiar dyads. Theoretically, both males and females may benefit from food sharing events occurring within the OMU; males may benefit by expressing their tolerance and retain females, while females may benefit by receiving access to a rare food source.

Female-biased dispersal is rare in mammals, yet social dispersal ("transfer") appears to be a ubiquitous aspect of Guinea baboons. Therefore, I went on to investigate the variables which drive female intrasexual relationships using a newly developed method which allows for assessing social relationship strength in dynamic systems. To determine if females might be negatively impacted by social stress connected to OMU membership, I investigated if faecal glucocorticoids varied with harem size or female rank. I found that female sociality was driven more by OMU membership than by genetic relatedness (based on autosomal microsatellites) or lactation status. However, despite the apparent social importance of OMU membership females from larger OMUs did not experience elevated faecal glucocorticoids.

Faecal glucocorticoid concentrations were also not related to female rank. My study indicates Guinea baboon females interact flexibly with each other in relation to their OMU membership, rather than being constrained by the ties of kinship.

In conclusion, I have performed the first comprehensive analysis of the social relationships of female Guinea baboons. This work provides insights into the dynamics of female-male and female-female social relationships and behavioural mating system. The mating system of Guinea baboons and the social dispersal of females are directly affected by male sexual strategies (likely male-male competition). However, females are able to engage socially with both males and females (potentially kin) outside of their OMUs. Although these relationships are minor in comparison to the more dominant relationships with their primary males, they are examples of free social choice which is not typically present in polygyn-monandrous mating systems. Multilevel systems are described as being evolutionary responses to ecological pressure through the fission and fusion of subgroups. In addition, social factors are also working to maintain subgroup integrity and females are active participants. Being able to quickly adjust to social change with low physiological costs may be an adaptation to highly dynamic social environments.

ZUSAMMENFASSUNG

Biologen und Psychologen sind bereits seit langer Zeit von geschlechtsspezifischen Verhaltensweisen fasziniert. Der Selektionsdruck erfolgt hauptsächlich über drei evolutionäre Mechanismen, die Männchen und Weibchen unterschiedlich beeinflussen können: sexuelle Selektion, soziale Selektion und natürliche Selektion. Man nimmt an, dass Phänotypen bei Männchen eher durch Prozesse der sexuellen Selektion entstehen, wie z. B. Merkmale, die mit dem Wettbewerb um Geschlechtspartner in Verbindung stehen. Wenn wir uns allerdings in erster Linie auf die sexuellen und auffälligen männlichen Merkmale konzentrieren, schränken wir unser Blickfeld bei der Untersuchung evolutionärer Kräfte und wie diese soziale Organisation und soziale Strukturen formen, ein. Dies kann dazu führen, dass wir entscheidende Mechanismen, die sich an der Grenze zwischen männlichen und weiblichen sexuellen und sozialen Strategien abspielen, übersehen. Es gibt überzeugende Beweise dafür, dass die von Darwin beschriebenen „passiven“ Weibchen überhaupt nicht passiv sind, sondern dass die evolutionären Einflüsse aktiver weiblicher Strategien oft übersehen wurden. Weibchen sind nicht nur einfach passiv, sondern ein aktiver Teil der Evolutionsgeschichte, den es zu beachten gilt.

In Rahmen dieser Dissertation wurde untersucht, wie es weiblichen Guinea-Pavianen (*Papio papio*) gelingt, in einer scheinbar männlich dominierten Gesellschaft, ihr soziales Umfeld zu gestalten. Es war bereits bekannt, dass Guinea-Paviane in einer einzigartigen, mehrstufigen Gesellschaft leben, die sich durch weibliches Dispersionsverhalten, Raumtoleranz der Männchen, männliche Zugehörigkeit und geringe männliche Aggression auszeichnet. Die Art der Beziehung zwischen Männchen und Weibchen und Weibchen und Weibchen war allerdings noch unerforscht. Aus diesem Grund wurde die Frage der sozialen Beziehungen zwischen Weibchen zum Fokus dieser wissenschaftlichen Arbeit. Anhand einer wilden Gruppe von Guinea-Pavianen im Parc National de Niokolo-Koba, Senegal, wurden Partnerwahl (sozial wie auch sexuell), soziale Auswirkungen der Dispersion und potenzielle Elemente des weiblichen Konkurrenzkampfes untersucht. Mein Ansatz umfasste die Integration einer Reihe von Methoden, um die genetischen, physiologischen und Verhaltenskomponenten der weiblichen sozialen Organisation dieser Spezies eingehend zu untersuchen.

Um die Rolle der intergeschlechtlichen Beziehungen zwischen Guinea-Pavianen zu untersuchen, beurteilte ich räumliche Nähe mithilfe von Netzwerkanalysen zur

Untersuchung intergeschlechtlicher räumlicher Distanz und teilte die Ergebnisse in drei Statuskategorien basierend auf der Vergleichsfrequenz innerhalb von 2 m fokaler Weibchen: „primär“, „sekundär“ und „andere“. Mithilfe dieser Statuskategorien fand ich heraus, dass weibliche Guinea-Paviane mit einem bestimmten adulten oder subadulten Männchen (das „Primärmännchen“) eine starke soziale und sexuelle Beziehung pflegen, aber auch soziale Beziehungen zu einem oder mehreren männlichen Freunden haben (die „Sekundärmännchen“). Die „one-male unit“ (OMU) bestand aus 1-4 Harem-Weibchen und ihrem Primärmännchen. Die Häufigkeit und Intensität der Kontakte zwischen dem Primärmännchen und seinen Weibchen variierte geringfügig, wobei säugende Weibchen mit geringerer Wahrscheinlichkeit begrüßt wurden als Weibchen, die gerade ihren Zyklus hatten oder trächtig waren. Obwohl das Sozialverhalten einheitlich war, konnte beobachtet werden, dass sich Weibchen oft in der Nähe von Männchen aufhielten (2-5 m), mit denen sie noch nie Kontakt hatten, was darauf hinweist, dass räumliche und soziale Beziehungen nicht immer einhergehen müssen. Es konnte ebenfalls beobachtet werden, dass Weibchen dazu neigen, ihr Primärmännchen zu wechseln, und dass die Dauer der jeweiligen Beziehung sehr variabel ist. Zwar war es mir nicht möglich, den genauen Zeitpunkt des Übergangs zu erfassen, aber ich konnte eine eindeutige Änderung der Vorliebe des Weibchens, die sofort wahrnehmbar war, nachweisen. Diese Studie bestätigt ferner die Einzigartigkeit der mehrstufigen sozialen Organisation des Guinea-Pavians im Vergleich zu anderen *Papionini* und gibt uns neue Einblicke in die intergeschlechtlichen sozialen Strategien, die von Weibchen angewandt werden und inwiefern sie dabei die freie Wahl haben.

Nachdem bestätigt war, dass Primärmännchen für alle Aspekte intergeschlechtlicher Beziehungen wichtig waren, befasste ich mich weiterhin mit den intergeschlechtlichen Beziehungen von Guinea-Pavianen, indem ich das Auftreten und die Verhaltensauswirkungen des Tötens und Fressens monopolisierbarer Wirbeltiere untersuchte. Ich beobachtete, dass die Männchen die primären Jäger waren, und dass die Jagd opportunistisch war und keine Gruppenkoordination stattfand. Daher hatten die Männchen auch immer zuerst Zugang zu Fleisch, allerdings konnten Harem-Weibchen in mehreren Fällen Stücke des Kadavers von ihren Primärmännchen ergattern. Danach analysierte ich das Auftreten von passiver Fleischteilung zwischen Männchen und Weibchen, wobei sich herausstellte, dass die Mitgliedschaft bei einer „one male unit“ wichtiger war, als der Fortpflanzungsstatus des Weibchens. Diese Analysen bestätigten Ergebnisse aus Studien über andere Primatenarten, die darauf schließen lassen, dass soziale Beziehungen wichtig für das Teilen von Nahrung sind. Im Besonderen ist es wichtig zu erwähnen, dass soziale

Beziehungen räumliche Toleranz in vertrauten Dyaden schaffen. Theoretisch können Männchen wie Weibchen von der Nahrungsteilung innerhalb der OMU profitieren; Männchen können durch den Ausdruck ihrer Toleranz punkten und Weibchen bei sich halten, während Weibchen vom Zugang zu einer seltenen Nahrungsquelle profitieren.

Weibliches Dispersionsverhalten ist bei Säugetieren selten und doch scheint die soziale Dispersion („Transfer“) bei den Guinea-Pavianen allgegenwärtig zu sein. Aus diesem Grund untersuchte ich Variablen, die intergeschlechtliche weibliche Beziehungen beeinflussen, mithilfe einer neu entwickelten Methode, die die Beurteilung der Stärke sozialer Beziehungen in einem dynamischen System ermöglicht. Um festzustellen, ob Weibchen möglicherweise aufgrund ihrer OMU-Zugehörigkeit unter negativem sozialem Stress leiden, untersuchte ich, ob Glucocorticoide im Stuhl je nach Harem-Größe und Rang des Weibchens variieren. Ich stellte fest, dass die weibliche Sozialität mehr von der OMU-Zugehörigkeit als von genetischer Verwandtschaftsbeziehung (basierend auf autosomalen Mikrosatelliten) oder Säugungsstatus abhängt. Dennoch wiesen Weibchen trotz der scheinbar großen sozialen Bedeutung der OMU-Zugehörigkeit keine erhöhten Glucocorticoide im Stuhl auf. Die Glucocorticoidkonzentrationen im Stuhl standen auch nicht mit dem Rang des Weibchens in Verbindung. Meine Studie zeigt, dass weibliche Guinea-Paviane eine flexible Beziehung untereinander in Bezug auf ihre OMU-Zugehörigkeit pflegen und nicht durch Verwandtschaftsbande eingeschränkt sind.

Diese Studie stellt die erste umfassende Analyse der sozialen Beziehungen weiblicher Guinea-Paviane dar. Diese Arbeit gibt Einblicke in die Dynamik sozialer Beziehungen zwischen Weibchen und Männchen und Weibchen und Weibchen sowie über das Paarungssystem. Das Paarungssystem der Guinea-Paviane und die soziale Dispersion der Weibchen werden direkt von den sexuellen Strategien der Männchen beeinflusst (wie dem männlichen Konkurrenzverhalten). Weibchen sind allerdings in der Lage mit Männchen wie auch Weibchen (potenziell verwandt) soziale Beziehungen außerhalb ihrer OMU einzugehen. Obwohl diese Beziehungen im Vergleich zu den dominanteren Beziehungen mit ihren Primärmännchen nicht so bedeutend sind, sind sie doch Beispiele einer sozialen Entscheidungsfreiheit, die für polygyn-monandrische Paarungssysteme nicht typisch ist. Mehrstufige Systeme sind bekannt dafür, ökologischem Druck durch Spaltung und Fusion von Untergruppen nachzugeben. Zudem beeinflussen soziale Faktoren die Integrität der Untergruppe und Weibchen spielen in diesem Zusammenhang eine aktive Rolle. Die Tatsache, dass sie sich schnell an soziale Veränderungen anpassen können, ohne hohe

physiologische Kosten davonzutragen, kann als eine Anpassung an ein hoch dynamisches soziales Umfeld angesehen werden.

CHAPTER 1: General Introduction

Attempts to understand the social role of females have gone on for millennia. Aristotle saw females as “mutilated male[s]”, passive and lacking authority in the face of masculine strength (Aristotle 350 BCE, as translated in Platt 1912). Yet, despite this view Aristotle understood that women were integral to society and a complement to men (Aristotle 350 BCE, as translated in Rhys Roberts 1912). Aristotle’s view of women has been echoed repeatedly by scholars and is reflected in the way that noted biologists have viewed females across a variety of species. Darwin at least added the possibility that females could, in rare cases be choosy and accept males based upon “who pleases [them] most”:

“Sexual selection depends on the success of certain individuals over others of the same sex, in relation to the propagation of the species. The sexual struggle is of two kinds; in the one it is between the individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; whilst, in the other, the struggle is likewise between the individuals of the same sex, generally the females, which no longer remain passive, but select the more agreeable partners” (Darwin, 1871)

Here Darwin portrays females in simple two paradigms: the “passive” female and the “choosy” female. Bateman (1948) saw females in a similar light:

“The female, with the rarest exceptions, is less eager than the male . . . she is coy, and may often be seen endeavouring for a long time to escape.” (Bateman, 1948)

These perspectives try to incorporate female and male sexual strategies, but treat females as audience members rather than as members of an ensemble cast. Fortunately, these perspectives are slowly being replaced by evidence that females can be choosy in spite of male competition and that female social strategies are complex and worthy of continued study (Small, 1993).

In the following sections I will give the general framework for my thesis by outlining factors which shape female social relationships. I begin by introducing some of the main concepts determining intersexual relationships and then continue with intrasexual relationships. I will then go on to describe how patterns of dispersal influence group composition and bring these variables together using an integrated theory of selection. As social systems have a profound impact on social relationships, I will define multilevel systems before introducing Guinea baboons. Lastly, I outline the overall aim for my thesis and the objectives of each study.

Intersexual relationships

Anisogamy & Sexual Conflict

Mathematical models indicate that sex roles are a direct result of anisogamy (or gamete dimorphism), the sexual reproduction of two gametes differing in size and/or form (Lehtonen et al., 2016). As the anisogamy ratio increases, the sex with the smaller gamete experiences stronger selection pressure on sexually competitive traits (Lehtonen et al., 2016); by definition, the sex that produces the smaller gamete has been coined the “male” and sex with the larger gamete is the “female” (Parker et al., 1972). In addition to anisogamy, the associated sex-specific investment in reproduction also contributes to the generation of deviating life history trajectories for males and females (Lehtonen et al., 2016; Schärer et al., 2012; Trivers, 1972). The evolution of males and females did not come about due to random evolutionary processes, but is rather a direct result of sex-specific selection originating with anisogamy (Schärer et al., 2012).

Selection pressures, originating from anisogamy and sex-specific investment in reproduction have resulted in biological variation between the sexes and an inherent state of sexual conflict which influences all facets of reproductive interactions between males and females (Kokko and Jennions, 2014; Wedell et al., 2006). Sexual conflict occurs in reproductive behaviour from mating (Parker, 2006) and fertilization (Parker, 2006) to the investment in offspring (Harrison et al., 2009; Parker, 2006; Penn and Smith, 2007). Sex-specific reproductive strategies lead to different resource requirements (Trivers, 1972) and differing costs of reproductive investment in terms of time and energy (Kokko and Jennions, 2014). Although present in many taxa, sexual conflict is perhaps best epitomised in mammals, where females invest highly in offspring throughout gestation and lactation. In some

mammalian species males often mate-guard females in order to exclude reproductive competitors (Parker, 2006). This exclusionary strategy, though potentially ensuring paternity, carries the risk of injury, reduction in feeding time and physiological stress (Alberts et al., 1996; Girard-Buttoz et al., 2014a, 2014b, 2014c). On the other hand, females may evolve behavioural or physiological means of controlling reproduction by mating with multiple males (Small, 1990; Young et al., 2013), showing physical signs of fertility in non-fertile periods (Young et al., 2013) or concealing ovulation (Marlowe and Berbesque, 2012). Such female counter strategies may have evolved to incite competition and confuse paternity (Wolff and Macdonald, 2004). Sexual conflict can also occur regarding investment in offspring. At this stage, both sexes have already invested time, energy and/or nutrition in fertilisation and gestation. However, in species producing more altricial offspring there is the additional consideration of parental investment during development into adulthood (or at least independence). The amount of maternal vs paternal investment in offspring appears to be related to the frequency of extra-pair paternity (Møller and Thornhill, 1998; Shackelford and Goetz, 2009; Trivers, 1972). Trivers (1972) suggests that the relative amount invested by each sex dictates the direction and intensity of sexual selection (the preference in one sex for specific traits) in the less discriminating sex. Sexual conflict is a ubiquitous aspect of sexual reproduction and anisogamy (Hosken and Stockley, 2005; Parker, 2006) and may lead to substantially different life history optima for males and females, as suggested by the work of Tobias and colleagues (2012).

Sex differences in social and physical environments

Recent evidence suggests that although females and males may live in the same social group or habitat, they are not necessarily experiencing equivalent evolutionary pressures. This is due to the fact that the sexes differ in the way they experience their environments. Ecological preferences for certain geographic features (e.g. jaguar, *Panthera onca*: Conde et al., 2010), spatio-temporal dynamics of habitat use (e.g. grey seals, *Halichoerus grypus*: Breed et al., 2006), foraging distance (e.g. parti-coloured bat, *Vespertilio murinus*; Safi et al., 2007) and forage type (e.g. African elephant, *Loxodonta africana*: Stokke and Toit, 2000) may contribute to sex-based variations in habitat selection and use. In addition, one sex may be dominant over the other, resulting in differences in competitive ability and different social spheres (e.g. chacma baboon, *Papio ursinus*: (Kitchen et al., 2009); northern giant petrels, *Macronectes halli*: González-Solís et al., 2000; Ring-tailed lemurs, *Lemur catta*: von Engelhard et al., 2000).

Female Mate Choice

Regarding the potentially conflicting sexual strategies of males, the strategy which turns out to be the most profitable for females critically depends on the strategy that males are employing, as intrasexual competition among potential mates can influence intersexual mate choice (Wong and Candolin, 2005). In mammals, female competition tends to favour the manifestation of low risk competitive strategies (e.g. chimpanzee, *Pan troglodytes* Pusey and Schroepfer-Walker, 2013; human, *Homo sapiens*: Benenson, 2013; Campbell, 2013; Vaillancourt, 2013). Aspects of female competition and female mate choice may be overshadowed by the more overt behaviour of males. Male competition then facilitates or obscures the assessment of potential mates by females, and therefore female mate choice, resulting in the perception of male dominance driving mating patterns (Wong and Candolin, 2005). In addition to male competition, a preference for females to mate with dominant males may also result from female mate choice (Wong and Candolin, 2005). However, there are a few mammalian species, such as the spotted hyena (*Crocuta crocuta*: Goymann et al., 2001; Watts et al., 2009) and the ring-tailed lemur (*Lemur catta*: von Engelhard et al., 2000), where competition between females has resulted in female social dominance and female sexual and social strategies overshadowing male strategies.

Female Intrasexual Relationships

Affiliation & Cooperation

There is a high degree of variation in the intensity of adult female relationships across mammals. Social relationships are typically measured using social behaviour, proximity and group membership. At one end of the spectrum close social bonds among females are often typified in the highly selective and differentiated relationships of many Cercopithecine primates (e.g. Swedell, 2011). Recent evidence indicates that the same is true for male bonds (e.g. Assamese macaques, *Macaca assamensis*: Kalbitz et al., 2016). Female social bonds in savannah baboons are highly affiliative relationships which are maintained over time and equitable between individuals (Silk et al., 2006a, 2006b, 2010a). These long-term affiliations have high fitness benefits to the participants: enhancing longevity (Silk et al., 2010a), increasing offspring survival (Silk et al., 2003a, 2009) and perhaps also coping with stressors

(Crockford et al., 2008; Wittig et al., 2008). In other species, such as African and Asian elephants, social relationships are assessed more loosely using group membership criteria (Charif et al., 2005), yet females will maintain close spatial and social relationships throughout their lives (Sukumar, 2003; Wittemyer et al., 2005). On the opposite end of the continuum are species, such as rodents, in which females show high degrees of intolerance and aggression (Wolff, 1993). In both scenarios females are competitive, but the form of competitive exclusion for resources aiding in increasing reproductive output and fitness take on two distinct forms: individualistic (e.g. small mammals: Wolff, 1993) and cooperative (e.g. lion, *Panthera leo*: Packer et al., 1990). The difference lies in that females who maintain affiliative relationships are able to benefit from sociality by increasing their reproductive success and longevity (e.g. chacma baboon, *Papio ursinus*: Silk et al., 2009, 2010a; horse, *Equus caballus*: Cameron et al., 2009). These long-term benefits may result from the cooperative behaviours associated with stable social groups, such as increasing access to potential mates, assistance in territorial maintenance and alloparenting (e.g. lion, *Panthera leo*: Packer and Pusey, 1983; Verreaux's sifakas, *Propithecus verreauxi*: Koch et al., 2016; saddle-back tamarins, *Saguinus fuscicollis*: Goldizen, 1987).

In spite of being theoretically constrained by ecological selection pressures, females invest highly in maintaining affiliative relationships when they live in social groups. By definition, all social animals have social relationships. In some cases, these relationships involve repeated close social contact (e.g. grooming: Dunbar, 1991; Silk et al., 2006a, 2006b) and in others social contact is rare or challenging to record, but close spatial proximity is common (Archie et al., 2011; Best et al., 2014; Kerth et al., 2011; de Silva et al., 2011). “Social bonds” is a term used to describe a subset of close social relationships (Silk, 2002); they are equitable, stable over time and differentiated (Silk et al., 2010b). The majority of relationships do not fit under the criteria of close social bonds. They may be influenced by season (e.g. Japanese macaques, *Macaca fuscata*: D’Amato et al., 1982) or individual attributes (e.g. Barbary macaques, *Macaca sylvanus*: McFarland and Majolo, 2011).

Many primate species live in stable multimale-multifemale social groups which allow philopatric females the opportunity to preferentially affiliate with kin (Seyfarth et al., 2014; Silk et al., 2010b; Tinsley Johnson et al., 2013). In this scenario social relationships are strongly nepotistic, coalition formation (agonistic support) and cooperative acts are common (Silk et al., 2004, 2010b) and participants benefit through reinforcing the existing dominance hierarchy (Perry, 1996; Silk et al., 2004).

Social support and affiliation can serve as a buffer against long-term stress and have been shown to impact offspring survival (Cameron et al., 2009; Silk et al., 2003a, 2009), health (Archie, 2013; Beaulieu et al., 2014; Cohen and McKay, 1984; Cohen and Willis, 1985; Cohen et al., 2000; DeVries et al., 2003; Sapolsky, 2004, 2005) and longevity (Silk et al., 2010a). Close social relationships also help individuals to cope with stressful events (Crockford et al., 2008; Kanitz et al., 2014; Wittig et al., 2008) and also reduce the harassment received from males (Cameron et al., 2009; Newton-Fisher, 2006; Packer and Pusey, 1983).

Competition

Females compete for access to resources that allow them to survive and reproduce. The desired resources may be social (e.g. Assamese macaque: (Haunhorst et al., in prep) or ecological (e.g. Rondani, *Pachycrepoides vindemmiae*: Goubault et al., 2007; tree swallow, *Tachycineta bicolor*: Rosvall, 2008). For example, experimental and field data support the high importance of food for female reproduction and that females compete directly over access (e.g. chacma baboon: King et al., 2009; olive baboon: Barton and Whiten, 1993; primates: Koenig, 2002; wolverine, *Gulo gulo*: Persson, 2005). Proponents of the socio-ecological model and its modern day variants state that ecological variables (primarily food distribution and predation pressure) drive females' distribution patterns and that males distribute themselves in accordance with female patterns (Altmann, 1990; Clutton-Brock, 1989a; Emlen and Oring, 1977; Isbell, 1991; Isbell and Young, 2002; Sterck et al., 1997; Wrangham, 1980). By controlling interindividual spacing patterns these factors ultimately impact a species' social organisation and social structure.

Female birds and mammals are highly selective and are not just competing for access to any mate, but select males based on male quality (Altmann, 1997; Halliday, 1997; Petrie, 1983; Rosvall, 2011). Mate quality has been found to be important to females living in both single-male and multi-male groups (e.g. Altmann, 1997; Haunhorst et al., in prep, under review; Monard and Duncan, 1996; Rosvall, 2011; Scott, 2014). High quality males may provide direct benefits, such as access to territories (Andersson, 1994; Orians, 1969), enhanced nutrition (Haunhorst et al., under review; Lewis et al., 2004; Marlowe, 2001, 2003), reduced aggression (Haunhorst et al., under review), or parental care (Cheney et al., 2012; Clutton-Brock, 1991; Huchard et al., 2009; Møller and Thornhill, 1998; Palombit et al., 2001; Slagsvold and Lifjeld, 1994). Particular males may provide females with indirect benefits,

such as “good” genes (Mays and Hill, 2004; Prokop et al., 2012; Ziegler et al., 2005), which may also bring about intrasexual competition.

Female competition occurs both between and within groups (Stockley and Bro-Jørgensen, 2011). Inter-group competition takes the form of agonist intergroup encounters and territorial behaviour (Stockley and Bro-Jørgensen, 2011). Intra-group female competition is often manifested in avoidance (e.g. Assamese macaque: Heesen et al., 2014), infanticide (e.g. chimpanzee: (Pusey et al., 2008); mammals: Stockley and Bro-Jørgensen, 2011; yellow baboon: (Kleindorfer and Wasser, 2004) and aggression (e.g. Pusey and Schroepfer-Walker, 2013; Stockley and Bro-Jørgensen, 2011). In addition to direct competition, females may compete directly for mates via reproductively suppressing subordinates (Clutton-Brock and Huchard, 2013; Clutton-Brock et al., 2006; Fitzpatrick et al., 2008; Wasser and Barash, 1983). Reproductive suppression may be mediated through a number of social cues: mate guarding/interference, pheromonal suppression and neuroendocrine hormones (Abbott et al., 1997; Hamilton, 2004; Wasser and Barash, 1983). For social females living in competitive environments, social stress, resulting from low rank and repeated agonistic attacks, can serve to suppress the reproduction of subordinates (Wasser and Barash, 1983). Suppression resulting in delayed reproduction and increased interbirth intervals has a direct impact on inclusive fitness (see Wasser and Barash, 1983). Evidence for female competition for resources and mates, and the resulting fitness consequences which have been demonstrated across a variety of taxa show strong support for female competition serving as a selective principle under which sexual selection functions (Rosvall, 2011).

Selection Theory

Tobias and colleagues (2012), in an effort to understand the evolution of ornaments and weaponry in females, have described a conceptual framework, based on West-Eberhard (1979, 1983), consisting of three graded levels by which selection functions: natural selection, social selection and sexual selection. Sexual selection, the competition for mates, results in sex-specific adaptations which assist in mate acquisition (Shuker, 2010; Tobias et al., 2012; West-Eberhard, 1983). These may include morphological or behavioural characteristics, such as antlers (Jennings et al., 2004) or nest building (Barber et al., 2001; Borgia, 1986; Borgia et al., 1985). Within this framework, sexual selection is a part of social selection (Tobias et al., 2012; West-Eberhard, 1979, 1983); social selection being the selective force which shapes

social behaviour. As competition and choice operate under both social and reproductive contexts, the mechanisms which act upon social and sexual selection are similar (Lyon and Montgomerie, 2012; McGlothlin et al., 2010; Moore et al., 1997; Tanaka, 1996; West-Eberhard, 1983; Wolf et al., 1999), while natural selection is an all-encompassing process working in diverse ways (Kappeler and Schaik, 2004). The end result is that for females and males the same factors (for example, mating, social dominance or parental care), may have sex-specific impacts on trait evolution.

Evidence suggests that the process of sexual selection acts more strongly in males than females due to its interactions with anisogamy, asymmetrical parental investment and variance in mating success (Bateman, 1948; Emlen and Oring, 1977; Kokko et al., 2003; Lehtonen et al., 2016; Rosvall, 2011; Trivers, 1972; Wade and Shuster, 2005). Where sexual conflict is strong and males have more control over matings, females may attempt to resolve conflict by increasing their control over reproductive decisions via subtle or cryptic strategies that allow them to manipulate their social environments and reproductive options (Drea, 2005; Kuester and Paul, 1992; Parish, 1996; Perry, 1997; Smuts and Smuts, 1993; Tang-Martinez and Ryder, 2005). When the operational sex ratio is limiting or when typical sex roles are reversed (Cheney et al., 2012; Eens and Pinxten, 2000; Emlen and Oring, 1977; Kvarnemo and Ahnesjö, 1996) females compete for access to mates, indicating that sexual competition is influenced by elements of a species' social organisation (Kappeler and van Schaik, 2002).

Dispersal and Philopatry in Social Animals

Patterns of dispersal and philopatry influence intrasexual social relationships; the sex which is dispersing tends to favour antagonism and intolerance, while the sex which is philopatric tends to favour affiliation and cooperation (Greenwood, 1980). For example male philopatry and female-biased dispersal is favoured in chimpanzees (Mitani et al., 2002). Male chimpanzees engage in a variety of cooperative behaviours which promote high degrees of male affiliation and tolerance (Mitani et al., 2000). On the other hand, female chimpanzees are combative, have low levels of affiliation and tolerance, and typically engage in agonistic interactions which can have direct fitness consequences (Pusey and Schroepfer-Walker, 2013; Pusey et al., 2008).

There are four types of dispersal commonly used in the literature; natal and breeding/secondary dispersal refer to the timing and order in which dispersal events occur, and locational and social dispersal refer to the occurrence of geographic or social transfer (Dobson, 2013; Isbell and Van Vuren, 1996). Dispersal is a process which determines which individuals reside together in the same group. In the literature, dispersal is often used synonymously with migration (Johnson and Gaines, 1990). However, here I am making a distinction between the seasonal-cyclic movement of animal aggregations for access to resources (Alerstam and Lindström, 1990; Holdo et al., 2009; Pagès and Fuchs, 2003) and the smaller scale permanent movement of individuals resulting in demographic and/or locational change. Dispersal may be density dependent (Matthysen, 2005) and dispersal events may occur once or repeatedly over an individual's lifetime (Greenwood, 1980). In addition, individuals may disperse on their own or in groups (Bradley et al., 2007; Greenwood, 1980).

A dispersal syndrome in a population or species describes the attributes correlated with dispersal patterns (Clobert et al., 2009). The spatio-temporal profitability of dispersal varies among individuals, promoting a plastic strategy (Bowler and Benton, 2005; Marty et al., accepted). Individuals may disperse as juveniles (Dobson, 1982) or wait until they have reached sexual maturity (Marty, 2015). Dispersal patterns may also vary throughout a species' range and are influenced by the dynamics of range expansion, with individuals at the core dispersing over shorter distances than those on the periphery (Phillips et al., 2010). Dispersal within demes (or "local populations") varies more than dispersal between demes, and the occurrence of leptokurtic dispersal has been directly associated with behavioural traits influencing fitness (Fraser et al., 2001; Réale et al., 2000; Sih et al., 2004). This region-specific (geographic) variation in dispersal consequentially influences the genetic imprint of a population (Phillips et al., 2010).

Additionally, social structure, dyadic relationships and individual attributes (e.g. sex, age and social status) all play key roles in driving the occurrence of dispersal in social species (Ajrouch et al., 2005; Hirsch et al., 2013; McPherson et al., 2001; Smolker et al., 1992). Individuals may disperse from their social groups or territories for a variety of reasons: to maximise lifetime reproductive success by increasing their access to mates and resources (Greenwood, 1980), in response to eviction from previously cooperative relationships (e.g. meerkats, *Suricata suricatta*: Stephens et al., 2005) or they may "choose" to explore reproductive options in another group (e.g. crested macaques, *Macaca nigra*: Marty, 2015).

Mortality events may also result in the dissolution of reproductive groups and the dispersal of its members (e.g. western lowland gorillas, *Gorilla gorilla gorilla*: Stokes et al., 2003).

Transferring between groups or to a new location is potentially costly (Bonte et al., 2012) and in mammals, this is an endeavour typically taken on by males (Greenwood, 1980). The sex-bias in dispersal is directly influenced by a species' mating system (Greenwood, 1980; Lawson Handley and Perrin, 2007). The mating system consists of two components: the mating behaviour observed and the genetic outcome produced (c.f. Kappeler and van Schaik, 2002). The major categories of mammalian mating systems (monogamy, polygyny, polyandry and polygynandry/promiscuity) (Clutton-Brock, 1989a) refer to the number and sex of partners involved in mating behaviour, but do not necessarily reflect the genetics of offspring (Cohas and Allaine, 2009; Cohas et al., 2006; Scelza, 2011). However, these categories should be considered more as a continuum, as some species/populations exhibit flexibility in the sex ratio of breeding groups or even exhibit variation in mating strategies depending on environmental conditions (e.g. chacma baboon: Byrne et al., 1987; great reed warbler, *Acrocephalus arundinaceus* Bensch and Hasselquist, 1992; guinea pig, *Cavia aperea*: Asher et al., 2004; great gerbil, *Rhombomys opimus*: Randall, 2005; hoary marmots, *Marmota caligata*: Kyle et al., 2007). Variation may simply be a reduction in possible partners due to decreases in population density (e.g. chacma baboon: Byrne et al., 1987; Henzi et al., 1990; Whiten et al., 1987) or due to variations in competitive ability (e.g. guinea pig: Asher et al., 2004). Dispersal patterns serve to reflect these mating systems and for some females dispersal might not be so costly as it may lead to such benefits as reduced female feeding competition and inbreeding avoidance (Clutton-Brock, 1989b; Kahlenberg et al., 2008a; Korstjens and Schippers, 2003; Moore, 1984; Pusey and Schroepfer-Walker, 2013; Sakamaki et al., 2015; Stokes et al., 2003).

Multilevel Systems

“Certain environmental factors determine the degree to which mates can be defended or monopolised. In effect, *ecological constraints impose limits on the degree to which sexual selection can operate.*” (Emlen and Oring, 1977). As a result of ecological and social factors, nature displays a wide array of social systems from those containing solitary foragers to others in which group membership varies in its permanency.

Fission-fusion dynamics are an inherent aspect of group structure and comes from the fluid process of individuals negotiating their way through their physical environments

(Couzin, 2006). However, travel paths are not random and preferential associations between individuals result in higher-order social structures (Couzin, 2006). Multilevel (or modular) systems are those in which preferred associates maintain persistent social and spatial contact throughout group fission and fusion events, generating at least two spatially and at times temporally divided subgroups (Grüter and Zinner, 2004). In a variety of species, subgroups layer upon each other to form a hierarchical structure in which grouping patterns vary in the extent of their associations (Grüter and Zinner, 2004; Hill et al., 2008; Kirkpatrick and Grueter, 2010; Mac Carron and Dunbar, 2016; Schreier and Swedell, 2011; de Silva and Wittemyer, 2012; Snyder-Mackler et al., 2012a; Wolf et al., 2007). The multilevel systems of marine and terrestrial mammals are increasingly under investigation and comparative studies on multilevel systems indicate that they may be better equipped to balance the costs and benefits associated with group living (Grueter and van Schaik, 2009). In some species sex-segregated groups seasonally come together to reproduce (Breed et al., 2006; Fabiani, 2004; Hoffman et al., 2007; Wolf et al., 2007) while others live year round in bisexual breeding groups (Chapais, 2013; Dunbar, 1984; Imamura, 2015; Kirkpatrick et al., 1998; Kummer, 1968; Monard and Duncan, 1996; Rubenstein, 1994; Swedell, 2002). As the type of multilevel society nearly co-varies with the number of species which exhibit them, I will focus on those that have polygyn-monandrous mating systems and persistent intersexual associations.

Multilevel societies containing reproductive groups (i.e. one male units (OMUs)) contain a primary (dominant) breeding male with potentially secondary (subordinate) males and offspring (e.g. geladas (*Theropithecus gelada*) (Dunbar, 1984; Mori, 1979a), hamadryas baboons (*Papio hamadryas*) (Kummer, 1968; Swedell, 2002), horses and zebra (*Equus caballus* and *Equus*) (Monard and Duncan, 1996; Rubenstein, 1994; Rubenstein and Hack, 2004), humans (*Homo sapien*) (Chapais, 2013; Imamura, 2015) and the Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) (Kirkpatrick et al., 1998)). Secondary males may also acquire some reproductive access to OMU females (Chowdhury et al., 2015; Feh, 1999; Snyder-Mackler et al., 2012b) and are tolerated near the OMU to assist in territorial or female defence (Kummer, 1968; Linklater et al., 1999; Mori, 1979b; Rubenstein and Hack, 2004). Immature or non-breeding males form bachelor groups (or all male groups) which threaten the OMU holder's retention of females (Dunbar, 1984; Pappano et al., 2012). In these societies females may be philopatric (e.g. Chang et al., 2014; Guo et al., 2014; le Roux et al., 2011), but female dispersal is more common (e.g. Hammond et al., 2006; Matsuura, 2015; Monard and Duncan, 1996; Swedell et al., 2011).

Guinea baboons

In evolutionary history Papionins appeared approximately 11.6 million years ago after diverging from Cercopithecines (Raaum et al., 2005) and likely lived in female-bonded multimale-multifemale groups (Di Fiore and Rendall, 1994). The majority of extant Papionins still follow this ancestral pattern: chacma (*Papio ursinus*), Kinda (*P. kindae*), olive (*P. anubis*), and yellow (*P. cynocephalus*) baboons (after Swedell, 2011). However, the Guinea baboon (*P. papio*), hamadryas baboon (*P. hamadryas*) and gelada (*Theropithecus gelada*) all exhibit a derived (or newly evolved) trait of multilevel social systems. Because of their long and independent evolutionary history (Delson, 1993; Liedigk et al., 2014; Newman et al., 2004), the multilevel social system of hamadryas baboons and geladas most likely evolved independently (Grueter et al., 2012). Variations in dispersal pathways as a result of the expansion and contraction of savannah habitats make the evolutionary history of *Papio* unclear (Zinner et al., 2011).

Although Guinea baboons (*P. papio*) occupy a narrow range of highly variable habitat at the north-western edge of the baboon distribution (Galat-Luong et al., 2006; Oates et al., 2008) they share some morphological and behavioural features with the hamadryas baboon in the north-east (Anderson and McGrew, 1984; Boese, 1973, 1975; Dunbar and Nathan, 1972; Galat-Luong et al., 2006; Jolly, 2009; Jolly and Phillips-Conroy, 2006). Guinea baboon groups vary greatly in their size and composition, frequently demonstrating a high degree of fluidity (Boese, 1973, 1975; Galat-Luong et al., 2006; Patzelt et al., 2011; Sharman, 1982). Previous behavioural research in captivity and on unhabituated groups in the wild have suggested that they may also be a species with a multilevel social system (Boese, 1973; Galat-Luong et al., 2006; Maestripietri et al., 2005, 2007). The strongest hints regarding the Guinea baboon social system have come from observations of mating behaviour in captivity (Boese, 1973; Maestripietri et al., 2005, 2007) and descriptions of the high level of fluidity in terms of group size in the wild (Boese, 1973; Galat-Luong et al., 2006). A recent study from (Patzelt et al., 2014) confirmed that not only do Guinea baboons live in a multilevel social system consisting of at least two distinct levels, but that they also show unique traits of male spatial tolerance and male affiliative relationships. Aggression rates between males are also low in comparison to chacma baboons (Kalbitzer et al., 2015) and males engage in ritualistic greeting interactions (also known as “notification” behaviour) across multiple social levels

(Dal Pesco, 2013; Kalbitzer et al., 2015; Patzelt et al., 2014). Evidence from studies sampling various locations in their geographic distribution strongly support female-biased dispersal (Kopp et al., 2014, 2015).

Study Aims

Little is known about Guinea baboons in comparison to the tomes which have been devoted to other Papionins. This is particularly true for Guinea baboon females, as the majority of studies in which sthe wild have focused on the behaviour and genetics of males. Female dispersal is rare in mammals (Greenwood, 1980) and its occurrence, along-side male tolerance, in Guinea baboons provides an opportunity for comparing the evolutionary mechanisms which drive the evolution of social groups. My aim was to contribute to a better understanding of the social system of Guinea baboons by clarifying the role of males in female social life and to evaluate how dispersal patterns and female-female competition might be contributing to the maintenance of the social structure.

In study 1 (**Chapter 2**) I investigated the nature of intersexual relationships in Guinea baboons from the female perspective in order to definitively determine if one male units form the social basis of this society. To accomplish this, I first scrutinised the spatial relationships of female-male dyads using social network analyses in order to determine if females have preferred male neighbours. I then used the frequency of close proximity as an indicator by which to assign males to status categories. I assessed the status assignments using behavioural measures in order to determine if there were also behavioural preferences and to what extent behaviours varied with female reproductive state. I described female social dispersal events and the resulting impact that they had on intersexual relationships. I went on to discuss the implications of my results towards our understanding of the social system, social organisation and mating system in this species. Lastly, I considered what is known about intersexual relationships in a number of extant Papionins, the potential evolutionary implications and the extent to which Guinea baboons fit into the “typical” baboon behavioural models.

In study 2 (**Chapter 3**), I used information regarding intersexual relationships to investigate the rare phenomenon of vertebrate prey consumption and meat sharing in baboons. First, I described how Guinea baboons acquired and captured vertebrate prey,

including who participated in the killing and what prey species were captured. Subsequently, I built upon the discoveries from study 1 and determined if specific social relationships or the reproductive state of females influenced who had access to meat, as well as how meat was obtained by the females. Lastly, I discussed the potential implications that social relationships have on cooperative food sharing events and how females may benefit.

In Study 3 (**Chapter 4**), I conducted the first investigation of female-female social behaviour in Guinea baboons by assessing covariates associated with social preferences and female competition. Based on knowledge acquired in study 1, as well as the assessment of a novel technique for analysing dynamic social data, I accomplished this aim through investigating affiliative, agonistic and spatial data. Furthermore, I assessed if one-male unit size or female rank predict faecal glucocorticoid levels as a proxy for physiological stress levels. By way of discussion, I addressed what may be inferred from these results and how they fit into our understanding of how dispersal and mating patterns influence social partner choice.

I made a summation of the results from Chapters 2, 3 and 4 in the general discussion (**Chapter 5**) and set them within the context of the Guinea baboon social system and the larger context of social behaviour in dispersal for females in multilevel societies. I then discussed the relevance of my findings in relation to sexual conflict and female selection. Lastly, I made overall conclusions and formulated suggestions regarding future avenues of research.

**CHAPTER 2: Sex and friendship in a multilevel
society: behavioural patterns and associations between
female and male Guinea baboons**

Adeelia S. Goffe, Dietmar Zinner and Julia Fischer

{Cognitive Ethology Laboratory, German Primate Center, Göttingen, Germany}

Behavioural Ecology and Sociobiology (2016)

DOI: 10.1007/s00265-015-2050-6

Abstract

One key question in social evolution is the identification of factors that promote the formation and maintenance of stable bonds between females and males beyond the mating context. Baboons lend themselves to examine this question, as they vary in social organisation and male-female association patterns. We report the results from the first systematic observations of individually identified wild female Guinea baboons. Guinea baboons live in a multilevel society with female-biased dispersal. Although several males could be found within 5 m of females, each female chiefly associated with one “primary” male at the 2 m distance. Social interactions occurred predominantly with the primary male, and female reproductive state had little influence on interaction patterns. The number of females per primary male varied from 1-4. During the 17-month study period, half of the females transferred between different males one or multiple times. A subset of females maintained weaker affiliative nonsexual relationships with other “secondary” males. Units composed of primary males with females, and occasional secondary males, apparently form the core of the Guinea baboon society. The social organisation and mating patterns of Guinea and hamadryas baboons may have a common evolutionary origin, despite notable differences in relationship quality. Specifically, Guinea baboon females appear to have greater leverage in their association patterns than hamadryas baboon females. Although we cannot yet explain the lack of overt male control over females, results generally support the notion that phylogenetic descent may play an important role in shaping social systems.

Significance Statement

The wide range of variability in intersexual relationships across species makes the identification of key factors driving relationship formation and maintenance challenging. From the female perspective, we provide comprehensive data on the intersexual relationships and spatial associations of wild Guinea baboons, a little studied baboon species with a multilevel social system, female-biased dispersal and high levels of male-male tolerance. Our data indicate that one or more females are closely bonded to a “primary” male with whom they affiliate and copulate. The occurrence and intensity of these relationships varied minimally with the oestrous phase of females. Females exhibited spatial freedom, indicating some element of female choice. A subset of females maintained weaker nonsexual friendships with “secondary” males. Although superficially similar, there may be a common

evolutionary origin for the social organisation and mating system of hamadryas and Guinea baboons.

Keywords *Papio papio*, intersexual relationships, mating system, pair bond, social organisation

Introduction

Social relationships between females and males vary widely in their temporality, intensity and modes of expression. According to socioecological theory, males compete for access to fertile females, while females may aim for high quality males, access to resources and/or paternal care (Emlen and Oring, 1977; Greenwood, 1980). Males' ability to monopolise females depend on a number of factors, including the size and distribution of females' home ranges, the distribution of feeding patches and food quality, or the length and synchrony of the females' breeding cycle (Davies and Lundberg, 1984; Ridley, 1986; Sterck et al., 1997). Thus, for the majority of mammals, social interactions between females and males are restricted to courtship and mating. This is the most pronounced in solitary foraging species in which females and males come together for brief periods to mate (e.g. honey badger, *Mellivora capensis*: (Begg et al., 2006); orang utan, *Pongo pygmaeus*: (Mitani, 1990); polar bear, *Ursus maritimus*: (Molnar et al., 2008)). In gregarious species that live in bisexual groups, there is the potential for social contact at all phases of the female reproductive cycle, but intersexual interactions may still vary with changes in female reproductive state (e.g. eastern chimpanzee, *Pan troglodytes schweinfurthii*: (Muller et al., 2007); spotted hyaena, *Crocuta crocuta*: (Szykman et al., 2003, 2007); Grevy's zebra, *Equus grevyi*: Sundaesan et al. 2007).

Baboons (genus *Papio*) lend themselves for investigating the link between mating and relationship patterns in societies with different social organisations. Commonly known as "savannah" baboons, chacma (*P. ursinus*), olive (*P. anubis*) and yellow baboons (*P. cynocephalus*) live in multi-male multi-female groups with female philopatry and male dispersal. Their mating system can be regarded as polygynandrous, whereby male rank predicts mating success and reproductive skew (Swedell, 2011). Intersexual associations are conspicuous and vary with female reproductive state. During consortships, oestrous females and males stay in close proximity (Swedell, 2011). Lactating females with dependent infants maintain affiliative "friendships" with specific males, most likely as a measure against harassment and infanticide risk (Lemasson et al., 2008; Palombit, 2009).

In contrast, hamadryas baboons (*P. hamadryas*) have a multilevel social system in which all females, regardless of reproductive state, maintain close proximity to specific males (the "leader males"), one-male units (OMUs). One or more females spatially, socially and sexually affiliate with one male, resulting in the formation of OMUs. OMUs are spatially segregated from other OMUs, partly through male enforcement (Kummer, 1968; Schreier and Swedell, 2009) and form the social core of these societies (Kummer, 1968). Some OMUs may also have follower males, which are significantly less social with females than are leader

males (Chowdhury et al., 2015; Kummer, 1968; Pines et al., 2011; Swedell, 2006). Multiple OMUs together form higher nested social levels which vary in size and composition (clan, band, troop; see (Swedell, 2011) for review). Furthermore, in contrast to savannah baboons, hamadryas baboon males are predominantly philopatric but both sexes may disperse (Städele et al., 2015; Swedell et al., 2011).

Until recently, much less was known about Guinea baboons (*P. papio*). Observations of male-male association patterns revealed that they live in a multilevel social system in which several males form parties, which in turn regularly aggregate into gangs (Patzelt et al., 2014). Males exhibit high levels of tolerance and maintain relationships with other males (Patzelt et al., 2014). Genetic evidence suggests that, similar to hamadryas baboons, there is female biased dispersal (Kopp et al. 2014, 2015). To date, work regarding intersexual relationships had been conducted on either unhabituated populations in the wild or on captive groups, and had led to conflicting conclusions regarding the social system of this species. Some researchers proposed a multi-male multi-female social system similar to that of some savannah baboon populations (Sharman, 1982). Others assumed weak substructuring in which OMUs are sometimes present (Dunbar and Nathan, 1972), or a multilevel social system containing OMUs (Boese 1973; Maestripieri et al. 2005, 2007; Galat-Luong et al. 2006).

Here, we present data from the first systematic observations from individually identified female Guinea baboons, with respect to their association and interaction patterns with males. The goal of this study is to clarify the intersexual social relationships and mating patterns of this species. Of primary interest was whether female-male associations conformed generally to the savannah baboon model, where intersexual relationships are mainly confined to the oestrous period and lactation, or whether females associated with males throughout their reproductive cycle, as in the case of hamadryas baboons. We conducted social network analyses based on proximity scans to identify substructures within the social group, and investigated interaction patterns between females and males, with a specific interest in the temporal dynamics of intersexual associations.

Methods

Field Site and Study Subjects

Research took place at the Centre de Recherche de Primatologie (CRP) field station in the Parc National du Niokolo Koba, Senegal (as described in Maciej 2013) from January

2012 to July 2013. The Guinea baboon population around the CRP field station consisted of >400 individuals, comprising 5-7 gangs varying in degree of habituation. We observed members of the Mare gang, which included 3 parties (party IDs 4, 9 and 10), because they were the best habituated gang at that time. At the onset of the study, all individuals in the focal gang could be followed by the observer (ASG) from a distance of 10-12 m. Other gangs in the community were not as well habituated, but could be followed easily at a distance of ≥ 20 m. By the onset of focal sampling in April 2012 all individuals in the Mare gang could be followed even through dense vegetation at a distance of <5 m, if necessary, and by May 2012 it was possible to observe this gang when feeding/travelling in aggregations of >200 baboons without causing obvious disruption. Gang size and composition varied during the study period. The study gang consisted of 15-16 adult females, 0-2 subadult females, 11-12 adult males and 3-6 subadult males. Variation in gang composition was due to maturation, mortality and migration events.

Data collection

Our study involved focal observations of wild animals in the field making it impossible to use blinded methods to record the data. Electronic forms for data collection were created using Pendragon 5.1.2 software (Pendragon Software Corporation, USA) and run on HP Tungsten Palm E2 handhelds (Hewlett-Packard Company, USA). As a part of the daily census a single observer, ASG, recorded the presence and health status for all individuals in the study group, with female reproductive status noted for all focal females (Gauthier, 1999; Higham et al., 2009). Females observed to suckle dependent offspring were categorised as lactating; pregnant females were distinguished by reddening of the anogenital area (AGA) and the paracallosal skin (PCS). Cycling females were partitioned into four categories: C0 (an absence of swelling in the AGA and PCS), C1 (small vertical swelling of the AGA), C2 (a medium (vertical and horizontal) swelling of the AGA and a small swelling of the PCS) and C3 (full outward distention of both the AGA and the PCS, however, the width at peak swelling did not extend beyond the outer extremities of the ischial callosities as it does in other *Papio* species (Gauthier, 1999; Higham et al., 2009)).

Ad libitum data on intersexual grooming, greeting, copulation and aggressive interactions were collected during ~2,100h over the course of 489 observation days (2012 =328 and 2013=161) from 06:00 to 13:00 and 15:00 to 19:00. Focal data (totalling 1,262 completed samples of 30 min each) were collected over the course of 256 study days from 16 adult females from April to August 2012 and December 2012 to June 2013.

As proximity distances have been suggested as good indicators of social relationships (Fernando and Lande, 2000; Kummer, 1968; Lusseau, 2003), 4 scans were conducted per 30 min follow in order to record the location of all adult and subadult males within 1-2 m (henceforth referred to as 2 m) and $\geq 2-5$ m (henceforth referred to as 5 m) of the focal female. One scan was conducted at the start of each focal protocol, with subsequent scans occurring at 10 min intervals; a total of 5,048 proximity scans were analysed to assess spatial proximity, irrespective of the occurrence or quality of social interactions. From previous studies, we knew that spatial and interaction networks do not necessarily correlate (Castles et al. 2014; Patzelt et al. 2014); although social interaction is contingent upon spatial proximity, the reverse is not necessarily true.

Focal observations of 30 min in duration were conducted for each female 1-3 times per week during morning and afternoon sessions, throughout which the occurrence of all approaches (within 2 m), retreats, supplants (approach-retreat interactions in which individuals maintain close proximity for less than 5 seconds), grooming, greeting, aggression and copulation events were recorded (Altmann, 1974). Grooming bout durations were recorded to the closest second and involved either bilateral or unilateral grooming of one or both partners. Bouts were defined as episodes that were not interrupted for more than two minutes or by an active social interaction with another individual. Greetings, approach-retreat interactions often involving affiliative “grunt” vocalizations (Maciej et al., 2012) were also recorded and involved at least one element of contact (e.g. ventral embrace, genital touching or sniffing, or mounting). As aggression events varied in duration and were often polyadic in nature, aggression events were determined to have ended when one of the participants retreated from the other or affiliative behaviours were observed between the two individuals. Copulations were recorded for all tumescent (with a sexual swelling) adult females ad libitum; in order to distinguish between socio-sexual and reproductive sexual behaviours, only full mountings that occurred (most likely) with intromission while a female was tumescent were recorded as copulations. Mounts with non-tumescent females were categorised as greetings.

Data analyses

All statistical analyses were conducted in the R environment version 3.1.2 (R Core Team, 2014) and RStudio interface (RStudio, 2012). The individual citations for functions and packages utilised are given below.

Intersexual network structure

As grouping patterns varied throughout the study period, we confined the social network analysis to a stable two-month period from April-June 2012. The analysis is based on 1,360 scan samples, ranging from 84 to 96 per female, for two different proximity distances: 5 m and 2 m. We calculated degree centrality, density, and applied community identification algorithms (spin glass and walktrap). Degree centrality was used to determine the number of immediate neighbours for each individual and we then ran a Mann-Whitney U test with the function *wilcox.test* in the stats package (R Core Team, 2014), to determine whether males differed in terms of the number of their female partners. Proximity networks were undirected and weighted in order to visualise the varying intensity of connections. The success of intersexual pairings was assessed for each female individually by comparing the subgroup assignment to the male node, which had the highest number of connections. Figures were generated using the Fruchterman Reingold layout (Fruchterman and Reingold, 1991) and the calculation of network metrics were performed in R using available functions in the package igraph (Csárdi and Nepusz, 2006): *graph.strength*, *graph.density*, *spinglass.community* and *walktrap.community*. Additional details regarding these methods are included in the supplementary material.

Identification of male partners

In order to assess if females have preferred male associates, we analysed 5 m and 2 m proximity scans collected over the entirety of the study period (ranging from 160 to 344 scan samples for each female). We individually assessed whether each female revealed preferential associations with specific males, which included 20 subadult and adult males, using a Friedman average rank test, a nonparametric test for repeated measures (Demšar, 2006; Friedman, 1940). We then used the Nemenyi post-hoc test to test the difference in rank for all pairwise comparisons (Demšar, 2006); see details in the supplementary material. Tests were conducted using the functions *friedman.test* from the stats package (R Core Team, 2014) and *posthoc.friedman.nemenyi.test* in the PMCMR package (Pohlert, 2014).

Two meter scans collected throughout the course of the study were used to visualise weighted proximity networks using the package igraph (Csárdi and Nepusz, 2006) with the Fruchterman Reingold layout, which clusters more strongly connected sets of nodes together (Fruchterman and Reingold, 1991). As there may be temporal changes in intersexual associations, data were pooled every two weeks and the top male for each female (the male who was recorded most often within 2 m) was assigned as her “primary male”; other males

were categorised as “secondary” if they were observed within 2 m or “unaffiliated” (with any female) if they were never observed within 2 m of a female. This method resembles the one used for determining preferred intersexual partners in Grevy’s zebra (Sundaresan et al. 2007).

In order to determine if females were more likely to interact with males of different status categories (primary, secondary and unaffiliated) we looked at the occurrence of social contacts during focal observations. Social behaviours of interest included grooming, greeting, aggression and infant handling. Every focal observation (40 to 86 samples per female) received a yes/no score for each of the possible 20 subadult and adult males. We then ran generalized linear mixed models (GLMMs) (function *glmer* from the statistical package lme4; (Bates et al., 2013)) controlling for female and male identity, as well as the random slope for status and male identity. Due to the small amount of variability in the number of dyads observed to copulate it was not possible to compare this behaviour statistically.

Directionality of relationship maintenance

From 1,262 focal samples we determined the overall percentage of approaches performed by females towards their primary and secondary males. In addition, we calculated the Hinde index (Hinde, 1977; Hinde and Atkinson, 1970), in order to determine which individual was responsible for maintaining proximity, and potentially, female social partner choice (Soltis et al. 2001). The index was calculated using the equation:

$$\text{Hinde Index (HI)} = A_f - R_f$$

Where A is the proportion of approaches performed by the female and the R is the proportion of retreats performed by the female; supplants were not included in the calculations. Proportions were calculated from the total number of approaches or retreats a female experienced. HI scores range from -1, indicating male driven relationships to +1, suggesting female driven relationships. As only dyads having ≥ 10 approach-retreat interactions were included, one dyad containing a primary male and 16 dyads containing secondary males were excluded due to a low number of interactions. We tested the variability between dyads containing different male status categories while controlling for female and male identity with a GLMM using the function *lmer*.

Temporal dynamics of female-male associations

In order to assess the temporal stability of intersexual relationships during periods when focal scans were not collected ad libitum grooming, greeting, copulation and aggression data were used. For females who interacted with more than one male on a regular basis, it

was necessary to observe an interaction that was not surreptitious (that is, an interaction which occurred when the primary male was in the direct line of sight of the pair) in order for her to be recorded as changing from one primary male to another. Otherwise, it was assumed that the identity of the primary male had not changed.

Female reproductive state and intersexual relationships

To investigate the influence of female reproductive state on the probability of grooming, greeting or aggression occurring between females and their primary males, we ran three GLMMs (Baayen et al., 2008), with binomial error structure (occurrence yes/no). The predicted probability (based on the proportion of number of observations) of grooming, greeting and aggression occurring was modelled based on focal samples from 16 females observed in 1-6 reproductive states. In order to investigate the variability in the intensity of social interactions a second set of models including only the observations during which grooming or greeting occurred (227 and 345 focal observations, respectively). The grooming duration and the greeting frequency per 30 minute focal observation were assessed using GLMMs with Gaussian and Poisson error structures, respectively. In the Poisson model utilizing counts of the number of greeting events, a log transformed offset term was used (the number of focal observations per female).

Comparisons of the estimates of the models based on all data with estimates with effects excluded individually revealed that all the models were relatively stable. Variance inflation factors (Field, 2009) for both variables in all three models did not indicate that collinearity was an issue; none of the data sets were found to be overdispersed. All models were implemented in R using the functions *lmer* and *glmer* in the package *lme4* (Bates et al., 2013). Female and male identity were always included as random effects (Kreft and de Leeuw, 1998).

Results

Intersexual network structure

Males were located within 5 m of females in 43.7% of scans and within 2 m in 20.9% of scans. Social network analysis of 2 months of focal data revealed different structures for each of the bipartite proximity networks (Table 1). The social network visualisation of the 2 m scans partitioned the network into two large subgroups (parties), while visualisation of the 5 m scans appeared relatively cohesive and included all individuals at the level of the gang

(Figure 1). The 5 m network contained more individuals, more dyads, had a higher degree and a higher density than the 2 m network (Figure 1; Table 1). Comparisons of degree centrality values between primary and secondary males revealed that for the 5 m network, secondary males had significantly higher degree centrality than primary males (median degree centrality for 7 primary males = 3.0; median degree centrality for 6 secondary males = 3.5; $W=10.5$, $P<0.05$). However, this relationship was untestable for the 2 m network due to the small number of secondary males observed ($N=3$) in comparison to primary males ($N=6$). The modularity values indicated less substructuring between the subgroups identified in the 5 m network compared to the 2 m network (Figure 1; Table 1). Both community detection measures identified comparable numbers of subgroups within the two networks, although the assignment of the individuals to subgroups varied slightly. In the 2 m network each female was assigned to her primary male, the male with whom she had the strongest tie. Each 2 m subgroup consisted of 1 primary male, 0-2 secondary males, and 1-4 adult females. For the 5 m network community assignment algorithms failed with only 33.3% of females being assigned to the same primary males as has been identified in the 2 m network.

Similar results were obtained for the global assessment of ~10 months of focal data. We found a significantly preferred associate only for 2 of 16 females when we assessed the 5 m scans, while we identified as preferred associates for 13 of 16 females when we assessed the 2 m scans (Friedman and Nemenyi tests; a subset of the results are available in Figure S1).

Table 1 Weighted network size and metrics based on 5 m and 2 m proximity scans between intersexual dyads.

Variables	Proximity	
	5 m	2 m
Total no. individuals	28	24
Total no. dyads	91	48
Degree range	1-12	1-7
Degree mean	6.5	4
Density	0.24	0.17
Modularity - spin glass	0.03	0.07
Total no. subgroups - spin glass	6	6
Modularity - walktrap	0.07	0.56
Total no. subgroups - walktrap	5	7

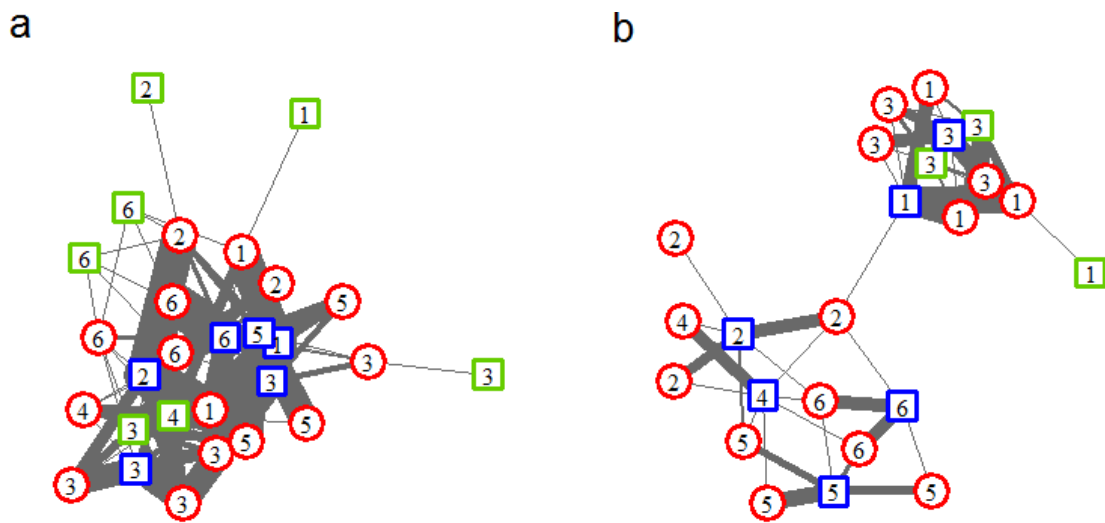


Figure 1. Two weighted association networks calculated from scan sampling of female-male dyads at two different distances: (a) 5 m (N=28 individuals, 91 dyads) and (b) 2 m (N=24 individuals, 48 dyads). Data were aggregated over a two-month period of stability. The nodes identify sex and status categories: females= red circle, primary males=blue square and secondary males=green squares. The width of the edges connecting female-male dyads indicates the frequency at which a dyad was observed. The numbers in each node indicate

the community to which that node was assigned based on spin glass community identification.

Intersexual social behaviour and male social partner status

During focal sampling, grooming bout length varied between 0.07-23.15 min with a mean bout length of 3.51 min. In 76% of total grooming time observed, females were actively grooming males. On average females groomed with primary males 1.26 min/h of focal observation time and with secondary males 0.16 min/h. A typical grooming bout lasted 3.52 min (± 0.10 min) with primary males and 2.85 min (± 0.08 min) with secondary males. Females groomed significantly more frequently with primary than with secondary and unaffiliated males ($\chi^2=29.87$, $df=2$, $P<0.001$; Figure 2a, Figure S2). Greeting events occurred at a rate of 0.85 per h. Ninety percent of greetings occurred between females and primary males and greeting probability was significantly influenced by male status with females greeting significantly more with primary than with secondary and unaffiliated males ($\chi^2=39.27$, $df=2$, $P<0.001$; Figure 2b). Aggressive behaviours, occurring at a rate of 0.10 events per hour (mean per female, ranging from 0-0.27 events per hour), customarily involved males behaving aggressively towards females; however, in 20% of bouts females were also observed to act aggressively towards males. Aggressive interactions occurred significantly more with primary than with secondary and unaffiliated males ($\chi^2=38.22$, $df=2$, $P<0.001$; Figure 2c). Ad libitum data indicate that females in all reproductive states either actively or passively participated in aggressive behaviour with males and some counter-aggressive behaviours involved female-female coalitions. Primary males were responsible for 59% of all infant-handling events by males with infants of focal females. Male status predicted the probability of infant handling events, with primary males handling infants significantly more than secondary and unaffiliated males ($\chi^2=13.46$, $df=2$, $P<0.001$; Figure 2d).

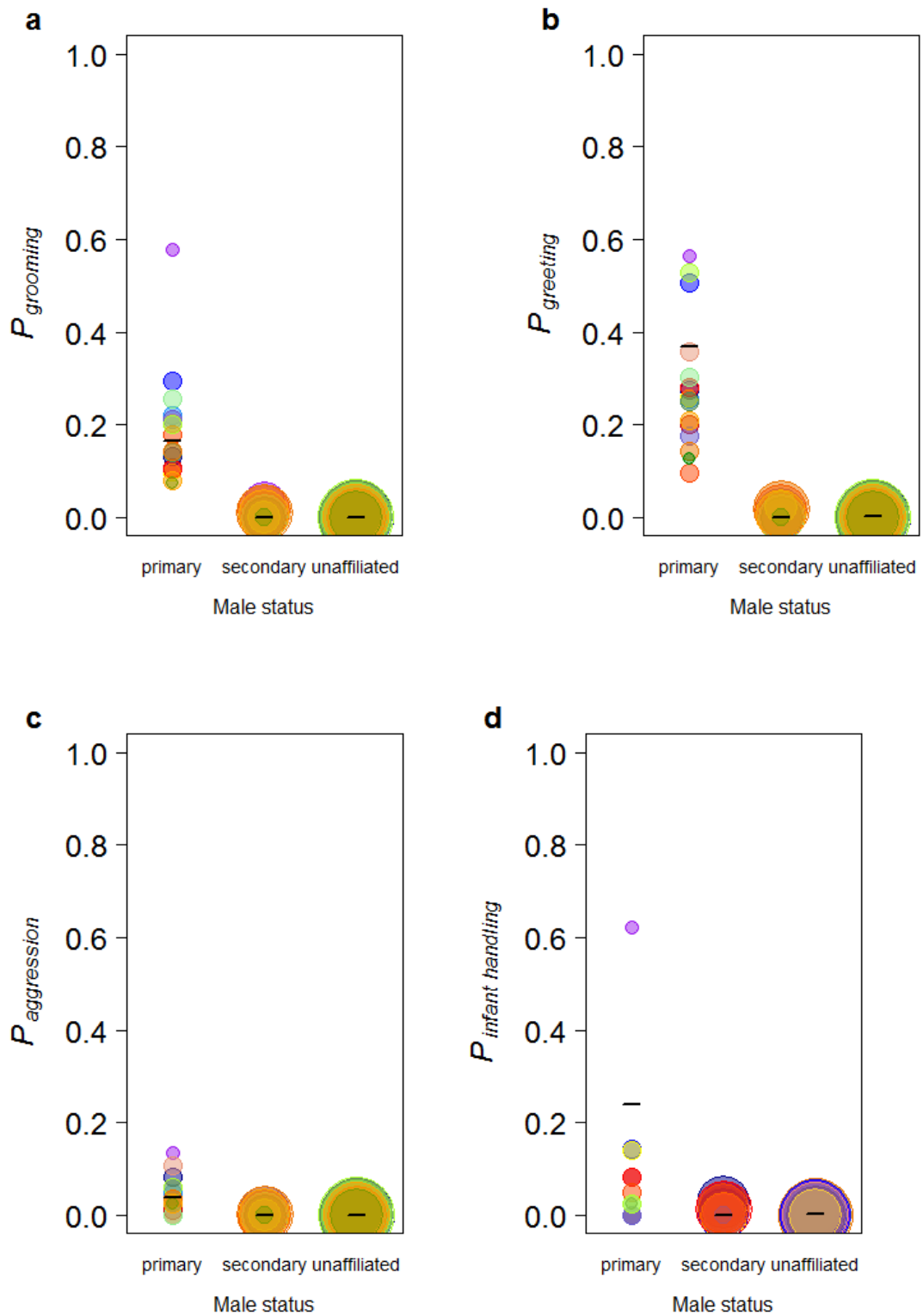


Figure 2. The mean probabilities of observing a grooming, b greeting, c aggression and d infant handling between females and males of different status categories. Horizontal black lines show the models' predicted values. Circles represent the proportion of focal

observations in which the respective behaviour was observed. The circle area is proportional to the number of observations and each female is represented by a different colour.

From six females, we were able to collect focal observations when they were tumescent. These females copulated with a total of 7 different males, 6 of which were adult and one subadult. Two females copulated with 1 male only; 4 females with 2 or more males, but were consistent with copulation partner within any respective oestrus period. For these 6 tumescent females copulations occurred at a mean rate of 0.69 times per focal hour. The small sample size did not allow for assessing if male status influenced the number of copulations in the same manner presented above, therefore we looked at the total number of copulations observed throughout the study period.. Of 493 copulations observed ad libitum between 11 tumescent females and 12 males (10 adult and 2 subadult), 98.6% occurred between females and their respective primary male.

On average, 4.9 secondary males (range=0 to 10) were assigned to each female based on 2 m proximities. Yet again proximity did not necessarily imply social interaction as females typically interacted with far fewer secondary males (e.g. mean number of secondary male grooming partners=0.52; range=0 to 3).

Directionality of relationship maintenance

Primary males were responsible for 60% of all approaches (25 dyads), while secondary males initiated 76% of all approaches (33 dyads). The HI ranged from -0.66 to 0.26 (mean=-0.17) for intersexual dyads containing primary males and -0.88 to 0.07 (mean=-0.36) for those with secondary males, indicating that in the majority of dyads, males were responsible for maintaining proximity to females (in 18 of 24 dyads containing primary males and 15 of 16 dyads containing secondary males; Figure 3). No difference was found in the HI scores for dyads containing primary males vs. secondary males ($\chi^2=1.19$, $df=1$, $P=0.28$).

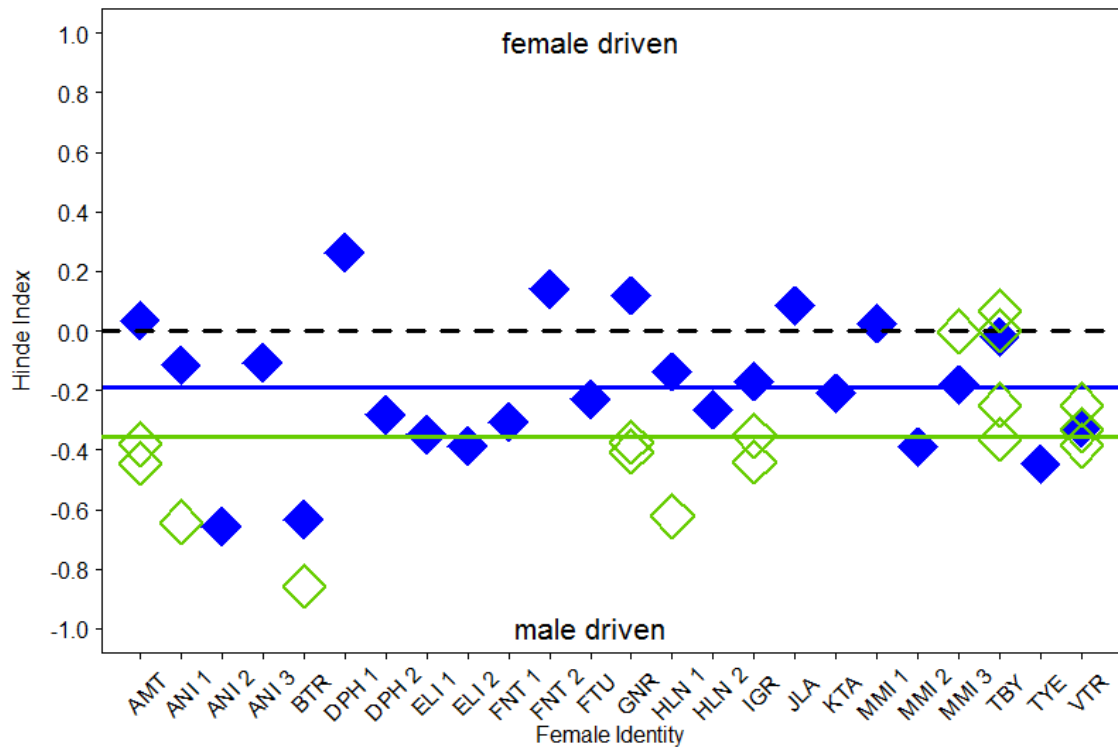


Figure 3. The Hinde Indices for intersexual dyads in which at least 10 approach-retreat interactions were observed over the course of the study period. The blue filled diamonds represent dyads containing females and primary males and the green open diamonds represent dyads containing females and secondary males; group means for male status categories are indicated in blue (primary males) and green (secondary males). The black dashed line indicates 0, where the responsibility for relationship maintenance is equal between females and males.

Female reproductive state and intersexual relationships

GLMMs of the probability of observing specific behaviours indicated that female reproductive state only minimally impacted the probability of social behaviours with primary males. The grooming probability ($\chi^2=7.98$, $df=5$, $P=0.16$) and aggression with primary males ($\chi^2=8.18$, $df=5$, $P=0.15$) did not vary significantly in relation to female reproductive state. However, female reproductive state significantly influenced greeting probability ($\chi^2=16.10$, $df=5$, $P<0.01$; Figure 4). Post-hoc analyses indicated that lactating females greeted with primary males significantly less often, while there was no difference between pregnant and cycling females (Table 2). The analysis of the duration of grooming bouts between females and primary males revealed no relationship between female reproductive state and grooming ($\chi^2=6.69$, $df=5$, $P=0.25$); female reproductive state also did not influence the frequency of greeting events ($\chi^2=2.96$, $df=5$, $P=0.71$).

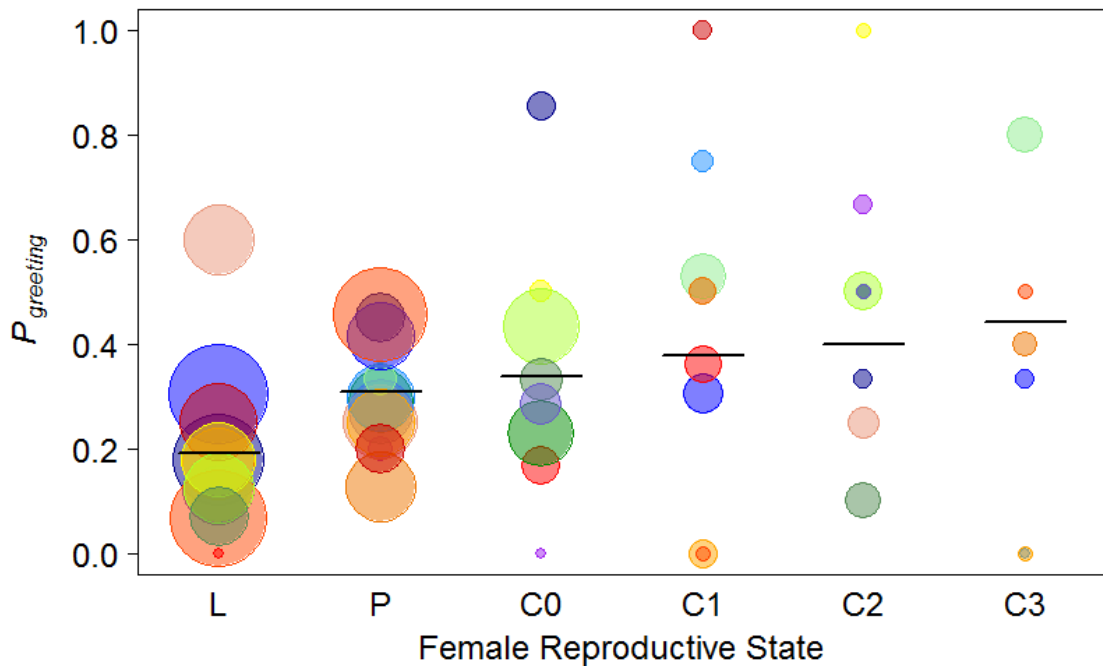


Figure 4. The mean probabilities of observing females greeting with their primary males in relation to the females' reproductive states. Horizontal black lines show the models' predicted values. Circles represent the proportion of focal observations in which greetings were observed. The circle area is proportional to the number of observations and each female is represented by a different colour. Female reproductive state categories: L=lactating, P=pregnant, C0=cycling but detumescent, C1=tumescens size 1 (small), C2=tumescens size 2 (medium) and C3=tumescens size 3 (large).

Table 2 The effects of reproductive state on the occurrence of greeting probability.

	Estimate	Standard error	z value	P value
Intercept	-1.442	0.182	-7.907	<0.001
Pregnant	0.641	0.207	3.102	0.002
Detumescent C0	0.770	0.292	2.641	0.008
Tumescens C1	0.941	0.312	3.018	0.003
Tumescens C2	1.034	0.385	2.686	0.007
Tumescens C3	1.209	0.496	2.437	0.015

Results from a generalized linear mixed model with binomial error structure, in which female and male identity were included as random factors. The intercept represents lactating females

Seven of the focal females, in various reproductive states, maintained affiliative relationships (via grooming interactions) with males who were not their primary male (Figure S2S2). Of the 36 grooming bouts with secondary males observed during focal observations, 61% (from 13 of the 14 dyads) were non-surreptitious and females never received aggression from their primary males although it was apparent that the primary males were aware of these interactions (either because they were participants (42%), or were seated within 10 m and in a direct line of sight (19%). Some females were observed to share the same secondary males. Unfortunately, these interactions are too few to determine if secondary males are more likely to engage in social interactions with oestrus females.

An analysis of the influence female reproductive state on relationships with secondary males was not possible due to the small sample size. Ad libitum data indicate that females in all reproductive states were observed to groom and greet with secondary males, however.

Temporal dynamics of female-male associations

The use of ad libitum data allowed us to look at the changes in the identity of the primary males over a longer period than was possible with only focal data (Figure 5). Changes in female-primary male affiliation, based on the occurrence of grooming, greeting and copulations, were immediately obvious and females were observed to transfer between and within parties (intra-party transfers=10, inter-party intra-gang transfers=6, inter-gang=2-4 (2 inter-gang transfers may have been unconfirmed mortalities)). The sixteen females were distributed unevenly over 10 primary males in the focal gang and the majority of females shared their primary male with at least one other female, and as many as 4 adult females sharing the same male. Females were not observed to transfer to their secondary males, but rather to bachelors or already established primary males. Although the exact moments of transfer were not observed during focal observations there appears to be no graded period when females transferred from one primary male to the other. On two occasions, within a few hours or days of a transfer, social interactions between the new pair appeared to result in aggressive displays (i.e. stares and ground slaps) by the former primary male. In addition, during ad libitum data collection, dyadic male-male aggression was observed between a primary male and secondary male immediately following surreptitious affiliation. Seventeen changes were identified for females in various reproductive states (lactating, pregnant and cycling) and no infanticide was observed. Over the 507 study days, 8 females remained with

the same primary male, while 8 females changed primary males at least once (Figure 5). Changes in primary males occurred for females who did and did not have secondary male social partners at the time of transfer. As the exact moment that these transfers occurred was not observed it is unclear as to whether males or females were the instigators. Female tenure time with any single male varied from 15 to 507 days (the complete observation period; Figure 5). Median female tenure length was 200 days. However, this value may be a conservative estimate, as only 6 of 31 female tenures were not truncated by the study period (Figure 5, Figure 6). Females interacted with secondary males at a much lower rate than with primary males, thus making shifts in secondary male status more difficult to detect. Four females maintained social relationships with secondary males for periods of >300 days.

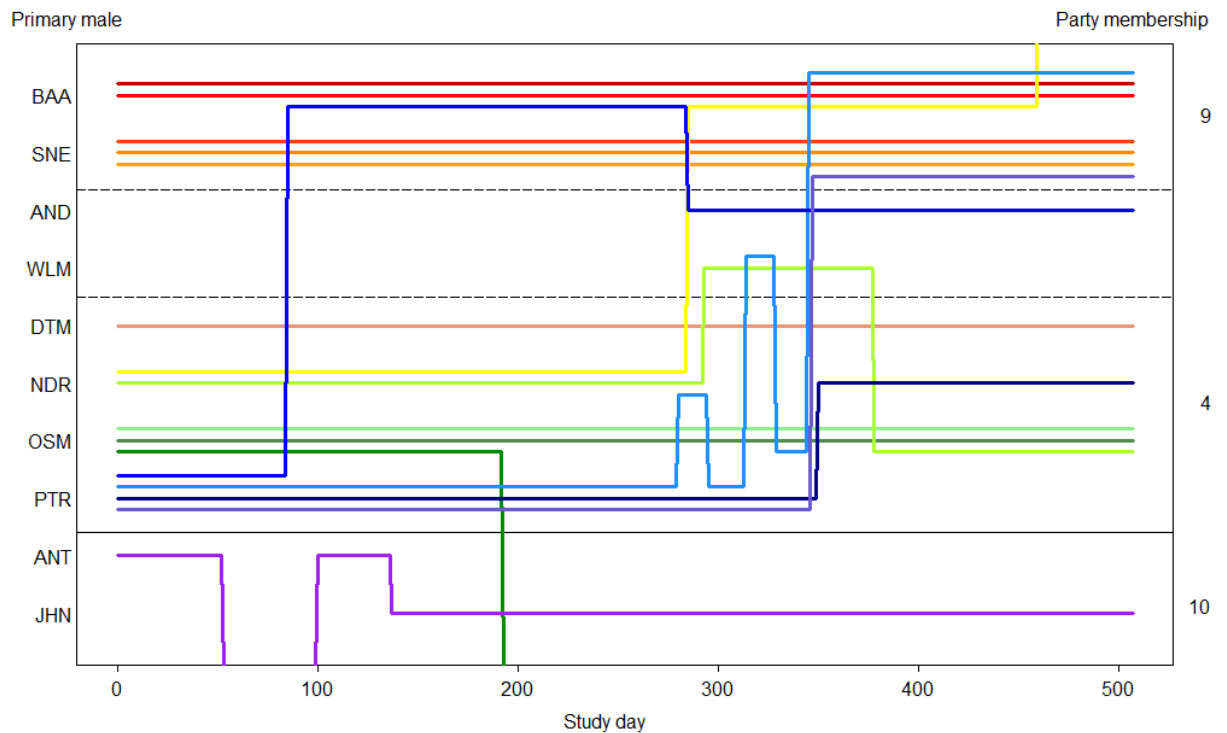


Figure 5. A schematic of the temporal changes in female associations with primary males. The identity of primary males is shown on the y-axis, with study females grouped on the inner y-axis by unit membership (as indicated by the three letter IDs of the primary males). The coloured lines represent different females with horizontal lines showing persistent unit membership and vertical lines showing transfer between males. Study day is indicated on the x-axis. Black horizontal lines distinguish between parties with consistent membership (separated by a solid line) and parties with males who changed their affiliation (separated by dashed lines): party IDs 4, 9 and 10.

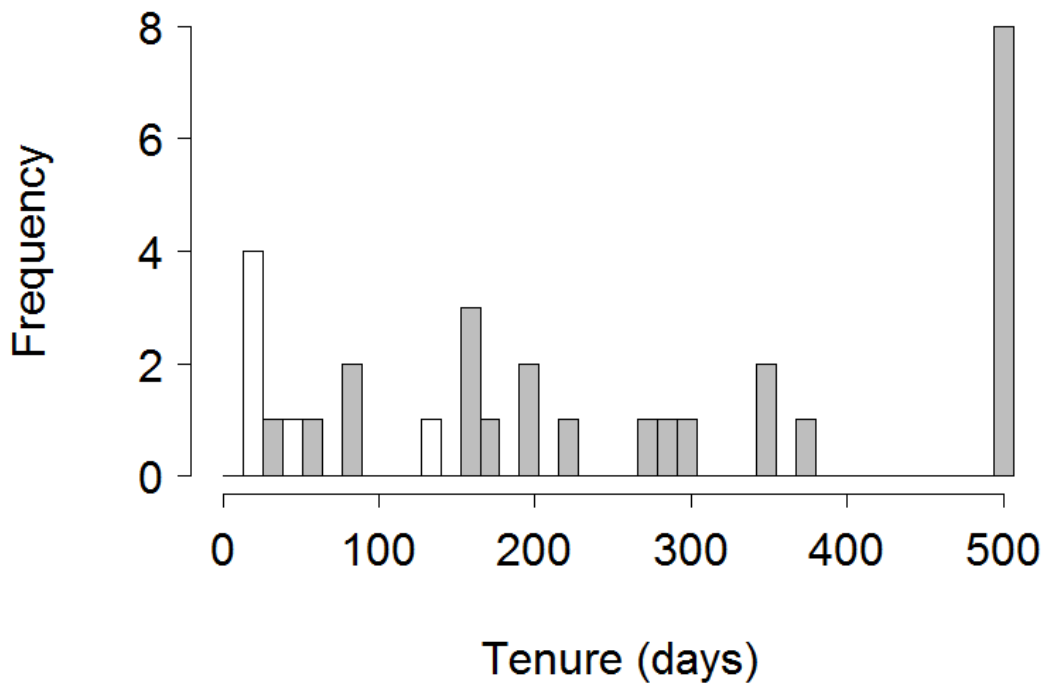


Figure 6. Histogram of female tenure length from ad libitum data. Grey bars indicate tenures which were truncated due to the study duration, and white bars indicate the tenures for which the start and the end were observed.

Discussion

The primary aim of this study was to provide comprehensive data on female-male relationships in wild Guinea baboons, to fill in the gaps in our understanding of this species' social system, and ultimately to contribute to a better understanding of primate social evolution. The social network analysis corroborated the existence of parties within gangs (Patzelt et al., 2014), but also identified further substructures (“units”) within parties, which comprised 1-3 adult and subadult males and 1-4 adult females. These units became only apparent when close spatial associations (up to 2 m), but not medium distances (up to 5 m) were considered. Within units, females showed strong spatial associations with one specific “primary” male and most of the social interactions were confined to that male. Some females groomed with other “secondary” males. These males were typically subadult, post-prime, or injured males. Some relationships with secondary males lasted throughout the study period.

Female reproductive state only marginally affected the frequency and type of interactions with primary males. The most striking finding was that although females spent substantial amounts of time outside a distance of 5 m from any male, mate fidelity was remarkably high, as almost all of the observed copulations were restricted to the primary

male. Thus, from the females' perspective, the mating system seems to be monandrous. Given these mating patterns and the social and spatial relationships between females and their respective primary male "OMUs" appear to comprise the core of the Guinea baboon society (Table 3), confirming earlier observations on mating behaviour in captivity (Boese, 1973; Maestriperi et al., 2005, 2007). At the level of the social organisation, some of the subunits constitute multi-male units, as there may be one or more secondary males (Chowdhury et al., 2015; Dunbar, 1984; Dunbar and Dunbar, 1975a; Kummer, 1968; Pines et al., 2011; Snyder-Mackler et al., 2012b). Multiple units are embedded within the party and two or more parties come together to form a gang. Gangs may be comparable to the bands of hamadryas baboons and geladas or troops in savannah baboons (c.f. Dunbar 1984).

Table 3. Features of intersexual relationships in *Papio* and *Theropithecus*.

Spatial and behavioural features	MM MF	OMUs		This study
	savannah baboons	hamadryas baboon	gelada	Guinea baboon
FRS predicts affiliation	strong ⁸	weak ⁹	weak ⁴	weak
Distance to male: L/P	n/a	mean=2.2±1.5 m ¹	13.0±4.0% at 2 m ²	18.8±1% at 2 m
Approaches by males	n/a	28% ³	male driven ²	76%
Grooming	n/a	L > F ¹	differentiated ^{4,5}	L > S
Aggression/herding (hourly rate)	n/a	>0.25 ⁶	0.23 ⁴	0.1
Female counter-aggression and coalitions	n/a	absent ⁷	present ^{4,5}	present
Female transfer	n/a	individual ⁹⁻¹²	group ⁴	individual
Range of OMU sizes	n/a	1-9 ¹	1-10 ⁴	1-4
Mean OMU size	n/a	2.6 ¹²	5.07-6.25 ¹³	2.14

n/a=not applicable; L=leader; F=follower; P=primary; S=secondary; FRS=female reproductive state

¹(Swedell, 2006); ²(Kawai and Mori, 1979); ³(Hans Kummer, 1990); ⁴(Dunbar and Dunbar, 1975b); ⁵(Dunbar, 1984); ⁶(Swedell and Schreier, 2009); ⁷(Swedell, 2011); ⁸(Seyfarth and Cheney, 2012); ⁹(Kummer, 1968); ¹⁰(Sigg et al., 1982); ¹¹(Swedell, 2000); ¹²(Swedell et al., 2011); ¹³(Snyder-Mackler et al. 2012a)

The comparative perspective

Intersexual relationships in Guinea baboons share some interesting similarities with hamadryas baboons (Table 3). Both species have superficially similar nested multilevel system containing OMUs, but there are also marked differences (Table 3). Notably, in hamadryas baboons, males enforce close female proximity through herding (Kummer, 1968; Swedell and Schreier, 2009), in a similar fashion as in other harem based societies, such as horses (*Equus ferus caballus*, (Monard and Duncan, 1996)). Hamadryas baboon females submit to male coercion through early conditioning and futility of opposition, and thereby learn to maintain close spatial proximity to their leader male (Hans Kummer, 1990; Swedell and Schreier, 2009), but it may also be in the female's best interest to stay in the proximity of a particular male. Takeovers of adult females in hamadryas baboons often involve male-male conflicts and are the result of the defeat of an older leader male. During male takeovers, OMUs are frequently split up, with females of the original OMU found in different OMUs afterwards (Kummer, 1968; Sigg et al., 1982; Swedell, 2000; Swedell et al., 2011).

Guinea baboon females spend substantial amounts of time away from any male, implying that females have a certain degree of freedom not available to hamadryas females. Interestingly, Guinea baboon females respond to male aggression with occasional counter-aggression and female-female coalitions, rather than the submissive behaviour characteristic of hamadryas females. Females take an active role in relationship continuity and are seemingly able to avoid advances by other males. In Guinea baboons, transfers of females between different primary males occurred individually. The level of the social system did not halt female transfers as females were observed to change between OMUs at all three social levels. Interestingly, sometimes, the transfer of one female was shortly followed by the transfer of other females, resulting in periods of social instability (see Figure 5; Table 3). This raises the question to which degree females compete over males, an aspect that has previously

often been neglected (Clutton-Brock and Huchard, 2013), although Kummer (Kummer, 1968) reported frequent female-female competition for access to the leader male in hamadryas baboons.

The multilevel social system of geladas (Dunbar, 1984; Mori, 1979b) offers an alternative female bonded social pattern, which has some similarities to Guinea baboons in that female counteraggression and coalition formation have been observed (Table 3). In contrast, gelada unit cohesion is explained by strong female kin-based relationships (le Roux et al., 2011). Gelada OMUs appear to be larger, are less spatially separated and may overlap with other OMUs (Kawai and Mori, 1979; Snyder-Mackler et al., 2012a). Further substructuring may be caused by the splitting/budding of OMUs as their size increases (Dunbar, 1984). Males commonly acquire females through taking over a group of closely related females (Dunbar, 1984; Dunbar and Dunbar, 1975a), and occasionally, followers may lure females from an OMU from which they are affiliated (Dunbar, 1984).

In sum, we conclude that female-male relationships in Guinea baboons differ fundamentally from those of savannah baboons, where females maintain close associations with males only during consortships, and with male “friends” when they are lactating, while they share greater similarities with those between hamadryas baboon males and females.

Female and male reproductive strategies

Male competition for access to mates (Dobson, 1982), and control over females varies substantially between species (Smuts and Smuts, 1993). In a number of multilevel species, prime males at their reproductive peak actively exclude male competitors and sequester females (Chowdhury et al., 2015; Linklater, 2000; Qi et al., 2014; le Roux and Bergman, 2012; Rubenstein, 1994). In cases where complete exclusion of outside males is not possible, dominant-prime males concede to the presence of other males who may assist in territorial or female defence (Kummer, 1968; Linklater et al., 1999; Mori, 1979b; Rubenstein and Hack, 2004). This may prolong leader male tenure, but may also result in reproductive concessions (Chowdhury et al., 2015; Feh, 1999; Snyder-Mackler et al., 2012b). Yet males may not concede, but rather cooperate to increase their reproductive benefit, such as in bottlenose dolphins (Wiszniewski et al., 2012).

High mate fidelity between Guinea baboon females and primary males indicates that primary males are not making reproductive concessions to other males, although paternity data will be needed to corroborate this assumption. The high degree of mate fidelity, the low overt competition by males for mating opportunities (Kalbitzer et al., 2015), and the fact that

Guinea baboon males show small relative testes (Patzelt, 2013) are consistent with a monogamous or polygyn-monandrous mating system where sperm competition does not play a major role (Jolly and Phillips-Conroy, 2003, 2006).

The adaptive value of friendships between females and secondary males in Guinea baboons presently remains unclear. Furthermore, our results raise the question why Guinea baboon males make hardly any overt attempts to control or takeover females from other males. One conjecture is that males forego competition over females because this might jeopardize their bonds with other males (Patzelt et al., 2014). The occurrence of closely related males within the party (Patzelt et al., 2014) may alleviate some of the costs associated with lost reproductive opportunities. Long-term data will be needed to assess the roles that females and males play in maintaining long-term relationships and the predictors of female transfers between males, to obtain a full understanding of female and male strategies.

Evolution of Social Systems

One major debate in the understanding of social evolution is the interplay between phylogenetic inertia (as outcomes of past selective pressures and genetic drift) and current ecological conditions. The standard socioecological model predicts that male mammals map themselves onto female distribution patterns, which are driven by resource distribution (Clutton-Brock, 1989a; Emlen and Oring, 1977; Jarman, 1974; Sterck et al., 1997). Grueter and van Schaik (2009) proposed that multilevel groups are better equipped to balance the costs and benefits of group living, which may not only apply to nonhuman primates, but also to some wild equids (Rubenstein 1986, 1994; Rubenstein et al. 2007), African and Asian elephants (de Silva and Wittemyer, 2012; de Silva et al., 2011), certain antelope species (Jarman, 1974) and perhaps giraffes (VanderWaal et al., 2014).

According to phylogenetic reconstructions, the ancestral state of the social system in Papionins was most likely a female bonded multi-male multi-female system (Di Fiore and Rendall, 1994). The multilevel system found in hamadryas, Guinea baboons and geladas thus represents a derived trait. Since geladas and baboons have a relatively long independent evolutionary history (Delson, 1993; Liedigk et al., 2014; Newman et al., 2004) it can be assumed that the multilevel systems of geladas and baboons evolved independently (Grueter et al., 2012). In contrast, hamadryas and Guinea baboons have a common ancestor which lived less than 2 million years ago (Liedigk et al., 2014; Zinner et al., 2009), indicating that the OMU based multilevel system of these species may be a synapomorphic trait already present in their last common ancestor. Jolly (Jolly, 2009) proposed that spatial dynamics

during that range expansion may have played a role in shaping baboon social systems. Conditions at the frontier of the range expansion might have favoured male philopatry and promoted a shift from the female-bonded to a male-bonded system (Jolly, 2009). The frontier population(s) constituted the ancestors of extant hamadryas and Guinea baboons.

While this scenario stresses the ecological and demographic conditions in the past, others have focussed on present day ecological conditions. Specifically, the social organisation of hamadryas baboons and geladas has been viewed as adaptations to extreme and somewhat marginal habitats (Dunbar, 1992; Schreier and Swedell, 2012). However, the ecology of the two species differs greatly and therefore, a simple relationship between particular ecological settings (i.e. spatial and temporal distribution of resources) and the respective social system cannot be inferred.

Taken together, there is still no single comprehensive model that integrates phylogenetic descent with present-day factors. Resource availability, predation pressure, infanticide risk, and bachelor threat may all have potentially affected the social dynamics and social evolution of the different variants of multilevel societies (Grueter et al., 2012; Grüter and Zinner, 2004; Rubenstein, 1986). We suggest that fundamental characteristics in social tendencies (e.g. aggressiveness and mating pattern) indeed have a genetic basis, while present day ecological conditions drive short-term variation in social organisation (Sharman, 1982). Hybrid zones may prove useful to investigate this natural interplay between these two factors. Behavioural studies of hamadryas-olive baboon hybrid groups (Beehner, 2003; Bergman and Beehner, 2004; Sugawara, 1979) have already indicated that there may be a genetic basis to male herding behaviour. Future work combining behavioural and genetic studies on Guinea-olive baboon hybrids would contribute to our understanding of the genetic basis of male physical coercion of females as well as the extent to which females can and do exhibit choice.

Acknowledgments

We would like to thank the *Diréction des Parcs Nationaux (DPN)* and *Ministère de l'Environnement et de la Protéction de la Nature (MEPN)* de la République du Sénégal for permission to work in the *Parc National de Niokolo-Koba (PNNK)*, as well as the conservateur of PNNK, Mamadou Sidibé, for his logistical support. We have much appreciation for the staff and researchers of the *Centre de Recherche de Primatologie Simenti*, in particular Cheikh Sané, Moustapha Faye, Armél Louis Nyafouna and Ibrahima Diatta for their companionship and Federica Dal Pesco, Ulrike Barnett and Matthias Klapproth for their assistance in the field. We also thank Roger Mundry and Holger

Sennhenn-Reulen for providing statistical aid and Robin Dunbar, Dorothy Cheney, Cédric Girard-Buttoz, Gisela Kopp and three anonymous reviewers for commenting on earlier versions of this manuscript. Funding from the Deutsche Forschungsgemeinschaft (DFG Fi707/9) is gratefully acknowledged.

Compliance with ethical standards

Approval and research permission was granted by the *Direction des Parcs Nationaux (DPN)* and the *Ministère de l'Environnement et de la Protection de la Nature (MEPN)* de la République du Sénégal (research permit numbers: 0383/24/03/2009; 0373/10/3/2012). Research was conducted within the regulations set by Senegalese agencies as well as by the Animal Care Committee at the German Primate Center.

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

CHAPTER 3: Meat sharing between male and female Guinea baboons (*Papio papio*)

A. S. Goffe and J. Fischer

{Cognitive Ethology Laboratory, German Primate Center, Göttingen, Germany}

Primate Biology (2016)

DOI: 10.5194/pb-3-1-2016

Abstract

Meat sharing in nonhuman primates has been linked to a variety of functions, including harassment reduction, mate provisioning and status enhancement. We present observational data regarding male prey capture and male-female meat sharing in wild Guinea baboons. Guinea baboons live in a multilevel society that comprises units of males with associated females and, sometimes, secondary males. Several males of different units maintain strong bonds, resulting in the formation of parties within gangs. Female-male relationships persist irrespective of female reproductive states, yet females may also switch between males at all stages of the reproductive cycle. Our data show that males capture and kill a variety of prey, including hares and antelope. Males shared meat passively only with females in their social and reproductive units. The occurrence of oestrus females in the gang did not influence whether or not sharing would occur in that males did not share with oestrus females unless an affiliative relationship already persisted, indicating that short-term currency exchanges of meat for sex are unlikely. We hypothesize that males may benefit from feeding tolerance by retaining females, while females may increase access to potentially nutritious and rare food sources. Alternatively, females may prefer males that are generally less aggressive and thus also more likely to share meat. Long-term data will be needed to ultimately distinguish between the two accounts. Although there is no evidence that males intentionally provide necessary resources to particular females during times of high energetic demands and decreased foraging efficiency, as has been found in humans, and meat sharing is generally rare, it may have subtle, yet important effects on the maintenance of bonds in Guinea baboons.

Introduction

Food sharing among nonkin has been invoked as an important facet in primate social evolution and has been described to take on two forms: active and passive. While the active form involves giving of a food item by the possessor to another individual, the passive form is limited to the tolerated removal of a food item from the possessor. Both forms have been shown to be associated with elevations in the oxytocin levels (Wittig et al., 2014), a neuropeptide linked to bond formation (Young and Wang, 2004). Intersexual food sharing in primates is assumed to have co-evolved with female mate choice (Jaeggi and van Schaik, 2011), indicating that sharing may be traded for enhancing reproductive success (Stevens and Gilby, 2004). Harassment reduction, mate provisioning, status enhancement and reciprocity

have all been proposed as causes of nonkin food sharing (Jaeggi and Gurven, 2013; Silk et al., 2013; Stevens and Gilby, 2004; Teleki, 1975). Therefore, the dynamics of repeated social interactions between individuals is important to understanding food sharing patterns. Although active sharing has never been reported in the genus *Papio*, the diversity within their social systems (Swedell, 2011) makes them an excellent model to investigate the social determinants of passive food sharing.

To date, carnivorous behaviours have been reported in five baboon species (Butynski, 1982; Teleki, 1975), although details regarding the social factors responsible for patterns in meat eating have not been fully investigated for all of them. “Savannah” baboons, chacma (*Papio ursinus*), olive (*P. anubis*) and yellow baboons (*P. cynocephalus*), live in multi-male multi female groups where males form a linear dominance hierarchy and compete for reproductive access to females (Swedell, 2011). Olive baboons show moderate levels of contest over carcasses (Strum, 1982) and occasional meat sharing between consort partners and female-male friends (Strum, 1981), while chacma baboons reportedly show high levels of contest between individuals and no sharing was noted (Hamilton and Busse, 1982). In contrast, hamadryas baboon (*P. hamadryas*) females and dominant leader males persistently associate, regardless of the oestrous phase of the female and one male units (OMUs) are imbedded within a multilevel system (Swedell, 2011). However, in spite of hamadryas baboons having been observed to eat meat (Swedell et al., 2008), meat sharing has not been reported in this species.

Here, we describe prey capture and meat eating behaviours in wild Guinea baboons (*Papio papio*), a little known baboon species living in western Africa, in which females have more spatial and social freedom than in the closely related hamadryas baboon that lives in a superficially similar multilevel system (Goffe et al., 2016). The Guinea baboons social system consists of units, parties, and gangs which show high fission-fusion dynamics (Goffe et al., 2016; Patzelt et al., 2014). Units are composed of a primary male and one or more females (in the case of OMUs) and occasionally secondary males (in the case of multi-male units (MMUs)); primary males have full sexual and social access to their females, while secondary males only have social access (Goffe et al., 2016). Thus, the system can be understood as having OMUs at the level of the mating system, and OMUs as well as MMUs at the level of the social organisation (sensu Kappeler and van Schaik, 2002). Male-male and male-female social relationships are differentiated, in that individuals have preferred social partners (Goffe et al., 2016; Patzelt et al., 2014) and population genetics studies indicate patterns of female

biased dispersal (Kopp et al., 2014, 2015). As has been found in hamadryas baboons, Guinea baboon males have not been shown to have a clear dominance hierarchy (Kalbitzer et al., 2015). There is also little evidence to date that males compete directly for copulations with receptive females. Rather, copulations rarely occur outside of the established social relationships within a unit (Goffe et al., 2016). Multiple units come together to forage, sleep and travel together 70-100% of the time and form parties (Goffe et al., 2016; Patzelt et al., 2014) and two or more parties associating 12% of the time or greater as in the same gang (Patzelt et al., 2014). As nonkin social relationships have been shown to influence food sharing patterns in a variety of species (Cantarero et al., 2014; Carter and Wilkinson, 2013; De Waal, 1997; Marlowe, 2003) we expected to find a similar pattern in Guinea baboons.

Methods

We collected observational data on wild Guinea baboons living around the Centre de Recherche de Primatologie Simenti, in the Niokolo-Koba National Park, Senegal from January 2012-August 2012 and December 2012-June 2013. The focal gang consisted of 80 individuals in three parties (party four, party nine and party 10) which separated into seven to eight units (Goffe et al., 2016). A single observer (ASG) recorded all behavioural observations on electronic forms created using Pendragon 5.1.2 software (Pendragon Software Corporation, USA) and run on HP Tungsten E2 handhelds (Hewlett-Packard Company, USA). Oestrous state was recorded daily based on colour and structural changes in the anogenital area and pericallosal skin: lactating (L), pregnant (P) and cycling (C0=detumescent; C1=small tumescence; C2=medium tumescence; C3=large tumescence; Goffe et al., in press). Social interactions and close spatial proximity (two metres) were used to identify unit members (Goffe et al., 2016). Therefore grooming, greeting, and copulation data were summarised daily from ad libitum and focal data protocols (Altmann, 1974) and primary males, were identified for each female (Goffe et al., 2016). Networks, generated from intersexual associations were created in R version 2.15.1 (R Core Team, 2014) using the igraph package (Csárdi and Nepusz, 2006) with the Fruchterman-Reingold layout (Fruchterman and Reingold, 1991).

Prey capture and meat eating events were observed opportunistically and when possible a distance of at least seven metres was maintained in order to not strongly influence foraging behaviours and group dynamics. Carcass weight was estimated based on juvenile

and adult bodyweights (Skinner and Chimimba, 2005) and the amount an individual obtained was estimated based on the percentage of the original carcass that remained. The volume of meat consumed was not easy to quantify, as the exact size of bites may have been obscured by vegetation or other group members; additionally, the amount of time in possession of a food item may not adequately reflect time spent feeding or the amount consumed. Therefore, where possible, the amount of meat transferred was estimated based on five-by-five cm tissue = 50 g (Gomes and Boesch, 2009).

Meat sharing was characterised as the tolerated transfer of a defensible item by food motivated individuals (Feistner and McGrew, 1989); we assumed that this was the case whenever meat transfer occurred in the absence of aggression and submission by either individual. “Hunters” were identified as individuals who chased and killed prey and were the first to possess the carcass. In addition to capturing the prey, an individual may have obtained a carcass through theft, aggressive acquisition, or scavenging, the acquisition of meat after it had been left behind (greater than two metres) by the possessor. Passive sharing occurred when meat was taken by the receiver while both the receiver and the possessor were within close proximity to each other (zero to two metres) without the pair engaging in aggression or supplanting. Supplants took place when an individual moved into the feeding position recently vacated by the possessor as a direct result of the approach. Other behavioural definitions can be found in Table 1. In order to determine if female reproductive state or unit membership influenced the occurrence of meat sharing two-tailed Fisher exact tests were performed using the function *fisher.test* in the R stats package (R Core Team, 2014).

Guinea baboons are considered near threatened by the IUCN (Oates et al., 2008). Our research was performed with the approval of Senegalese agencies and in compliance with their legal guidelines (research permit numbers: 0383/24/03/2009; 0373/10/3/2012). In addition, all research was conducted within the regulations given by the animal care committee at the German Primate Center (Göttingen, Germany), as well as the principles and guidelines for the ethical treatment of nonhuman primates set down by the International Primatological Society.

Results

Prey capture by Guinea baboons involved individual males opportunistically stalking and chasing prey. However, dense vegetation made it impossible to determine precisely how

prey were located or the distance over which chases occurred. On four separate occasions, a male was observed to chase potential prey within five metres of other individuals within the group and although other baboons looked and adjusted their body position towards the predatory activity coordinated group effort to acquire prey was not observed. Prey species were primarily the young of antelope (*Tragelaphus scriptus* and unidentified species; nine of 12 capture attempts), as well as a hare (*Lepus microtis*; one of 12 attempts) and birds (unidentified species; two of 12 attempts). Mammalian prey were estimated to weigh approximately two kg (hare) and from 10 to 14 kg (antelope). During fourteen months of observation seven of 18 adult and subadult males in the study gang were observed attempting to capture prey; five of these males were successful hunters. Within that select group, capture success was highly skewed towards a particular male who captured four antelope. Four attempts to kill two birds and two antelope were unsuccessful (Table 2).

Hunters were the first possessors of the carcass and either retained the carcass (seven captures) or lost it through male-male theft (one capture). The antelope carcasses were never consumed entirely by the hunter, but rather accessed secondarily by females through scavenging (four of seven) and sharing (four of seven), or by males through scavenging (two of seven) and theft (one of seven; Table 1). Overt aggression (e.g. chasing or biting) was not observed. During carcass consumption by a male, only females with whom he had an intimate social relationship were tolerated in close proximity to him and such individuals were often able to acquire meat without being threatened or attacked by him. All females in close proximity were OMU members. Intersexual meat sharing occurred on nine occasions within four dyads. Immature individuals also approached male possessors, although we do not have detailed focal data from immature individuals, ad libitum data indicate that infants and juveniles who regularly maintained close proximity to or groomed with the adult members of an OMU were the same who approached and maintained proximity to the OMU male during meat consumption. A male only approached a male possessor during one meat consumption event; repeated approach-retreat interactions, categorised as supplants, over the course of 10 minutes resulted in the eventual theft of the carcass. However, tolerated meat sharing was not observed between this male-male dyad and this was the only case of carcass theft observed during the study period (Table 2, Figure 1b).

Although females were not observed to capture prey they did manage to acquire substantial portions of the carcass, in some cases consuming an estimated 10-40% of the original carcass (Table 2). On five occasions, passive meat sharing was observed between

primary males and associated females (Figure 1a-e). These adult and subadult females were allowed to approach, maintain close proximity (zero to two metres) and feed on scraps while the male was feeding and also acquired the carcass when he was apparently satiated (Figure 2). On all occasions females were demonstrably affiliative: grunting, lip smacking, grooming and contact sitting with the feeding male while the male showed no signs of resistance. Females exclusively approached their own primary males. In seven of eight cases when a kill occurred, there was at least one oestrus female in the study gang. Females in various reproductive states were observed to eat meat, and oestrus state appeared to have no influence on the occurrence of meat sharing (Fisher's exact test: $P=0.55$; Table 3). However, males did preferentially share meat with females within their units ($P<0.001$; Table 3). Due to the small sample size it was not possible to assess whether female reproductive state influenced the likelihood of sharing occurring preferentially within the OMU. Although the exact duration of female tenure cannot be calculated due to the short-term nature of this study, female unit tenure at the time of sharing varied from four months to over two years.

Once a female became the possessor of a carcass she was not harassed or aggressed by other individuals, although other males were in the vicinity. Females retained carcasses until they were apparently satiated or dropped the carcass during the course of the group's daily foraging march. Any male which subsequently gained access to a carcass after a female had left acquired the carcass through scavenging (one case), rather than through aggression or theft.

Conclusions

Our field observations of Guinea baboons support the idea that existing non-kin social relationships influence food sharing patterns (Cantarero et al., 2014; Carter and Wilkinson, 2013; De Waal, 1997; Marlowe, 2003). As only males were observed to capture prey, females had no immediate access to meat, but acquired portions of the carcass via passive sharing by their primary male, with whom they had a pre-existing relationship. Meat sharing was not dependent on female sexual receptivity as males shared with cycling, lactating and pregnant females at rates comparable to what would be expected given the amount of time females spend in oestrus and anoestrus stages. Notably, although males show spatial tolerance with each other, they do not hunt cooperatively and meat sharing between males appears to occur rarely (Klapproth, personal communication; personal observation).

Individuals may vary in their tendencies to actively participate in hunting or to “free ride” on the motivations of others (Gilby et al., 2008). In our study, hunting proclivity was skewed as one primary male was captured most of the prey; this same individual was also able to steal a carcass from another adult male. With this small sample size, it is difficult to identify the predictors of hunting proclivity. Given that Guinea baboon males do not have a distinct linear dominance hierarchy, as has been reported in savannah baboon species (Kalbitzer et al., 2015), it seems unlikely that social dominance would be a crucial factor in determining hunting tendency.

We found no support for direct reciprocity in the short or long term, as females were not observed to capture prey and the direction of sharing occurred only from males to females. Meat was also not exchanged directly for copulations, as sharing occurred with anoestrus as well as oestrus females, as long as they were members of the male’s unit. The lack of direct reciprocity in this study does not rule out that there may be a long term service exchange (e.g. Gomes and Boesch, 2009) within unit relationships, nor that “proficient” male hunters may in the long term have increased access to females. Males may also receive direct reproductive benefits through provisioning females during times of nutritional need, as has been suggested for the Hadza (*Homo sapiens*) of Tanzania, where husbands provision their wives during the early party of lactation (Marlowe, 2003). The small quantities Guinea baboon females apparently obtain through sharing may not qualify as substantial “provisioning” by their primary males, but they did obtain much larger quantities through scavenging from their primary males. A full analysis of nutritional intake will be necessary to determine the benefits of meat sharing and scavenging for females.

In chimpanzees, sharing is also influenced by the extent to which the possessor is being harassed (Gilby, 2006). Although we are unable to test the sharing-under-pressure hypothesis here, neither overt aggression nor demanding gestures/vocalisations were observed in Guinea baboon females. Guinea baboon males show strong male biased sexual size dimorphism (Boese, 1973; Patzelt, 2013), as is also the case for chimpanzees (Leigh and Shea, 1995). In addition, behavioural data indicate that, although aggression rates are low (Goffe et al., 2016; Kalbitzer et al., 2015), males are dominant over females, with 80.6% of agonistic bouts involving primary males behaving aggressively towards their females (Goffe unpublished data). Females are also eating from portions of the carcass, which have already been picked over by their primary male. Therefore it is unlikely that intersexual meat sharing occurs as a result of female harassment of males, but rather as a direct result of the high

tolerance exhibited by bonded individuals. Our previous work indicates that females appear to have a higher degree of spatial freedom and experience relatively low levels of aggression from their primary males in spite of close intersexual proximity maintenance predominantly being male driven (Goffe et al., 2016). Therefore, males may benefit by tolerating or promoting the close proximity of their females, rather than engaging in potentially counterproductive behaviour that would result in increasing intersexual distances.

The coevolution of intersexual food sharing and the opportunity for females to exhibit mate choice in primates (Jaeggi and van Schaik, 2011) implies that sharing may be preferentially promoted between intersexual bond partners. It appears that females' access to vertebrate meat may largely depend on their primary males' ability to capture prey and tendencies to share. Yet, although here we focus on meat sharing, it is likely that primary males are tolerant of their females in a variety of feeding contexts. If this is the case, then females may be used to being within close proximity of their primary males while feeding and may gain nutritional benefits by doing so. By taking food females may test the male's tendency towards tolerance (van Noordwijk and van Schaik, 2009), thus food sharing tendencies would be indicative of some other valuable male quality (Jones and Ratterman, 2009). As such, males who do not tolerate and share with their females may risk losing social and sexual partners (Jaeggi and van Schaik, 2011) and males may therefore receive a long term benefit for tolerating their females and sharing with them during food consumption events. On the other hand, females may simply benefit from gaining increased access to food (Strum, 1981), which might result in reproductive benefits during times of nutritional need (Cantarero et al., 2014; Marlowe, 2003). However, these two hypotheses are not mutually exclusive. Guinea baboon males may be able to (unintentionally) buffer costs associated with female-female competition or seasonal shifts in food availability through sharing with their females while avoiding costs associated with overt aggression or rebuffing females (Jaeggi and van Schaik, 2011).

Neuro-endocrinological mechanisms play a role in bond formation and maintenance in a variety of species (Young and Wang, 2004) and may also facilitate cooperative activities and food sharing (Wittig et al., 2014). Whether passive meat sharing in Guinea baboons results in hormonal reinforcement of existing social relationships and serves to facilitate intersexual relationship maintenance in the absence of persistent physical proximity remains to be investigated. Depending on the specifics of a species' social system, males may employ different mating strategies. Under certain circumstances (e.g. short tenure length), male

contest competition may be the best strategy, while in other systems, it may be more beneficial for males to “beguile” females through investment in strong affiliative relationships. Taken together, the presence and form of food sharing behaviours in wild populations can offer additional insights into the social and reproductive strategies of group living primates.

Author Contributions

A. S. Goffe and J. Fischer designed the study and wrote the manuscript. A. S. Goffe collected the data in the field and conducted the analyses.

Acknowledgements

We would like to thank the *Direction des Parcs Nationaux* and *Ministère de l’Environnement et de la Protection de la Nature de la République du Sénégal* for permission to work, as well as the conservateur, Mamadou Sidibé, and the park agents of the *Centre de Recherche de Primatologie, Simenti*, Cheikh Sané, Moustapha Faye, Armél Louis Nyafouna. Dietmar Zinner and Cédric Girard-Buttoz provided helpful comments and opportunities for discussion. In addition, the authors gratefully acknowledge the suggestions from Jo Setchell and two anonymous reviewers whose comments greatly improved an earlier version of this manuscript.

Reviewed by: two anonymous referees

Table 1. Terminology of meat sharing and whether or not they were observed to occur between male-male and male-female dyads.

Observed behaviours	Definition	Male	Female
Attempted transfer	An individual attempts to take a portion of a food item from the possessor.	y	y
Supplant	An individual moves into the feeding position vacated by another individual.	y	n
Resist	An individual attempts to prevent transfer by moving or turning away, or by vocal or physical aggression or threat.	y	n
Scavenge	The acquisition of meat after it has been left behind (>2 m) by the possessor.	y	y
Steal	The food transfer occurs despite resistance by the possessor.	y	n
Transfer	Part or the entire food item changes from the possessor to the receiver while both are within close proximity to each other (0-2 m).	n	y

Table 2. Events of male hunting, intersexual meat sharing and scavenging episodes within Guinea baboon one male units.

Event	Prey	Hunter	Estimated carcass weight (kg)	Thief	Sharing episode				Scavenging episode		
					Possessor (male)	Receiver (female)	FRS	Consumed (g)	Carcass retained by	weight (kg)	Consumed (kg)
1	antelope (sp. indet)	OSM	10		OSM	JLA	L	300	JLA	5	4
					OSM	KTA	L	100			
2*	antelope (sp. indet)	NDR	n/a								
3	hare (<i>Lepus microtis</i>)	WLM	2								
4*	bird (sp. indet)	AND	n/a								
5	antelope (<i>Tragelaphus scriptus</i>)	NDR	12	OSM	OSM	JLA	S1	100	JLA	2	1
					OSM	KTA	P	50			
6	antelope (sp. indet)	OSM	10		OSM	JLA	P	nr	JLA	4	2
					OSM	KTA	P	nr			
7	antelope (<i>T. scriptus</i>)	OSM	10								

8	antelope (<i>T. scriptus</i>)	SNE	14		SNE	HLN	P	100	HLN	6	3.5
9	antelope (sp. indet)	BAA	12		SNE	HLN	P	50	SNE	5	~1
									HLN	4	~1
					DTM	RXN	S0	50	DTM	2	~0.5
10*	bird (sp. indet)	young adult male	n/a								
11	antelope (sp. indet)	OSM	10								
12*	antelope (sp. indet)	NDR	n/a								

FRS=female reproductive state

* unsuccessful hunt/prey not captured

n/a=not applicable

nr=no record

Table 3. Fisher exact test of the difference between the observed and expected values for the hypotheses that meat sharing occurs preferentially based on social relationships or female reproductive state.

Hypothesis	Expected frequency	Observed frequency (%)
Presence of social bond		
Within OMU	0.633	9 (100%)
Between OMU	8.367	0 (0%)
Female reproductive state		
Lactating	3.656	2 (22.2%)
Pregnant	3.656	6 (66.7%)
C0	0.563	0
C1	0.563	1 (11.1%)
C2	0.281	0
C3	0.281	0

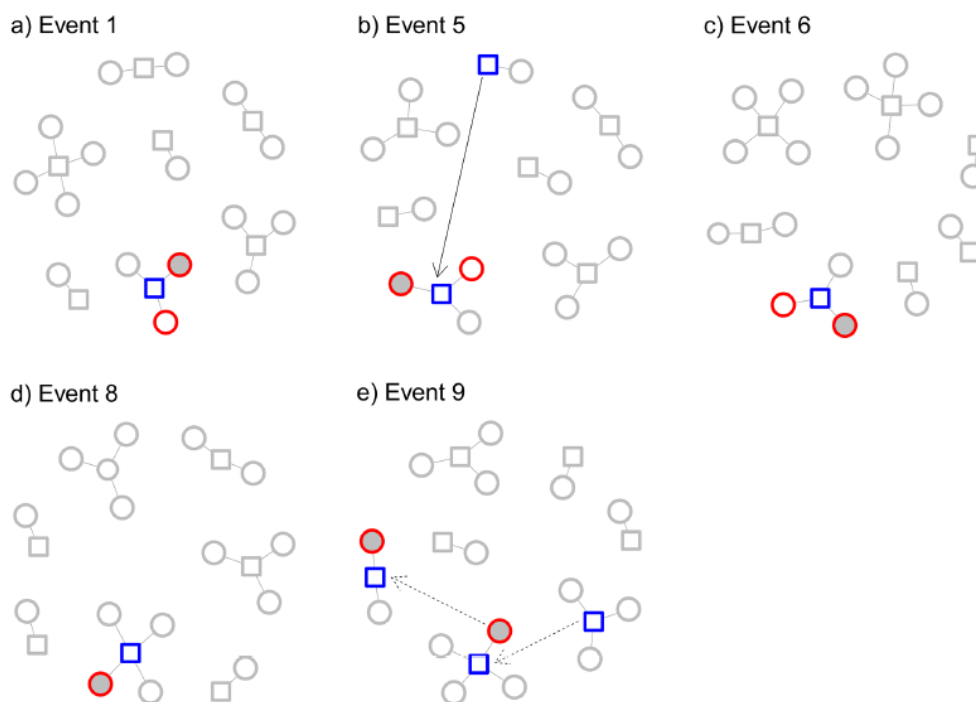


Figure 1. Five schematics of the movement of meat between and within one male units. Node shape denotes sex (females= \circ , males= \square), colour indicates meat consumption (nonmeat eaters= grey , male meat eaters= blue ; female meat eaters= red). The arrows show the movement of meat from one unit to another with the solid arrow showing the theft of a

carcass while the dashed arrows show the acquisition of meat by males through scavenging. Filled circles indicate females who also obtained meat via scavenging. Note that unit composition varied between the five events and that the secondary males have been excluded as no transfers occurred between primary and secondary males during the study period.



Figure 2. (a) Male-female meat sharing and (b) Female eating meat.

CHAPTER 4: Weak Forces: determinants and consequences of female-female relationships in Guinea baboons

A. S. Goffe^{1, 2}, Holger Sennhenn-Reulen^{1, 2}, Michael Heistermann³ & J. Fischer^{1, 2}

{1 Cognitive Ethology Laboratory, German Primate Center, Göttingen, Germany}

{2 Leibniz ScienceCampus Primate Cognition, Göttingen, Germany}

{3 Endocrinology Laboratory, German Primate Center, Göttingen, Germany}

Abstract

In social species, the maintenance of reliable affiliative relationships is important to long-term health and reproductive success. In societies with female philopatry and male dispersal, kinship is the most important determinant of female-female social relationships. Comparatively little is known about the determinants and consequences of female-female relationships in female dispersing species, however. Here, we used behavioural and genetic data to investigate the variables which influence spatial proximity and social behaviour among wild female Guinea baboons, *Papio papio*, a female-dispersing species living in a multilevel social system, with one-male-units (OMUs) at the base of the society. Additionally, we tested whether association patterns and aggression influenced physiological stress levels. To account for changes in association patterns in this relatively fluid system, we used dynamic indices including Elo rating. Females were mostly found in the proximity of and engaged socially with other females of their OMU. Although female kin were present within the same social group (“gang”), kinship only had a small effect on affiliation index scores but influenced spatial index scores. Remarkably, the presence of lactating females had only a marginal effect on female-female association. Aggression mostly occurred between females of the same unit but was not affected by relatedness or lactation status. We found no evidence that OMU size or rank influenced faecal glucocorticoid levels. Female relationship patterns in this species differ remarkably from female-bonded congeners and suggest that the determinants of reproductive success vary substantially with social organisation.

Key words: female social choice, Guinea baboon, glucocorticoid metabolites, kinship, multilevel society, one male unit

Introduction

Competition for access to environmental resources and mates is one of the chief costs of sociality (Greenwood, 1980) and is of particular importance to mammalian females (Clutton-Brock and Huchard, 2013). Group living species have managed to balance out the costs of sociality with the benefits. Indirect benefits may result from group membership or collaborative behaviours, such as territorial defence and decreased predation pressure (Isbell and Young, 2002; Rubenstein, 1978; Sterck et al., 1997).

Individuals receive direct benefits from the social support derived from maintaining relationships with others within their social groups. Highly affiliative, equitable and long-term social bonds have been shown to benefit individuals via stress reduction (e.g. chacma baboon, *Papio ursinus*: Wittig et al., 2008), coalitionary support (e.g. chimpanzee, *Pan troglodytes schweinfurthii*: Gilby et al., 2013) and third-party mediated reconciliation (e.g. chacma baboon: Wittig et al., 2007). The maintenance of strong bonds may enhance longevity (e.g. chacma baboon: Silk et al., 2010), infant survival (e.g. yellow baboon, *Papio cynocephalus*: Silk et al., 2003a; chacma baboon: Silk et al., 2009) and reproductive success (e.g. bottlenosed dolphin, *Tursiops aduncus*: Wiszniewski et al., 2012; chimpanzee: Gilby et al., 2013; gelada, *Theropithecus gelada*: Snyder-Mackler et al., 2012; hamadryas baboon, *Papio hamadryas*: Chowdhury et al., 2015; horse, *Equus caballus*: Cameron et al., 2009; lion: Packer et al., 2001).

Female dispersal, is rare in mammals and only a handful of species show this pattern (Dobson, 1982; Greenwood, 1980; Pusey, 1987). Therefore, much of the mammalian evidence supporting the trade-offs of maintaining strong bonds comes from female-bonded species. We know much less about the life-history determinants and reproductive success in dispersing females. Emigrants face challenges whether dispersal is social, locational or both (Isbell and Van Vuren, 1996). The age when individuals disperse is linked to a species' mating system (Dobson, 1982) and affects the social relationships of females (Clutton-Brock and Lukas, 2012). Females are driven to disperse for the purpose of incest avoidance if male tenure is longer than it takes females to reach sexual maturity (Clutton-Brock and Lukas, 2012; Lukas and Clutton-Brock, 2011), but the mechanism behind female dispersal in mammals varies. Females may disperse voluntarily (e.g. bonobo, *Pan paniscus*: Sakamaki et al., 2015; horse (Monard and Duncan, 1996); muriqui, *Brachyteles arachnoides*: Strier and Ziegler, 2000) or via eviction (e.g. banded mongoose, *Mungos mungo*: Gilchrist, 2006; redfronted lemur, *Eulemur rufifrons*: Kappeler and Fichtel, 2012) or abduction (e.g. hamadryas baboon, *Papio hamadryas*: Swedell et al., 2011). Yet regardless of the mechanism of female dispersal,

female immigration results in a potential conflict of interest between resident females and immigrants. Immigrant females may suffer more aggression in their new groups than their natal groups (e.g. horse: Monard and Duncan, 1996) and residents are more aggressive towards new immigrants than towards other residents (e.g. mountain gorilla, *Gorilla gorilla beringei*: Watts, 1994. Kahlenberg and colleagues (2008b) found high degrees of intrasexual competition among female chimpanzees with immigrant females ranking lower and having higher stress levels than resident females. In such instances female kin are absent or rare and females appear to “make do” socially, either cultivating intrasexual tolerance or affiliation, as found in bonobos, (*Pan paniscus*) (Furuichi, 2011; Kano, 1992; Sakamaki et al., 2015), various bird species (Riehl, 2013), and mountain gorillas (Watts, 1994)). Alternatively females may maintain high levels of intrasexual intolerance and aggression (e.g. chimpanzee: Kahlenberg et al., 2008; banded mongoose: Gilchrist, 2006).

A number of variables have been found to drive the differentiation of social relationships among mammals. Genetic relatedness (or kinship) between individuals for example, may result in general patterns of kin-biased affiliation with a further influence on bond strength and quality (Silk et al., 2006a). Group membership has also been shown to drive differences in interaction rates, with individuals associating more within than outside of their social group (e.g. hamadryas baboon: Swedell, 2002; horse: Sigurjonsdottir et al., 2012).

Outside of kinship and group membership, natal attraction is also purported to be an important factor dictating social interactions in mammals. The presence of mothers with infants influences affiliation patterns across social primates with individuals being engaging in grooming and infant handling interactions with mothers (e.g. black-and-white colobous (*Colobus vellerosus*): Bădescu et al., 2015; bottlenosed dolphin: Mann and Smuts, 1998; chacma baboon: (Silk et al., 2003b); olive baboon (*Papio anubis*): Frank and Silk, 2009).

Females are particularly sensitive to life events which risk their social relationships and social position (Engh et al., 2006a, 2006b; Sapolsky, 2005). Glucocorticoids have served as a biometric measure for assessing the physiological response to stressors in primates (e.g. Engelhard et al., 2002; Hämäläinen et al., 2014; Ostner et al., 2008), allowing the assessment of small and large scale stressors. For example, high levels of competition may negatively influence glucocorticoids (Girard-Buttoz et al., 2014b; Young et al., 2014) and have long term effects on reproductive success and fitness (Clutton-Brock, 2009; Lloyd and Rasa, 1989; Silk, 2007; Stockley and Bro-Jørgensen, 2011), in turn influencing immune function (Archie, 2013).

Here, we test to what extent kinship, reproductive group membership and female reproductive state influence the strength of social relationships among female Guinea baboons. In addition, we assessed whether females are stressed by demographic and social conditions. Guinea baboons provide valuable comparative data as – in contrast to female bonded savanna baboons - they live in a nested multilevel system (Patzelt et al., 2014). Their mating system is polygyn-monandrous (Goffe et al., 2016). At the lowest social level, the reproductive units (or one male units (OMUs)) consist of a primary male with one to four adult females (Goffe et al., 2016). Multiple units form a party (Goffe et al., 2016) and multiple parties form a gang (Patzelt et al., 2014). Behavioural observations and population genetic studies indicate that the dispersal pattern is female-biased (Goffe et al., 2016; Kopp et al., 2014, 2015) with females dispersing across all social levels resulting in the changing composition of OMUs (Goffe et al., 2016). Female tenure may vary from a few weeks to 2 or more years (Goffe et al., 2016), which allows us to assess the effects of changes in unit composition on female relationships and physiological stress response.

Based on current theory, we have three predictions regarding females' close spatial associations and affiliative behaviour. First, we expect that if kin are present in the gang, relatedness will predict females' association patterns. In this instance, relatedness should be the main factor driving social relationships and may also interact with OMU membership. Secondly, we predict that females will associate preferentially within their reproductive units. Thirdly, we predict that lactation status will result in increased association patterns. As female competition has been shown to influence stress levels (Stockley and Bro-Jørgensen, 2011), we expect that group size will influence stress with females in larger OMUs exhibiting elevated glucocorticoids (Markham et al., 2015; Pride, 2005). Furthermore, we predict that, if females compete for rank within their units, lower ranking females will have elevated glucocorticoid concentrations in comparison to high ranking females.

Methods

Study subjects

Research took place at the Centre de Recherche de Primatologie (CRP) field station in the Parc National du Niokolo Koba, Senegal, from January 2012 to July 2013. The Guinea baboon population (>400 individuals) around the CRP field station consisted of 5-7 gangs. We observed all 16 adult female members of the Mare gang (120 dyads), which included 3 parties (party IDs 4, 9 and 10).

Observational Data

Behavioural and census data were collected as previously described (Goffe et al., 2016). As a part of the daily census a single observer, ASG, recorded the reproductive status for all focal females according to morphological changes to the anogenital area and paracallosal skin. Individual females were categorised as detumescent, tumescent, pregnant and lactating. Female dyads were then put into three categories based on whether neither (N=100), one (N=111) or both (N=83) females were lactating on the day of observation; the number of dyads in each category vary with the days over which females were observed in each reproductive state.

Focal observations of 30 minutes in duration were conducted for each female 1-3 times per week during morning (06-13.00 h) and afternoon sessions (15-18.30 h). Focal data (1,262 completed samples) were collected over the course of 256 study days from 16 adult females from April to August 2012 and December 2012 to June 2013. In addition, ad libitum data were also collected during 2,100 contact hours in order to document agonistic interactions, which may occur at low frequencies. We determined females' residency status with co-resident dyads (N=29) sharing the same primary male and non-resident dyads (N=113) containing females with different males based on spatial association and affiliation patterns from ad libitum and focal data (Goffe et al., 2016).

Focal protocols included recording the grooming, greeting, contact-sitting and infant handling behaviours (Altmann, 1974). The durations of grooming and contact-sitting bouts were recorded and, in the case of grooming, involved either bilateral or unilateral grooming. Contact sitting bouts were determined to end when one of the participants shifted far enough for body contact to cease. Greetings were recorded when at least one element of contact (e.g. ventral embrace, or sniffing, or mounting) occurred within an approach-retreat interaction. We recorded infant handling when one female manipulated the dependent infant while it was within maternal body contact. Due to their short duration, greetings and infant handling events were recorded as frequencies. A general overview of social affiliation rates may be found in Table 1. The occurrence of keck vocalisations, supplants and agonistic interactions were recorded during focal sampling and ad libitum. The production of a keck (Cheney et al., 1995), crouching, or a retreat were scored as submissive signals. Screams were produced by both winners and losers and were not included in our determination of the dominance hierarchy as they may be used for recruitment for coalitionary support from a third party (Silk et al., 2004). We also conducted four proximity scans at minute 0, 10 20 and 30 during

each focal protocol and recorded the identity of all adult females in contact (0 m), within 1-2 m and ≥ 2 -5 m of the focal female; 5,048 proximity scans were performed. In relation to the focal female, 12.8%, 3.2%, 17.0% and 12.8% of scans contained at least one female in contact, 1 m, 2 m and 5 m, respectively.

Table 1. An overview of behaviours and proximities included in index calculations.

Behavioural category	Type	Rate (hourly)	Mean (min)	Minimum (min)	Maximum (min)
Groom	duration (min)	1.38	2.04	0.05	10.8
Contact sit	duration (min)	0.85	1.43	0.02	26.55
Greet	event	0.26	n/a	n/a	n/a
Infant handle	event	1.6	n/a	n/a	n/a

Microsatellite Genotyping & Relatedness Analysis

Faecal samples from 15 individually identified females were collected for microsatellite analysis. Collection occurred immediately after defecation and storage of faecal samples followed an established two-step protocol using ethanol and silica beads (Nsubuga et al., 2004; Roeder et al., 2004). As one female disappeared from the study group prior to faecal sample collection it was necessary to use a tissue sample collected previously; tissue sample collection and extraction followed the protocol described by Patzelt and colleagues (2014). At the end of the study period samples were shipped to the German Primate Center in Germany, where they were then stored at -20 C until extraction and analysis.

We isolated genomic DNA from 16 females and tested 25 polymorphic autosomal microsatellite markers used to characterise genetic variation in Guinea baboons (Patzelt et al., 2014). In brief, we extracted DNA from faecal samples using the QIAamp DNA Stool Mini Kit (Qiagen, Germany) and from tissue samples using the DNEasy Blood and Tissue Kit (Qiagen) as specified by the manufacturer's protocols. Extraction, polymerase chain reactions and sequencing were performed in separate rooms and monitored with negative controls in order to avoid contamination. PCR reactions were conducted using the Qiagen Multiplex PCR Kit using 24-48 ng of DNA. The amount of primer used varied as did the cycle conditions (Patzelt et al., 2014). Following capillary gel electrophoresis on an ABI 3130xL Genetic Analyzer (Applied Biosystems®, USA), microsatellite allele sizes were evaluated in comparison with the GeneScan™ -400HD size standard using Peak Scanner™

2 (Applied Biosystems®). We performed from 6-7 independent amplifications for each locus; homozygous alleles were identified in at least four interactions and heterozygous alleles were identified in at least two independent PCR reactions. When possible, we repeated the genotyping with the analysis of a second independently collected faecal or tissue sample.

All 25 markers were polymorphic with an average number of four alleles (range=2-8). We calculated the inbreeding coefficient (F_{is} ; following (Nei, 1987)) in the R-package *hierfstat* (Goudet and Jombar, 2015). We assessed the expected and observed heterozygosity, the extent of deviations from Hardy-Weinberg equilibrium, using the χ^2 test, and the presence of null alleles in *PopGenReport* (Gruber and Adamack, 2014). In order to test the extent of linkage disequilibrium (i.e. whether there is a non-random association of alleles at different loci) we used the T_2 test (Schaid, 2004) offered by the R-package *pegas* (Paradis, 2010). The number of alleles at each locus ranged from 2 to 8. The majority of autosomal loci (22 of 25) were found to be in Hardy-Weinberg equilibrium (HWE). Linkage disequilibrium results indicate that there is no link between observed alleles from different loci and that alleles combine freely ($T_2=4.85$, $df=4$, $P=0.30$). We found no evidence for the presence of null alleles. Additional details concerning the 25 autosomal alleles included in this study are provided in the supplementary information (Table S1).

Different relatedness estimators may vary due to the allele frequency distributions in a given dataset (Blouin, 2003). Therefore, dyadic relatedness coefficients were calculated using five non-likelihood (moment) estimators (Li et al., 1993; Lynch and Ritland, 1999; Queller and Goodnight, 1989; Ritland, 1996; Wang, 2002) and two likelihood estimators (Milligan, 2003; Wang, 2007) and subsequently compared using the R-package *related* (Pew et al., 2015). We estimated the genotyping error rate per locus to be 0.01 in order to account for the influence of undetectable genotyping errors which may be strongly influential in the number of locus polymorphisms detected (Hoffman and Amos, 2005). For the 3 loci found not to be in HWE we used a genotyping error rate of 0.03 (Schneider, 2016). We performed simulations containing datasets of 100 pairs of four relatedness categories (full sibling, half sibling, parent-offspring and unrelated) and then compared the observed and expected relatedness values using Spearman's correlation. The triadic likelihood estimator (Wang, 2007) performed best in these tests and was utilised in subsequent analyses. This method produced relatedness estimates which were highly skewed and ranged from 0 to 0.78 (median=0; Figure S1).

Misclassification of dyads based on relatedness estimates have been documented in a number of species (e.g. Blouin et al., 1996; Städele et al., 2016). This is most likely to occur by the assignment of dyads into strict categories based on values which could be strongly influenced by the extent of inbreeding or genotyping error. Rather than to risk assigning dyads incorrectly we conservatively grouped dyads into three categories broadly based on the estimated probability of altruistic acts (Chapais et al., 2001). Dyads with a relatedness estimate of ≥ 0.125 were considered to be related (N=17) and dyads with relatedness estimates of 0 were considered to be unrelated (N=64). Dyads with relatedness estimates between 0 and 0.125 may be misclassified and were thus placed in the “unclassified” category (N=39). All females were included in each category at least once.

Hormonal Analysis

From January to June 2013, faecal samples were collected every 1-2 weeks from 15 females. Hormone metabolites were extracted in the field using the method described and validated by Shutt et al. (2012), which has been used successfully in other studies (e.g. Hämäläinen et al., 2014; Rimbach et al., 2013), including a study on Guinea baboons (Kalbitzer et al., 2015). Sample extracts were shipped to Germany within 6 months of collection, where they were immediately stored at -20 C until analysis. We analysed fGC metabolite levels in 185 samples collected from January to April 2013 using an enzyme immunoassay for the measurement of immunoreactive 11-oxoetiocholanolone, a group-specific measurement of 5 β -reduced cortisol metabolites with a 3 α ,11-oxo structure (Möstl et al., 2002). The assay has been proven to detect changes in adrenocortical activity reliably in various mammal species (Ganswindt et al., 2003; Heistermann et al., 2006; Möstl et al., 2002) and has also been validated for Guinea baboons (see supplementary information). The assay was carried out on microtiter plates according to the procedures described in Heistermann et al. (2006). Sensitivity of the assay at 90% binding was 3 pg. Intra- and interassay coefficients of variation of high- and low-value quality controls were 4.0% (n=16) and 6.8% (n=11) (high), and 4.4% (n=16) and 8.9% (n=11) (low), respectively.

Behavioural Analysis: dynamic index measures

Matrix based ranking includes the inherent assumption that the relationships among individuals are transitive, datasets with missing interactions for dyads may appear to be linear

by chance (Appleby, 1983). This may cause particular challenges for populations/groups with low interaction rates, or in relationships that are random (Appleby, 1983). Therefore it is not statistically possible to have a linear hierarchy in a group of less than six individuals (Appleby, 1983) using matrix based methods. As OMUs in Guinea baboons typically consist of 1-4 females, we chose to analyse female rank relationships, affiliative interactions and proximity distances using two approaches more appropriate for both small numbers of individuals, as well as fluid social groups that experience high levels of demographic change. To assess the temporal variations in female-female relationships, we used the recently developed index for allowing the assessment of temporal variation in social relationships without a priori assumptions (Kulik and Mundry, in prep). In contradiction to static, matrix based calculations, this method generates an index which is updated following each dyadic interaction. We calculated a dynamic affiliation index (DAI) which included all affiliative social interactions relevant to females regardless of their oestrous stage. These affiliative behaviours included grooming (duration), contact sitting (duration) and greeting (event) and infant handling (event) and their inclusion was determined based on correlations conducted during a stable period. All dyads began at a neutral starting value of 0.5, with each affiliative interaction resulting in an increase in the DAI value for each dyad and a corresponding decrease in the value of all connected dyads:

$$gain_{ijk} = (GF - GF \cdot DAI_{ij\ k-1}) \cdot W_k$$

$$loss_{ijk} = 1 - \frac{gain_{ijk}}{n_{ijk} - 2}$$

where gain factor (GF) indicates the assumed importance of an interaction between individuals i and j on the social structure, and weight (W) indicates the standardised weight for the k^{th} behaviour. The gain is then used to calculate the loss, where n represents the number of possible interaction partners. For all dyads containing one of the interaction partners the loss is applied by multiplying their DAI scores by the loss. The values of this index range from 0 to 1, with higher values indicating dyads with higher degrees of affiliation. Additional details regarding this method are presented in the supplementary information.

Guinea baboons show high levels of spatial tolerance between female-male (Goffe et al., 2016) and male-male dyads (Kalbitzer et al., 2015; Patzelt et al., 2014), with individuals of different OMUs often sitting within 5 m of each other (Goffe et al., 2016). Therefore, we chose to assess spatial parameters separately from affiliative interactions. A dynamic

proximity index (DPI) using weighted proximity scans was calculated in order to assess the temporal variation in female-female spatial relationships. For each focal observation the proportion of scans in which a dyad was 0 to 1 metres were assigned a value of 2, scans in which a dyad was >1 to 2 metres were assigned a value of 0.667 and from >2 to 5 metres were assigned a value of 0.286 (after (Smuts, 1985), page 270-271). The DPI was calculated using the method developed by Kulik and Mundry (in prep).

Elo scores are used to assess dominance hierarchies in datasets with variable group size and containing unknown relationships (Albers and de Vries, 2001; Neumann et al., 2011). We calculated Elo scores to assess factors influencing temporal variability in female dominance ranks. To accomplish this, we included agonistic interactions observed during focal observations and ad libitum where the outcome was not determined by the interference of third parties and thus allowed for a clear distinction between the winners and loser of a given dyad (N=458). We calculated Elo scores using the R-package *EloRating* (Neumann and Kulik, 2015). All individuals were given the starting value of 1000 and a scoring constant (k) of 100. Elo scores were extrapolated so that values were generated for all study days regardless of whether a dyad was observed to interact.

Statistical models

As affiliation and proximity may not necessarily measure the same phenomena (Goffe et al., 2016), we chose to analyse DAI and DPI scores separately using the same model structure. To investigate which variables influenced the temporal variation in DAI and DPI scores for each dyad we ran linear mixed-effect models (LMMs) in the R-package *lme4* (Bates et al., 2013) using a log-transformed response, assumed to have a Gaussian distribution. In these models, relatedness, residency and lactation status were included as fixed factors, with a random intercept and slope for categorical day (representing the two study periods) and dyad. Our initial models included an interaction between relatedness and residency; however, this was removed from the model as it did not improve model fit. The residuals of one dyad are plausibly highly autocorrelated, therefore we conducted bootstrapping (Hastie et al., 2001) by blocks for dyad with 1000 replicates to generate unbiased confidence intervals for the fixed effects (Colquhoun, 2014; Halsey et al., 2015). We checked for the lack of correlation of covariates and the random intercepts, which is an assumption for mixed-effects models, by running a fixed effects model, as suggested by Clark and Linzer (2015). To check for the influence of heteroskedastic residuals we generalised additive models for location scale and shape (GAMLSS) in the R-package *gamlss* (Rigby and

Stasinopoulos, 2005). GAMLSS formulas were identical to those used in LMMs, with the addition that the fixed effects of categorical day with residency status were used as controls for heteroskedastic residuals. When the LMM and GAMLSS results were compared we found no relevant changes in the coefficients for the covariates and their respective confidence intervals, and therefore report the LMM results.

In a third model we used the occurrence of 453 dyadic agonistic events from which the outcome was clear to test whether residency patterns, relatedness or lactation status predict the occurrence (yes/no) of agonistic behaviour between females. To accomplish this we ran a generalised linear mixed model (GLMM) in R-package *lme4* (Bates et al., 2013) with dyad as random intercepts for grouping variable.

Lastly, we asked whether faecal glucocorticoid (fGC) metabolites are influenced by general aspects of female reproductive competition (i.e. number of females and female rank). To investigate whether harem size (the number of females in an OMU; range=1-4) or rank influenced fGC metabolite variation we ran a general additive mixed model (GAMM) in the R-package *gamm4* (Wood and Scheipl, 2014) using a log-transformed response for 185 fGC metabolite concentrations from 15 females. Due to the rarity of tumescent females in the various states of swelling we chose to combine tumescent females into one category and controlled for female reproductive state (Engh et al., 2006a; Weingrill et al., 2004; Wolff, 1993). We included a smoothing parameter for study day to consider the potential influence of seasonal variation in hormone secretion (Goymann, 2012; Polansky and Robbins, 2013). In order to account for the circadian rhythm of hormone secretion (Chung et al., 2011) we controlled for the time of day in which samples were collected by including the hour of collection as a random variable. Individual identity was taken into account by specifying random intercepts. We applied a 24 hour shift in the fGC metabolite data to allow for the time delay of hormone excretion in the faeces of baboons and other species (Heistermann et al., 2006; Möhle et al., 2002; Wasser et al., 2000, Heistermann unpublished data). Both the response and the Elo scores were z-transformed.

All statistical analyses were conducted in the R environment version 3.1.2 (R Core Team, 2014) and RStudio interface (RStudio, 2012). The use of P-values on their own is highly debated and, if used, should be reported alongside confidence intervals, which are comparable to P-values but not prone to the same statistical biases (Colquhoun, 2014; Wasserstein and Lazar, 2016). In addition, confidence intervals of 95% may not be substantially conservative (Colquhoun, 2014). Therefore, we report P-values and 99%

confidence intervals (where possible) for all regression models in an effort to make an appropriate assessment of whether or not the hypotheses are substantially supported. Autocorrelation has been shown to affect trends in data with temporal persistence (e.g. Schaubert et al., 2009; Yue et al., 2002) and may result in deflated effective degrees of freedom. Consequentially, for the DAI and DPI models, where index values are highly autocorrelated by definition, we report point estimates and nonparametric bootstrap percentile intervals (as defined by Efron and Tibshirani (1998)), as a replacement for confidence intervals. This adjustment takes into account autocorrelated observations, as reporting P-values unadjusted for autocorrelation would lead to specious conclusions.

Ethical Note

Our research was conducted with the approval and research permission of the Direction des Parcs Nationaux and the Ministère de l'Environnement et de la Protection de la Nature de la République du Sénégal (0383/24/03/2009; 0373/10/3/2012). This work adheres to the ASAB/ABS Guidelines for the Use of Animals in Research, the Guide to Ethical Information Required for Animal Behaviour Papers and the guidelines set by the ethics committee at the German Primate Center.

Results

Affiliation patterns

All 16 females affiliated directly or indirectly with each other and thus no dyad had a DAI score of 0. For the 120 dyads, DAI scores ranged from 0.29 to 0.98 (N=28,340, median=0.46; Figure S2). These scores were highly skewed with forty-six dyads (38%) in the third quartile (DAI scores ≥ 0.54 ; Figure S1), indicating that the majority of relationships were relatively weak. Twelve dyads, the top 10%, had DAI scores of 0.86 or greater.

We used these scores to assess whether relatedness, OMU residency or lactation status influenced affiliation patterns between female Guinea baboons. Inspection of the 99% confidence intervals from the LMM analysis revealed strong support for the hypothesis that residency status predicts DAI with DAI scores increasing 23.8% when female dyads changed from being non-resident to co-resident (Figure 1 & 2a). As the confidence intervals for the relatedness levels straddle the 0, we find only moderate support for the influence of relatedness on DAI scores with a potential 23.7% increase in DAI scores in unrelated vs.

related dyads (Figure 1 & 2a). No support was found for lactation status influencing DAI scores (Figures 1 & 2a). Medians and interquartile ranges (IQR) of the subgroups of categorical covariates are located in the supplementary information (Table S2). We then controlled for residency status to see if that would have an effect on the results and found no support for relatedness, but evidence that dyads containing one lactating female had higher DAI values than dyads containing two lactating females (Table 2).

Table 2. Results for the LMM predicting DAI scores, with residency as a control.

	Estimate	Lower limit	Upper limit
Intercept	-0.72	-0.86	-0.57
Unclassified	-0.05	-0.05	0.16
Related	0.09	-0.05	0.24
One lactating	0.01	0.00	0.02
Both lactating	-0.02	-0.03	-0.01

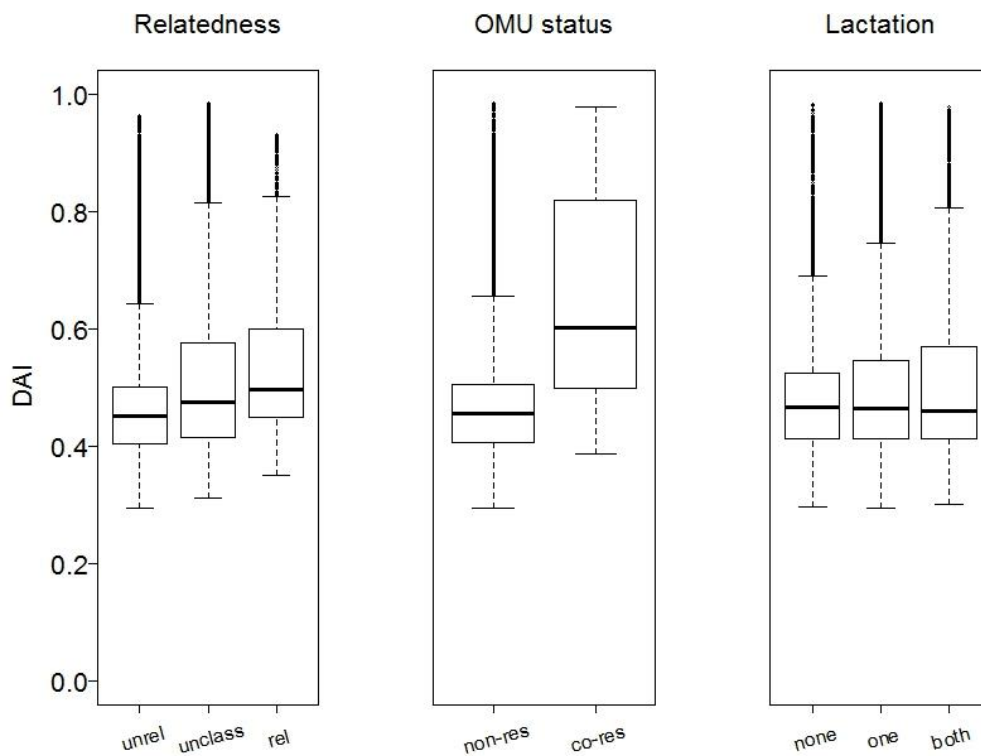
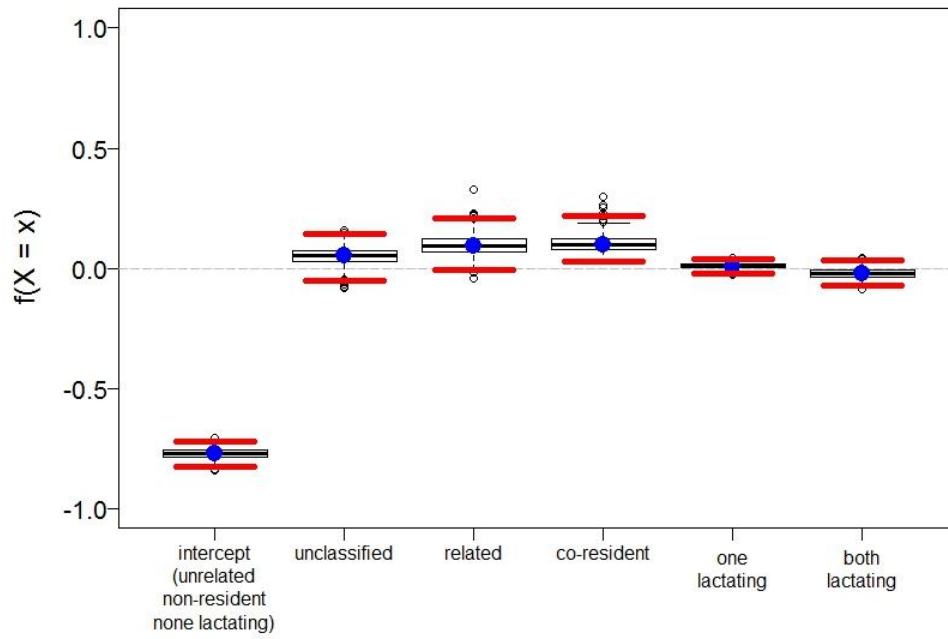


Figure 1. Tukey boxplots showing the relatedness, OMU status and lactation status of female dyads with weak to strong relationships based on daily dynamic affiliation index (DAI) scores. Subplots contain the categorical variables tested and the levels are specified on the x-axis; the levels for relatedness and OMU status are abbreviated: unrel=unrelated, unclass=unclassified, rel=related, non-res=non-resident, co-res=co-resident.

a)



b)

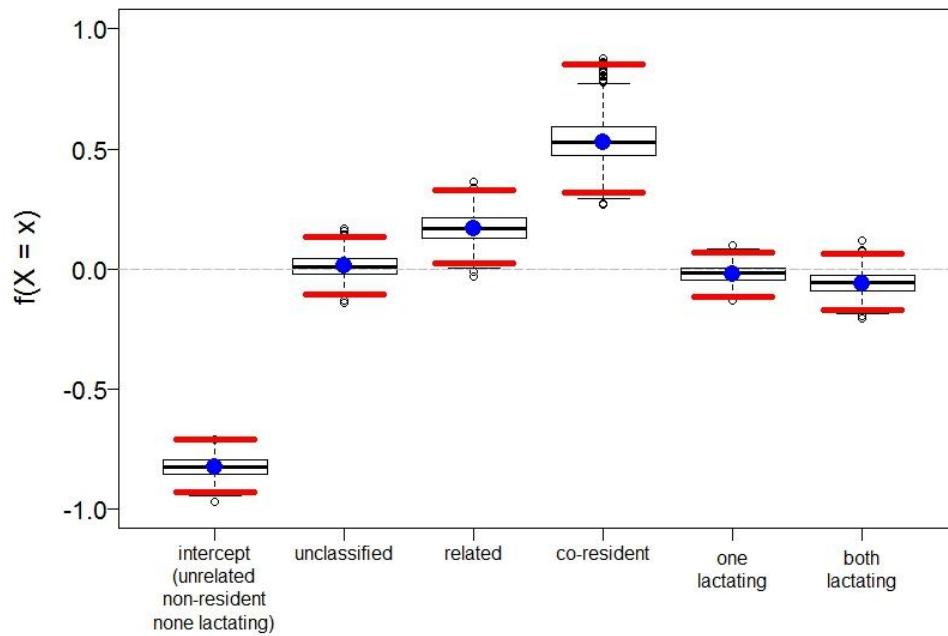


Figure 2. Results for the two models for which test which variable predict a) DAI and b) DPI scores. Tukey boxplots indicate the individual values as generated by 1000 bootstrap

replicates of the point estimates. The 99% bootstrap percentile intervals are indicated by the red horizontal bars. Coefficients for the models are designated by the filled blue circles.

Association patterns

DPI scores were also generated for the same dyads in order to determine if close spatial association is driven by the same predictors. Although not all 16 females were observed in close proximity with each other, no dyads received a score of 0 as all females were observed in close proximity to at least one other female (see methods). DPI scores ranged from 0.16 to 0.98 (N=28,340, median=0.44). These scores were highly skewed with forty-nine dyads (41%) in the third quartile (DPI scores ≥ 0.68), indicating that the majority of relationships were relatively weak. The top 10 % of dyads had DPI scores greater than 0.91.

LMM analysis of DPI scores revealed strong support for the hypothesis that residency status predicts DPI (Figures 2b & 3). P-values are not reported for the same reasons as mentioned above. Dyads which were co-resident had 38.5% higher DPI scores than dyads which were non-resident. The relatedness hypothesis was also strongly supported with related dyads having 27.0% higher DPI scores than unrelated dyads. Inspection of 99% confidence intervals did not reveal any support for the influence of lactation status (Figures 2b & 3). When we controlled for the effect of residency status on DPI scores we found no effect of lactation status and we lost the effect of relatedness.

Dyadic aggression

Ad libitum, 0.22 agonistic events per observation hour were observed between females during which there was no determinable third-party interference. Results from the GLMM showed that residency status predicted the probability of dyadic aggressive behaviour between females with co-resident dyads engaging in more aggression than non-resident dyads (estimate=2.36, standard error=0.18, z-value= 13.39, $P < 0.001$, 99% CI [1.91, 2.82]). No support was found for an influence of relatedness or lactation status on aggression rates.

Faecal glucocorticoid metabolites

From the beginning of January until the end of April 2016 we found a median faecal glucocorticoid concentration of 1578.0 ng/g (IQR=1196.0-1945.0); values varied widely for each female (Figure S3). Results from the GAMM indicated no support for the hypotheses that OMU size or female rank predicts fGC metabolite levels (Table 3).

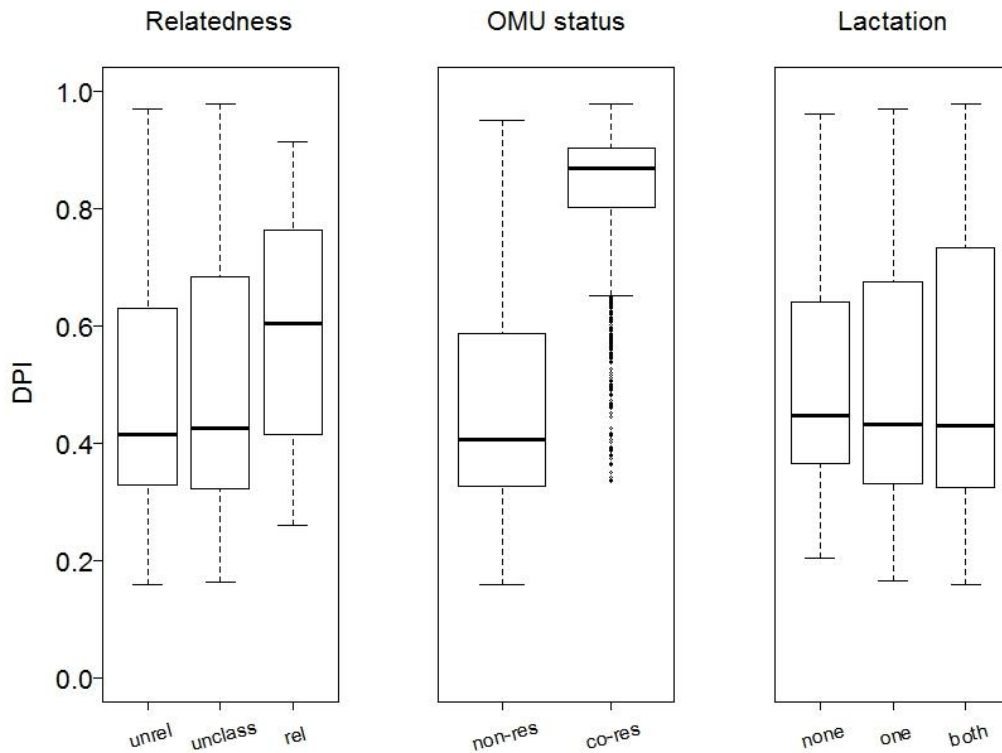


Figure 3. Boxplots showing the relatedness, OMU status and lactation status of female dyads with weak to strong relationships based on daily dynamic proximity index (DPI) scores. Subplots contain the categorical variables tested and the levels are specified on the x-axis; the levels for relatedness and OMU status are abbreviated: unrel=unrelated, unclass=unclassified, rel=related, non-res=non-resident, co-res=co-resident.

Table 3. Results for the GAMM predicting fGC metabolite concentration.

	Estimate	P-value	Lower limit	Upper limit
Harem size	0.04	0.57	-0.15	0.24
Elo score	0.35	0.45	-0.86	1.56

Discussion

Dynamic index measurements served to provide a general overview of female-female socio-spatial patterns and allowed for an assessment of variables affecting temporal variation. Overall, OMU residency was the most important factor predicting social patterns between Guinea baboon females, with relatedness playing a minor role. Females which were co-resident affiliated more and spent more time in proximity than non-resident females. Agonistic interactions similarly support the importance of OMU membership over kinship and lactation status for the social patterns of female Guinea baboons. However, lactation status was found to be important only when we controlled for residency. Although residency status influenced affiliation, close proximity and aggression patterns, we found no influence of female dominance score or the number of co-resident females on fGC levels.

The bias in social relationships to members of the same reproductive group is common in other polygyn-monandrous systems (e.g. gelada: Tinsley Johnson et al., 2013; guinea pig, *Cavia aperea*: Asher et al., 2004; hamadryas baboon: Schreier and Swedell, 2009; Swedell, 2002; horse: Sigurjonsdottir et al., 2012; Sichuan snub-nosed monkey, *Rhinopithecus roxellana*: Zhang et al., 2008), but the mechanisms behind this shared pattern differ. For example, targeted male aggression towards females in hamadryas baboons: (Swedell and Schreier, 2009) and horses (Sigurjonsdottir et al., 2012), and female philopatry in geladas (le Roux et al., 2011), have both been used to explain why females mainly socialise within their reproductive groups. Our results indicate that in spite of female Guinea baboons spatial freedom from their primary males (Goffe et al., 2016), females actively maintain relationships with OMU members regardless of kinship, and that the OMU membership is the most important factor for female social relationships. In spite of having room to choose, the OMU in which females reside is more important than the presence of kin.

Kinship does appear to play a minor role in the social relationships of female Guinea baboons. However, the extent of this relationship is unclear as the results from the DAI and DPI analyses are not fully concurrent. This is particularly interesting in that DPI is a weighted measure including a distance of up to 5 m. Distances were weighted in favour of those typically featuring social interactions and DAI and DPI scores show a strong positive correlation (Spearman's: $r=0.753$, $N=28340$, $P<0.001$). The slightly different results for the DAI and DPI analyses may be due to the low numbers of affiliative interactions combined with few related dyads, which may have resulted in a reduction of statistical power.

The function of dispersal may vary with the life history stage of individuals, as well as with the current social environment that they experience. Social factors linked with incest avoidance have been suggested as the force driving female dispersal from their natal groups (primary dispersal) (Clutton-Brock and Lukas, 2012). In multiple dispersing species, dispersal distance and the frequency of dispersal are likely driven by other ecological factors (Clutton-Brock and Lukas, 2012). Female biased dispersal is more common in monogamous species and females may disperse farther than males in socially monogamous mammalian species (Mabry et al., 2013). A simulation study by Tiedemann and colleagues (2000) indicates that female dispersal has a larger impact than male dispersal on genetic structure. The pattern throughout the Guinea baboon range in West Africa supports a historic pattern of female-biased dispersal (Ferreira da Silva et al., 2013; Kopp et al., 2014, 2015) and our previous work shows that Guinea baboon females disperse multiple times in their lives across various social levels (Goffe et al., 2016). In the course of data collection for this study two juvenile/subadult females were observed to change from their natal OMU to an OMU within their gang (Goffe, personal observation). Unfortunately we do not yet have comprehensive data concerning the natal dispersal of females in our study population and thus cannot accurately compare the first and subsequent dispersals. Female spatial proximities and social choices may be driven by the genetics of available partners rather than true kin selection.

Thirdly, even if genetic kin are present, individuals may be unable to differentiate between “related” and “unrelated” potential partners in their social groups. Taking into account that genomic variation depends on the pedigree and the extent to which alleles at different loci are identical by descent (Hill and Weir, 2011), it is clear that dyads of different relationship categories may share the same degree of genetic relatedness (Blouin, 2003; Hill and Weir, 2011). The term kin recognition has been used under a variety of definitions (Penn and Frommen, 2010) and has been shown to occur via a number of behavioural and physiological mechanisms: association (Breed, 2014; Rendall, 2004; Widdig, 2007), spatial patterns/use/location (Rendall, 2004), phenotype matching (Blaustein, 1983; Breed, 2014; Rendall, 2004; Widdig, 2007), and chemical and recognition alleles (Breed, 2014; Gardner and West, 2007; Getz and Smith, 1983). In some species kin recognition does not necessarily result in preferential behaviour (e.g. Fernandes et al., 2015)

Although genetic kin recognition is rare (Gardner and West, 2007), both maternal and paternal kin recognition have been noted for a number of species (Langergraber et al., 2007; Smith et al., 2003; Widdig, 2007). In closely knit matrilineal societies kinship and

proximity are strongly correlated and individuals frequently interact with those in close proximity to them (e.g. Kapsalis and Berman, 1996), which may result in the assumption that kin selection is the mechanism responsible for observed behavioural patterns when associations may in fact be random (Chapais, 2001, 2006). Female philopatry allows females to maintain close bonds with maternal kin; such relationships result in long-term knowledge of other individuals and a certain level of predictability regarding social interaction patterns (e.g. (Kalbitz et al., 2016; Silk et al., 2010a). Under these circumstances, kin recognition is relatively straight forward and self-perpetuating: with females benefitting from maintaining close bonds with kin (e.g. through increased reproductive success). Familiarity during ontogeny and the spatial distribution of individuals (e.g. group membership) both serve as potential mechanisms by which kin recognition is achieved (Rendall, 2004). Yet they act as confounds when trying to determine if kin selection or kin-biased mutualism is driving nepotistic support (Chapais, 2001). Kin selection, contingent reciprocity and mutualism may work together to contribute to apparent nepotistic biases in behaviour (Silk, 2009). On average, we found that non-resident dyads showed a higher mean relatedness than co-resident dyads, 0.05 and 0.03, respectively. The degree of average relatedness in a group is dependent upon the number of individuals and high average relatedness is only expected in small groups (Lukas et al., 2005). Therefore interactions among individuals in large groups may be driven by factors other than kin relationships (Lukas et al., 2005).

In Guinea baboons and other multilevel species, the question of group size is not as easily answered as in species with more coherent spatial relationships/groups. Due to the multiple layers of social subgroups with varying degrees of connectedness (e.g. Goffe et al., 2016; Mac Carron and Dunbar, 2016; Schreier and Swedell, 2009) the fission-fusion dynamics of multilevel societies allows for an independent assessment of the role of kinship which can be independent from group membership and incorporate aspects of individual spacing and choice which may not be as easily studied in other systems. In addition, the relationship between kinship and sociality appear to differ in species where dispersal is bisexual or female-biased, where female interactions driven by other factors than by kinship (e.g. Cameron et al., 2009; Milton et al., 2016). Future investigation including a more in depth genetic analysis would serve to illuminate the influence of maternal and paternal kinship on the social relationships of females in this population.

Regardless of the cause, the differential effect of OMU residency and kinship on dynamic index scores indicates that OMU residency is the most important factor for females'

socio-spatial relationships. Therefore, we looked more closely into OMU residency patterns and the potential physiological influences of female competition, but found no relationship between the number of resident females (i.e. harem size) or rank on faecal glucocorticoid levels. These results are surprising in comparison to the impact of group size on stress levels in other species (Markham et al., 2015; Pride, 2005), although the range in the number of adult females per OMU we report for Guinea baboons is at the low end of what has been reported in some polygn-monandrous species (Fabiani, 2004; Goffe et al., 2016; Kaseda and Khalil, 1996; Modig, 1996). Our values also fall within the range of what has been previously reported in captive zoo populations (Boese, 1973, 1975; Maestripieri et al., 2007), but at this time there is no comparable data on harem sizes from other wild populations.

Why lactation status plays such a small role in the social patterns of female Guinea baboons is unclear. Typically, natal attraction is investigated by looking at approach and grooming to mothers and infants (e.g. Henzi and Barrett, 2002). Female savannah baboons have been shown to “pay” for access to infants via grooming (e.g. chacma baboon: Henzi and Barrett, 2002; olive baboon Frank and Silk, 2009). Silk (1999) shows that bonnet macaques (*Macaca radiata*) are attracted to infants because adequate infant care is a highly selected trait in females. One would predict that this would be true for all female primates as infants are born altricial and highly depend on maternal care. This is particularly important as early maternal loss in yellow baboons can result in decreased survival chances of offspring (Tung et al., 2016). One possible answer might be that although infants are attractive, relationship strength does not change, but rather the directionality of grooming (e.g. olive baboon: Frank and Silk, 2009). The dynamic index we calculated was undirected and thus detecting shifts in relationship equity are not possible.

Various studies have found a differential relationship between rank and measures of cortisol secretion. A meta-analysis on cortisol variability in primates indicated that cortisol levels are elevated in subordinate individuals with reduced opportunities for kin support (Abbott et al., 2003). Differences in the fGC metabolite concentrations of female Guinea baboons in the pre- and capture period indicate that external stressors causing extreme social disruption do influence fGC metabolite levels (see supplementary information). Female chacma baboons have elevated fGC during times of social instability and the hormonal responses may be differentiated and depend on a variety of variables (e.g. female reproductive state) (Engh et al., 2006a; Weingrill et al., 2004). Evidence from male baboons suggests that it is the instability of relationships with individuals close in rank which causes

elevated cortisol in individuals (Sapolsky, 1992). Guinea baboon society is characterised as being highly tolerant regarding the inter- and intrasexual social and spatial relationships of males (Goffe et al., 2016; Kalbitzer et al., 2015; Patzelt et al., 2014). The hormone data we tested came from a period of social instability during which 5 transfers occurred between OMUs. Sapolsky (2005) outlines the ways in which societal characteristics dictate the influence of rank on the expression of physiological stress. In egalitarian societies rank has not been found to influence stress levels. These variables may have contributed to our inability to detect social causes of fGC metabolite variability.

Conclusions

In male dominated systems, females may have restricted social options to enhance their own reproductive success. In addition, variability in female social behaviour may be difficult to detect as they can be overshadowed by the more salient behaviours of males (e.g. aggressive control of hamadryas females: (Swedell et al., 2014) or modulated by ecological variables, as has been observed in *Pan* (Doran et al., 2002). Our results indicate that Guinea baboon females establish temporary relationships with nonkin which are based on OMU membership. Taylor and colleagues (2000) suggest that female mammals follow a “tend and befriend” pattern towards development and maintenance of social relationships which is linked to maternal attachment and caregiving. The flexible behavioural response of females to social stressors and demographic change may be linked to the neuroendocrine system (Crockford et al., 2013; Engh et al., 2006b; Taylor et al., 2000). The social adaptability under duress appears to be a character which is present in varying degrees in species with vastly different social systems and may be a beneficial strategy in the long term.

Particularly in systems with female-biased dispersal, fluctuations in group cohesion through fission-fusion dynamics may minimise the costs and maximise the benefits of sociality without influencing dispersal patterns, thus allowing for females to gain non-competitive benefits from fission-fusion dynamics (Lee and Strier, 2015). Social integration has been noted as a key component of reproductive success (Cameron et al., 2009; Silk, 2009; Silk et al., 2010a) and establishing affiliative/tolerant relationships with resident females may be key to group integration (Furuichi, 1989). Although female-female relationships in Guinea baboons are differentiated, they are not enduring, and thus cannot qualify under “social bonds” as the term is promoted by Silk (2006a, 2006b). Why females interact outside of their

own OMU at all, how their relationships develop over time and whether or not they are equitable, remain to be shown.

Acknowledgements

We would like to thank the *Diréction des Parcs Nationaux (DPN)* and *Ministère de l'Environnement et de la Protéction de la Nature (MEPN)* de la République du Sénégal for permission to work in the *Parc National de Niokolo-Koba (PNNK)*, as well as the conservateur of PNNK, Mamadou Sidibé, for his logistical support. We have much appreciation for the staff and researchers of the *Centre de Recherche de Primatologie Simenti*, in particular Cheikh Sané, Moustapha Faye, Armél Louis Nyafouna and Ibrahima Diatta for their companionship and Federica Dal Pesco, Ulrike Barnett and Matthias Klapproth for their assistance in the field. We thank Rasmus Liedigk and Andrea Heistermann for assistance in lab, and Cédric Girard-Buttoz for commenting on earlier versions of this manuscript. Funding from the *Deutsche Forschungsgemeinschaft (DFG Fi707/9)* and the *Leakey Foundation* is gratefully acknowledged.

CHAPTER 5: General Discussion

Females, mammalian females in particular, negotiate a social landscape which is highly impacted by their femininity. In **Chapter 1**, I have given the theoretical and empirical background regarding mechanisms driving variations in female social relationships. I then went on to address the aim of my thesis, which was to investigate the inter- and intrasexual relationships of female Guinea baboons. In **Chapter 2**, I clarified the behavioural mating system and social organisation of Guinea baboons, from the female perspective. I then went on to investigate a potential benefit, females may receive from maintaining relationships with a primary male (**Chapter 3**). Subsequently, I investigated the patterns of female-female social behaviour using a dynamic index in order to determine which variable influence female social structure (**Chapter 4**).

In this general discussion, I will begin by summarising empirical results and the contributions of this study towards our understanding of the Guinea baboon system, I will go on to discuss the implications of dispersal in a multilevel system. Subsequently, I will address the flexibility and adaptiveness of female social behaviour. Finally, I will propose a few avenues for future research, which would fill gaps in our understanding of the mechanisms driving the variability in female social relationships, with the aim of clarifying the give and take in the evolution of female social relationships and how they impact mating systems, social organisation and social structure.

The Guinea baboon system

Previous research has described the Guinea baboon as displaying behavioural and morphological features which are intermediate between those of hamadryas baboons and stereotypical savannah baboons (i.e. chacma, olive and yellow baboons) (Boese, 1973; Dunbar and Nathan, 1972; Sharman, 1982). However, captive and unhabituated populations limit our confidence in these descriptions when making inferences concerning the characteristics of a species' social system. Both have their drawbacks: restricted movement and artificial management practices, on one hand, and unidentified individuals behaving abnormally, on the other. Below, I will state where our current knowledge is regarding the

social system, social organisation, mating system and social structure (as per Kappeler and van Schaik, 2002) of Guinea baboons. Recent data from individually identified habituated baboons will be highlighted where possible, and some inferences will be drawn from unhabituated and/or captive individuals where warranted.

Social System

Previous results have shown that Guinea baboons have a multilevel social system containing multiple parties of two or more males nested within gangs (Patzelt et al., 2014). Some of these males are socially and sexually bonded to one or more females (the “primary males”), while other males only have social access to females (the “secondary males”) and males with no access (the “unaffiliated males”); thus indicating an additional social level to in Guinea baboons, the one-male unit (OMU) (**Chapter 2**; Goffe et al., 2016). Although these results were gleaned from one wild gang, other studies in captivity and in the wild have hinted at a potentially OMU-based multilevel system in this species. Two studies performed by Maestripieri and colleagues (2005, 2007) found that females have “concentrated” affiliative and mating interactions with a single male and concluded that OMUs or “harem-like” structures were present in this species. Other studies in the wild also hinted at a potential OMU based system, but were unable to come up with unequivocal evidence as individuals were unhabituated and unidentified (e.g. Boese, 1973, 1975; Galat-Luong et al., 2006). These studies used group counts to insinuate social relationships among unknown individuals.

However, there is evidence that females also maintain close proximity to secondary males and are observed to affiliate and travel with them (**Chapter 2**; Goffe et al., 2016; Goffe, personal observation). In addition, Guinea baboon females have more spatial freedom than hamadryas baboon females (**Chapter 2**; Goffe et al., 2016). Friendships with secondary males are obvious enough that assuming OMU membership based on short-term group composition our group counts may lead to an inaccurate assignment of females to OMUs. The overall picture indicates that the Guinea baboon society consists of three social levels: OMU, party and gang (**Chapter 2**; Goffe et al., 2016; Patzelt et al., 2014). Although data from unhabituated Guinea baboons indicate a high level of fission-fusion of subgroups and changes in group membership (e.g. Boese, 1973, 1975, Patzelt et al., 2011, 2014), it is not clear if additional social levels exist in this species.

Social Organisation

Guinea baboons have a social organisation (following the definition proposed by Kappeler and van Schaik, 2002) with variable group size and composition, resulting from a high degree of fission-fusion dynamics (Boese, 1973, 1975; Dunbar and Nathan, 1972; Galat-Luong et al., 2006; Patzelt et al., 2011, 2014; Sharman, 1982). Group size in the wild ranges from four to more than 425 individuals (Boese, 1973; Patzelt et al., 2011; Sharman, 1982) with some variability linked to season (see Sharman, 1982 for details). Variations in group size have been attributed to habitat structure, with larger groups fissioning and fusing in order to negotiate habitat features (Boese, 1973). Group composition consists of both single-male and multi-male groups (Boese, 1973; Patzelt et al., 2011), but composition is highly variable with 46% of groups changing composition during travel (Patzelt et al., 2011). Groups may contain varying numbers of males and females, however the multi-male group is the most common (Patzelt et al., 2011). Sex roles and mating systems are influenced by the adult sex ratio (Székely et al., 2014). When comparing studies from different wild Guinea baboon populations the adult sex ratios, the ratios of males to females, are vary slightly: 1:1.4 (Boese, 1973; Sharman, 1982), 1: 1.9 (Dunbar and Nathan, 1972) and 1:1.5 (Goffe, unpublished data).

In addition to large-scale group fission-fusion events, small scale interindividual distances can also give insight into the spatio-temporal cohesion of a species. In **Chapter 2**, I showed that in intersexual spatial relationships (based on proximity scans) 2-m differs from 5-m regarding the density and identity of individuals. Although these data were used to classify males into three categories for later analyses, differences in the two networks gives us insight into aspects of interindividual spatial dynamics. Unfortunately, there are no comparable analyses of intrasexual spatial relationships in males or females. However, the differences in the 2-m and 5-m intersexual networks highlights the difficulties which can be faced when using proximity distances without knowledge of a species' social organisation.

Repeatedly in the literature Guinea baboon males are described as being “tolerant”; male tolerance is used to apply to both the intrasexual and intersexual relationships of Guinea baboons. Tolerant intrasexual behavioural patterns include grooming, contact sitting and close spatial proximity (≤ 1 m) (Boese, 1973; Dal Pesco, 2013; Kalbitzer et al., 2015; Patzelt et al., 2014). Primary males also exhibit tolerance towards the social behaviour (see section 5.1.4) of, and spatial relationships to, their females (**Chapter 2**; Goffe et al., 2016). Weak intersexual spatial relationships have also been noted in other studies in the wild (Dunbar

and Nathan, 1972; Sharman, 1982). However, the use of the word tolerant implies that there is an element of negative emotion or disagreement associated with a particular individual's behaviour or spatial proximity. The empirical analyses (e.g. physiological and emotional effects) concerning male affiliative associations and female spatial freedom have not been presented to support this claim. Rather, the use of the word tolerant attempts to juxtapose the Guinea baboon system with the other baboon species which have entirely different social systems (for a review of baboon social systems see Swedell, 2011).

Mating System

The mating system describes social interactions directly related to copulatory behaviour and is divided into genetic and behavioural components (Kappeler and van Schaik, 2002). To date there is no data concerning the genetic mating system of Guinea baboons. However, we do have some idea of what constitutes the behavioural mating system. The analysis of 18 months of ad libitum mating behaviour indicate that females are serially monogamous (**Chapter 2**; Goffe et al., 2016). Extra-pair copulations occurred rarely and never in front of the primary male (**Chapter 2**; Goffe et al., 2016). No other study has continuous data on female sexual behaviour in Guinea baboons so it is not possible to compare tenure length or temporal aspects of the mating system across studies. There are a few short term studies in the wild and in captivity which have found that the majority of copulations go to one male, but that females will also copulate with a small number of other adult or subadult males (Boese, 1973; Maestriperi et al., 2005). Although these authors state that males had nearly exclusive access to females, the number of additional male sexual partners was higher than observed in this study and indicate that some females may be promiscuous. It is not clear if this difference is linked to natural variation in the Guinea baboon mating system or if it is an artefact of captive management practices (e.g. vasectomization of males). Although castration is a tool for captive management (Asa and Porton, 2010), it causes a variety of morphological, physiological and behavioural effects in males of various species and may result in modification of male behaviour, including reduced sexual behaviour and reduced aggression (for review see Folstad and Karter, 1992; Knol and Egberink-Alink, 1989, but see Epple, 1978). A promiscuous mating system for Guinea baboons was noted in another study on unhabituated individuals in the wild (Dunbar and Nathan, 1972), but as they did not distinguish between copulations and sociosexual behaviour (e.g. greeting-mounts), it is not clear to what extent their results were influenced

by the social structure (see section 5.1.4). Thus, it seems apparent that Guinea baboons display a polygyn-monandrous mating system.

One key feature of mating systems is the sexual signals exhibited by both males and females. Female baboons produce two signals which have been shown to serve reproductive functions. Copulation calls are auditory signals which are ubiquitous across animals and serve a reproductive function, signalling the timing of ovulation and the competitive strength of the male copulation partner in yellow baboons (Semple et al., 2002). Sexual swellings (morphological changes in the anogenital area (AGA) and paracallosal skin (PCS) of females) are visual signals which also serve a reproductive function. In chacma, olive and yellow baboons, sexual swellings serve as a graded signal which give males access to information regarding female ovulation (Higham et al., 2009; Nunn, 1999; Weingrill et al., 2003; Wildt et al., 1977). Chacma, olive and yellow baboons have a very different social systems and social structures in comparison to Guinea baboons (see Swedell, 2011 for review of savannah baboon systems). Female hamadryas baboons also have sexual swellings, which have been shown to be related to the probability of ovulation and female copulation rates with leader males (Nitsch et al., 2011). One would expect that, with the close spatial proximity hamadryas baboon leader males maintain to their females (see Swedell, 2006), sexual swellings would be potentially hazardous for maintaining male tenure (inciting male-male competition). Additionally, although morphological changes in the AGA and PCS are hormonally linked in some primates (e.g. chacma baboon: (Gillman, 1940); olive baboon: (Higham et al., 2008); macaques: (Zuckerman and Parkes, 1939)), they are potentially costly for females to produce and may advertise female quality (e.g. Domb and Pagel, 2001). In both the wild and in captivity Guinea baboon females have been shown to exhibit sexual swellings (Boese, 1973; Sharman, 1982; **Chapter 2**; Goffe et al., 2016; **Chapter 3**; **Chapter 4**). The presence of this trait across baboon species indicates that the sexual swelling is an ancestral trait. Though it is not clear to what extent this trait serves the same function in a polygyn-monandrous species as it did in a promiscuously mating species. However, more cycling (both tumescent and detumescent) than lactating or pregnant females were observed to transfer OMUs, indicating that there may be some effect of reproductive state on the timing of transfers (Goffe, unpublished data). (“Transfer” is a neutral term, referring to the period between emigration (departure) and immigration (settlement) (Bonte et al., 2012). The use of this term does not divulge information regarding the proximate or ultimate mechanisms behind dispersal.)

Social interactions between females and males not directly related with mating may be influenced by female reproductive state. Primary males were more often observed at the 2-m proximity distance when their tumescent females are most likely to be in oestrus (see tumescent state “S3”: **Chapter 2**; Goffe et al., 2016) and show stereotypical mate guarding during this timeframe (Goffe, unpublished data). This result contradicts the observation from another study in the wild that oestrous females associated weakly with adult males (Sharman, 1982). As this point directly influences our view of both the mating system and the social structure I will address it here. Firstly, the results in Sharman (1982) may be confounded by his classification of all tumescent females as being in oestrus. In multiple species of baboons females copulate and groom with immature males (e.g. chacma baboon: Cheney, 1978; Guinea baboon: Goffe, unpublished data; olive baboon: Higham et al., 2009). Potentially, immature males may not produce viable sperm (e.g. olive baboon: (Jolly and Phillips-Conroy, 2003); yellow baboon: (Albert and Altmann, 1995); but see the hamadryas baboon: (Jolly and Phillips-Conroy, 2003; Zinner et al., 2006)) and thus may not be perceived as a reproductive threat to the primary male. Secondly, Sharman (1982), unaware of the true social system of Guinea baboons did not take into account that not all males necessarily have access to or compete for oestrus females (see below regarding the dyadic and polyadic aspects of male-male aggression (section 5.1.4.1) and differentiated intersexual interactions (section 5.1.4.2)). Finally, Guinea baboon primary males may have access to information regarding when a female will ovulate and may thus focus their reproductive behaviour around the timing of ovulation. In olive baboons, swelling size and colouration are good indicators of the timing of ovulation (Higham et al., 2008). Adult male olive baboons appear to use this visual signal to time mate guarding, but not copulatory behaviour (Higham et al., 2009). Copulations in olive baboons were more closely linked to the more narrow window of female fertility and the timing of ovulation (Higham et al., 2009). These patterns would be easily explained if sociosexual behaviour (e.g. genital inspection) occurring during consortships gives Guinea baboon males access to olfactory or visual indicators of the exact timing of ovulation. However, there has yet to be a study looking specifically at the reproductive parameters of Guinea baboons.

The operational sex ratio (OSR) can also give insight into a species' mating system. In **Chapter 2** (Goffe et al., 2016) and **3**, I report the OSR of 1:2.3 (calculated from the ratio of primary males to OMU females). Although there is no comparable data from a wild population, this value differs substantially from the adult sex ratio reported in section 5.1.2. Three of the four males which result in the discrepancy were secondary males to at least one

female (**Chapter 2**; Goffe et al., 2016) and the other male was seen within 5 m of at least one focal female but was never observed to interact with her during focal observations (and was thus considered to be unaffiliated) (**Chapter 2**; Goffe et al., 2016). Some of these males were also members of at least one all-male group (Goffe, unpublished data).

Social Structure

In the previous section (5.1.3) I wrote about some aspects of the mating system which relate to social structure. Aside from mating behaviour, there are a variety of other social interaction patterns which can give us insight on the social structure of Guinea baboons. Although immature individuals are important to all aspects of social structure and would give excellent insight into social relationships in this species, I have chosen to exclude them from the discussion of this topic as much of the data at this point is highly speculative. Therefore, I will focus on male-male, female-male and female-female social relationships in turn.

Male Intrasexual Relationships

Evidence from the wild clearly shows that Guinea baboon males have highly differentiated affiliative social relationships with each other, consisting of grooming exchanges and contact sitting (Dal Pesco, 2013; Patzelt et al., 2014), which corroborate results previously reported from captivity (Boese, 1973). Males also engage in elaborate greeting exchanges (see **Chapter 2**; Goffe et al., 2016 for a definition). The function of greeting behaviour has not yet been determined in this species, although it is clear that its use extends beyond exchanges with highly affiliative or agonistic social partners as males who never groomed together did engage in greeting interactions (Dal Pesco, 2013; Patzelt et al., 2014; see Dal Pesco, 2013 for discussion). Agonistic behaviour can also tell us something about the relationships among males. Guinea baboon males appear to have a complicated network of agonistic relationships. Males have been found to exchange comparatively low levels of dyadic agonistic interactions (Kalbitzer et al., 2015), which can challenge traditional attempts at determining if there is a linearly significant dominance hierarchy (Appleby, 1983). Polyadic agonistic interactions also occur (Boese, 1973; Goffe, personal observation) during which males often form coalitions (Galat-Luong et al., 2006; Patzelt et al., 2014; Sharman, 1982), although there is no data available comparing the rate of polyadic vs dyadic

interactions or the situations under which each occur. Guinea baboon males are philopatric (Kopp et al., 2015) and the general patterns of high affiliation, low aggression and cooperation among males is what would be expected from a system in which males are likely to associate with kin (see Hamilton, 1964).

Intersexual Relationships

What we know of male-male social relationships in Guinea baboons paints a complicated picture of affiliation and aggression which is still unclear. However, some additional insight may be gained from what we have thus far observed in studies which have investigated intersexual relationships. As mentioned in sections 5.1.1, the basal social unit in this social system is the OMU (**Chapter 2**; Goffe et al., 2016). Within OMUs primary males engage repeatedly in grooming, greeting (including sociosexual behaviour) and agonistic interactions with females within their units (**Chapter 2**; Goffe et al., 2016). Females groom, greet and engage in infant handling interactions with their respective primary and secondary males (**Chapter 2**; Goffe et al., 2016). However, most social interactions occur with a female's primary male (**Chapter 2**; Goffe et al., 2016). Grooming is bidirectional, thus including the active participation of both males and females (Goffe, unpublished data), but it is thus far unclear to what extent the proportion of active grooming time may vary with female reproductive state. Interestingly, female-male greetings are highly correlated with grooming interactions (in contrast with male-male greetings), indicating that there may be a different function of greetings in different categories of intra-vs intersexual dyads (but see **Chapter 4**). Both primary and secondary males were observed to engage in sexual and nonsexual mounting (Goffe, unpublished data).

Although both primary and secondary males exhibit aggression towards females (e.g. supplant and ground-slap), complicated patterns of aggressive behaviour indicate that male Guinea baboons do not dominate females in all social situations (**Chapter 2**; Goffe et al., 2016). Females receive the vast majority of aggressive interactions from their primary males, but have also been observed to engage in counter-aggressive and retaliatory behaviours (e.g. chasing and threatening) (**Chapter 2**; Goffe et al., 2016). In addition, polyadic agonistic interactions also occur. Primary males have been observed to engage in coalitions with their OMU females against other males, as well as interfere in female-female agonistic interactions (Dal Pesco, personal observation; Goffe, personal observation). Anecdotal evidence indicates that secondary and unaffiliated males may sometimes be inhibited in their

aggression towards females in the presence of their primary male, as females have been able to supplant secondary and unaffiliated males over food in the presence of their primary male (Goffe, personal observation).

Overall, these results corroborate with studies from captivity which state that females engage in affiliative and agonistic interactions with predominantly 1 or 2 males (Boese, 1973; Maestripieri et al., 2007), indicating that in spite of the social disruption caused by captivity (e.g. restricted movement and reproductive management) the core behavioural patterns of wild Guinea baboons are still evident. However, it must be noted that studies which have tried to infer social behaviour from sex ratios and group composition data have concluded that females were not constrained to interact with one male and could not have a society in which males are able to monopolise subgroups of females (e.g. Sharman, 1982). As spatial relationships in Guinea baboons do not necessarily reflect existing social relationships (**Chapter 2**; Goffe et al., 2016; **Chapter 4**) one must therefore caution the use of non-behavioural data to infer aspects of social structure in this species.

Female Intrasexual Relationships

In Guinea baboons, intersexual relationships and intrasexual relationships for females are closely linked, with OMU membership playing a key role in female-female association and behavioural patterns. Females across a number of captive and wild studies have been observed to engage socially with other females (e.g. Boese, 1973; Frank, 2015; Maestripieri et al., 2007; Sharman, 1982; **Chapter 4**). Females' intrasexual relationships incorporate a variety of social interactions (see **Chapter 4**). Patterns of social interaction are highly differentiated but unstable, with the strength of dyadic relationships changing with OMU membership (**Chapter 4**). Although some closely related kin ($r > 0.125$) are present within the study gang, females had higher dyadic affiliation index scores with those females which were in their OMUs. Also, dyads in the same OMU ("coresidents") were more likely to be in close spatial proximity than those from different OMUs ("nonresidents") (**Chapter 4**). The importance of OMU memberships is also important regarding patterns of aggressive behaviour, with females more likely to engage in agonistic behaviour with coresidents (**Chapter 4**). Unfortunately, there are no comparable studies in the wild. However, observations of OMU-like grooming, proximity and aggressive behaviour patterns have been observed in captivity (Boese, 1973; Maestripieri et al., 2007).

Dispersal

As stated in the General Introduction (**Chapter 1**), dispersal patterns and mating relationships are closely tied as they both have profound impacts on the genetics of a population. Theoretically, one of the reasons why individuals disperse is to avoid inbreeding (Bowler and Benton, 2005). Yet, dispersal is costly and individuals face social and environmental risks (Bonte et al., 2012). In the following section I will give a brief review of dispersal patterns in Guinea baboons. I will then go on to discuss the possible mechanisms influencing dispersal and then continue with how dispersal functions within this multilevel system.

Female-biased Dispersal in Guinea baboons

Population genetics studies in Guinea baboons indicate dispersal is female-biased (Ferreira da Silva et al., 2013; Fickenscher, 2010; Fickenscher et al., 2011; Kopp et al., 2014, 2015). Field observations support this finding and suggest that females dispersal events are predominantly social rather than locational (**Chapter 2**; Goffe et al., 2016). As females engage in social interactions outside of their OMUs (**Chapter 4**) and maintain close proximity with males which are not their primary male partners (**Chapter 2**; Goffe et al., 2016), they are exposed to potential reproductive and social opportunities outside of their current OMUs. In addition, both Both cycling and pregnant females were observed to change to OMUs at multiple social levels: same party, different party-same gang and different gang (**Chapter 2**; Goffe et al., 2016). However, transfers (see section 5.1.3 for definition (cf. Bonte et al., 2012) occurred most often when females were cycling (**Chapter 2**; Goffe et al., 2016).

Do females choose or do males select?

Mate choice is multidimensional and occurs prior to as well as after the act of copulation. Theoretically, females prefer males of high reproductive value (Kokko et al., 2002; Mays and Hill, 2004). The relative importance of mating success vs. offspring survival depends upon the costs that females incur from choosing (Kokko et al., 2002). However, female preferences for mates may be restricted under the consequences of male competition (Clutton-Brock and McAuliffe, 2009). Spatial associations, friendships with secondary males

and patterns of agonistic behaviour in Guinea baboons (**Chapter 2**; Goffe et al., 2016) give evidence in support of pre-copulatory mate choice. Pre-copulatory mate choice may be influenced by spatial freedom as females, able to have relationships independent of their primary male, may be able to copulate secretly or initiate transfers. Intersexual friendships may also be a form of pre-copulatory mate choice, albeit with a long-term wait for rewards (e.g. hamadryas: Pines et al., 2011). Aggression levels in the wild and in captivity are universally low (e.g. **Chapter 2**; Boese, 1973; Goffe et al., 2016; Maestripietri et al., 2007). Different patterns of aggressive behaviour between primary males and their females may not serve the same purpose or function in the same ways in Guinea baboons as it may in hamadryas baboons (see **Chapter 2**; Goffe et al., 2016 for comparison and discussion).

In spite of evidence for female choice, male sexual selection may still play a role in female transfers in Guinea baboons. The presence of sexual dimorphism (Patzelt, 2013) indicates that male sexual selection is a factor influencing morphological traits in males and females (Mitani et al., 1996). Dyadic male contests over the possession of females have been observed, a few of which have resulted in male injuries (Goffe, personal observation). Cooperation between dominant and subordinate male geladas, horses and hamadryas baboons has been shown to support leader/dominant males in their defence of females, resulting in increased tenure length and reproductive success of dominant males (Chowdhury et al., 2015; Feh, 1999; Snyder-Mackler et al., 2012b). Such social alliances may serve to counter female choice through the generation of reproductive alliances. Although studies have shown that reproductive alliances result in increased male tenure length, there is no knowledge of how this male strategy influences females.

I would like to propose an alternative hypothesis for female transfer in Guinea baboons. Evidence from the first few hours/days following transfers indicates that immigrant female-primary male dyads groom and contact-sit frequently (Goffe, personal observation). The “conditioning” (through repeated aggressive behaviour/”herding”) which apparently performed by some hamadryas baboon leader males towards their new females (e.g. Swedell and Schreier, 2009) has not been reported in wild Guinea baboons. Overall, patterns of affiliation and aggression (section 5.1.4.2) indicate relaxed intersexual social relationships. In addition, females appear to receive additional benefits for maintaining close proximity to their primary males (**Chapter 3**; Goffe and Fischer, 2016). I suggest that males may be using social strategies other than just aggression and herding to influence reproductive outcomes; rather maintaining highly affiliative relationships with females and allowing females free social movement is a strategy by which males may be able to retain

females. Combined with male philopatry resulting in the promotion of kin selection, females may be choosing more “tolerant” males.

Dispersal in a Multilevel Context

Dispersing individuals face many challenges. However, within multilevel systems dispersal appears to be easier as Guinea baboon gangs have overlapping home ranges (Patzelt et al., 2014) and as females interact and spatially associate with females from other parties and gangs they have social knowledge outside of their own social group (**Chapter 2**; Goffe et al., 2016). In addition, the large aggregations reported for Guinea baboons may make transfers easier for both females and males as risks associated with dispersal become entirely social (i.e., risk of predation (without the benefit of group defence or the dilution effect) and locating resources in a novel environment are negligible). Multilevel systems may serve to make dispersal easier for females and males; large aggregations of Guinea baboons are a regular occurrence (Boese, 1973, 1975; Galat-Luong et al., 2006; Patzelt et al., 2011; Sharman, 1982) potentially providing the opportunity for dispersal to occur. Sharman (1982) found that there may be an ecological/seasonal component to fluctuations in group size—if so, this may influence the timing of dispersal. The fission-fusion dynamics of this species means that individuals may be socially familiar with others outside of their reproductive units (e.g. **Chapter 4**). For males and females this means increased access to individuals from other parties or gangs. It is not yet apparent to what extent individuals are knowledgeable of others outside of their own social unit (but see Maciej, 2013; Maciej et al., 2012).

Conclusion and Future Work

Through the use of behavioural and non-invasive sample collection I was able to improve our understanding of the Guinea baboon social system through investigating female inter- and intrasexual relationships. My project provides the first evidence from the wild that Guinea baboons have a one-male unit (OMU) based multilevel social system. Females have profound relationships with males which influence various aspects of their social lives. However, their relationships with males are permissive in that females are allowed considerable social freedom from their primary males and can engage in friendships with other males as well as with females outside of their OMU. The high degree of overlap in the mating system and social structure are of key importance. The traditional OMUs of many

species are spatially, if not also behaviourally discrete (e.g. hamadryas baboons). The fact that socially, females perpetuate the potentially OMU-based multilevel system indicates that there are highly selective forces which serve to maintain this social level. In closing, I will address a few key remaining questions which have emerged during the course of completing this work.

Although females appear to have strong relationships with their primary males, the seemingly fast adjustment following a transfer is surprising--a better understanding of the mechanism of transfers are essential. This could be sought in a number of ways. Firstly, male quality is theoretically of great import to females and females may select males based on different parameters: personality, rank or permissiveness. Future studies addressing this question could be conducted in the wild (observation) or in captivity (using preference tests). Secondly, as transfers appeared to occur quite smoothly in regard to intersexual relationships, neuropeptides should be explored in order to understand the potential roles of oxytocin and vasopressin in bond development, maintenance and termination.

Plato observed that “similarity begets friendship” (Plato 360 BCE, translated by Jowett, 1993). The concept of homophily is present throughout nature. Hamilton (1964) recognised this when he formulated his mathematical model based on kinship and this concept can also be observed in the prevalence of assortative mating in animals (Jiang et al., 2013). Different rules serve to generate a natural sense of group membership. In humans, ethnicity, age and religion dominate peoples’ social worlds (McPherson et al., 2001). Evidence from **Chapters 2 & 4** raise the question to what extent females end up in OMUs which minimise conflict. “Successful” OMUs may contain females with something in common: age-mates, peers or kin. On the other hand, over time initially combative females may reach a consensus (which would be signified by a cessation in hostilities) and eventually become allies and cooperate against new immigrants. Long-term data regarding female social relationships within and between OMUs are essential for addressing this question.

Little data exist on dispersing primate females. A thorough behavioural and genetic analysis of multiple gangs from both overlapping and geographically distinct regions is necessary in order to investigate the ecological and social factors influencing dispersal patterns. This would require not only a long-term study, but also a collaborative effort in order to gather data on female reproductive success, female tenure length and female-female competition. Such a long-term study in the wild would allow for the testing of maternal characteristics said to influence offspring maturation and reproductive potential (e.g. Albert

and Altmann, 1995). Female Guinea baboons, with their changing reproductive and social groups may be able to adapt more readily to the disruptions accrued by transferring groups.

Taking a step back, although we now recognise three social levels in the Guinea baboon system, only the OMU has an obvious function. It has been proposed that multilevel societies are better equipped to deal with harsh environments. This leads me to ask what is the purpose of the party and the gang? These levels are based upon male proximities and are clearly not random, but to what extent do these levels overlap with female and male social networks? How are they influenced by ecological variables and habitat characteristics? What are the most important to the baboons?

APPENDIX

Supplementary information – Chapter 2

Intersexual network structure

Network density calculates the proportion of connections/edges between two nodes given the number of possible connections in a network and gives a global value of the interconnections within the network. Density values range from 0, relatively solitary individuals with no connections, to 1, a closely knit network where all individuals are equally connected to each other (Wasserman and Faust, 1994). Traditionally, clustering (also called transitivity) is used to determine fine scale substructuring within a network. However, as our data contain only intersexual dyads it was not possible to base subgroup assignment on triadic connections. Therefore we used two other methods from community detection to identify subgroups within the two networks, as subgroup assignment based on a modularity maximising algorithm is not always biologically relevant (Kasper and Voelkl, 2009). Spin glass, an approach from statistical physics based on the Potts model, optimises clustering through a process of simulated annealing based on the modularity of the network (Reichardt and Bornholdt, 2006). The walktrap algorithm utilises random walks to identify subgroups in dense graphs (Pons and Latapy, 2005). Both of these measures calculate modularity, or the reliability of the subdivisions of a network into smaller subgroups (Newman and Girvan, 2004) and variations in modularity values are dependent on the splitting techniques used by the specific algorithms. As we wanted to consider the frequency at which males were present and unweighted edges may result in spurious results (Fagiolo et al., 2008), as well as lead to a reduction in the amount of data, we chose to use weighted edges in all analyses. Subgroup assignments of intersexual dyads derived from the spin glass (set at 500 spins) and walktrap algorithms were compared to the manual assignment of primary males described in the main text.

Identification of male partners: Friedman test and Nemenyi test

The Friedman average rank test (Friedman, 1940) is a nonparametric repeated measures ANOVA which is performed by “ranking” different conditions in multiple observations and

then determining the average rank (Demšar, 2006; Field, 2009; Friedman, 1940). The null hypothesis is that all conditions are equivalent in their ranks. If the null hypothesis is rejected, that is the P-value is significant, then a Nemenyi test may be performed to identify which condition(s) differ (Demšar, 2006). In R, the Nemenyi test reveals a matrix of P-values for all possible pairwise comparisons in each dataset. Here, for each female we treated the 20 males as the condition and the number of observations varied depending on how many scans were performed. Two data sets were run for each female (5 m proximity scans and 2 m proximity scans). We then rejected the null hypothesis in all cases as the Friedman test indicated significant values for all 32 tests (16 females, 2 dataset per female) and performed the Nemenyi postdoc analysis.

Supplementary Figures

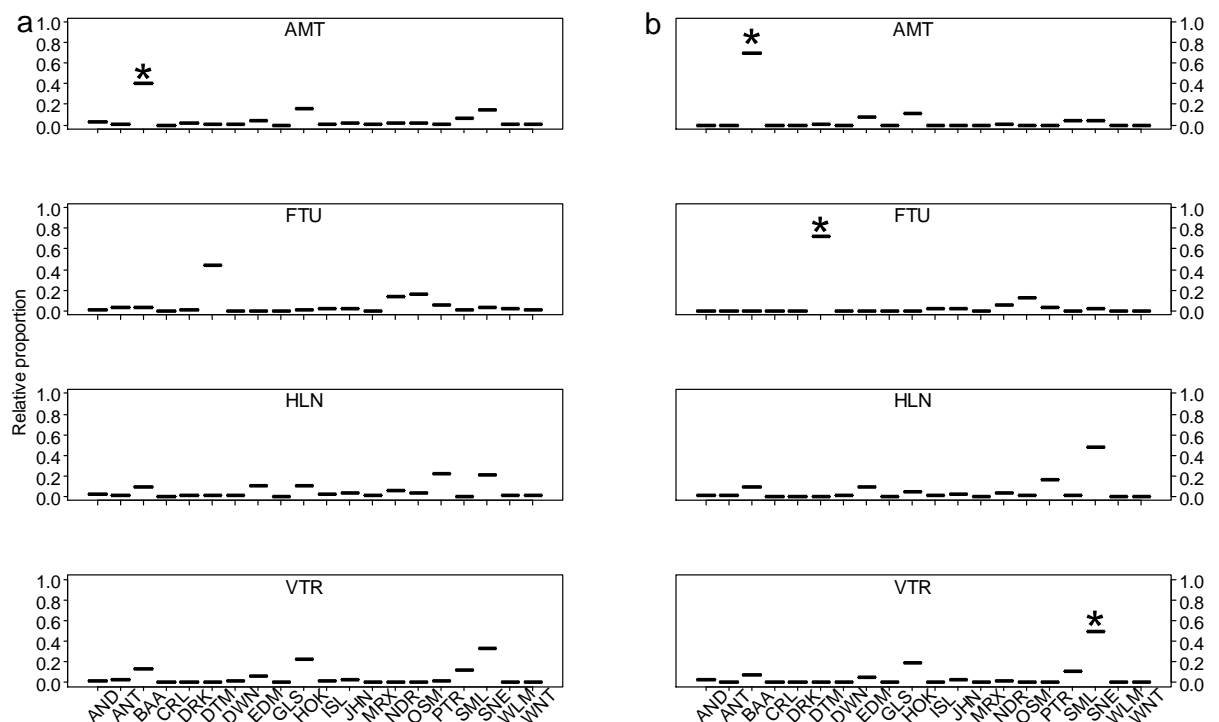


Figure S1. Relative occurrences of 20 adult and subadult males from (a) 5 m and (b) 2 m of four of the sixteen focal females. Three letter codes indicate individual baboons. Asterisks indicate males who were significantly more likely than others to be located within 5 m or 2 m of a given focal female according to the Nemenyi posthoc test

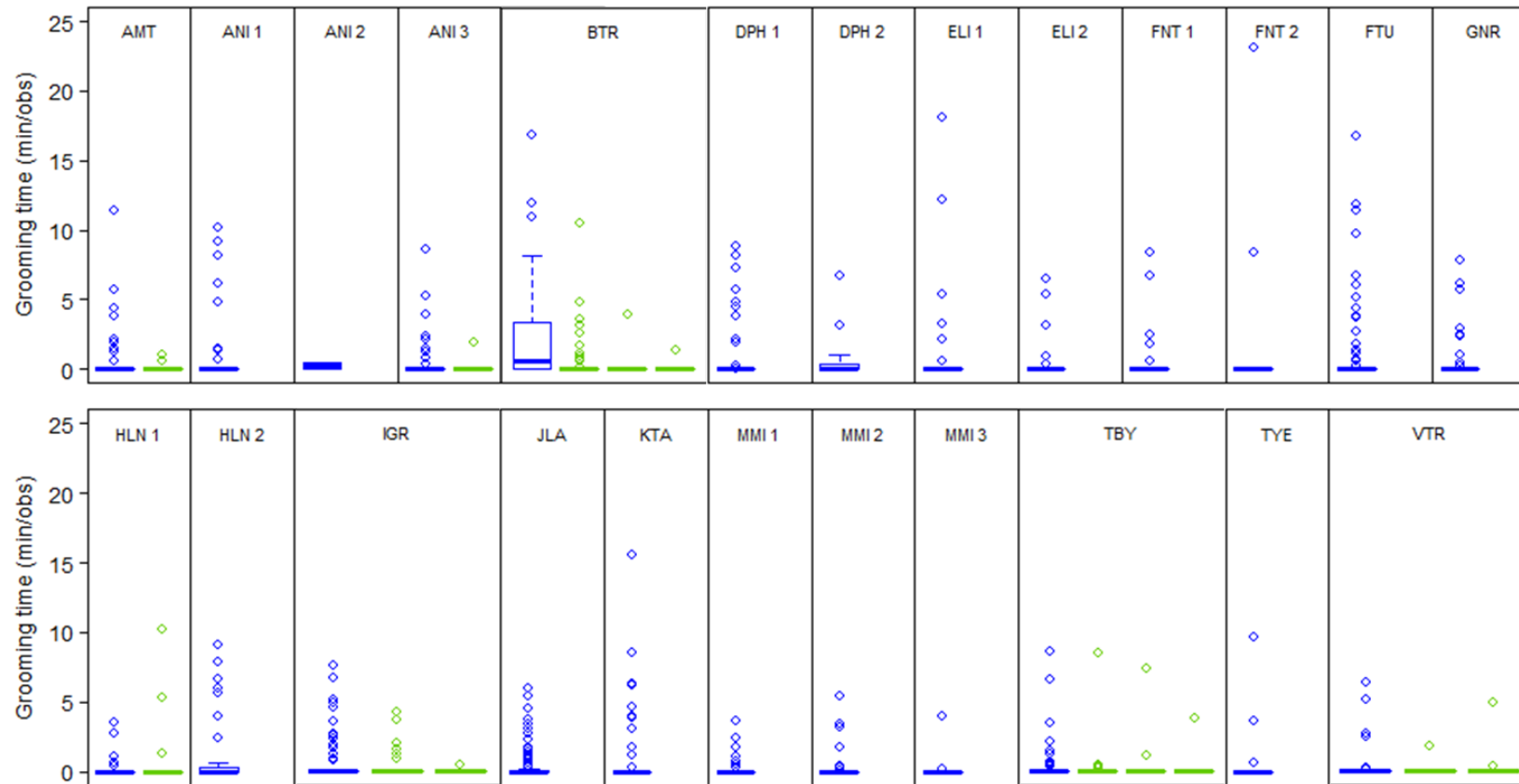


Figure S2. The amount of grooming time recorded during focal observations for intersexual dyads, ordered by male status. Each subplot includes that data for one female during the period she was with a specific male; female identities are indicated by the three-letter code at the top of each subplot and numbers differentiate between different OMU periods for transferring females. Primary males are in blue and secondary males in green. Although spatially available (see Figure 1 and Figure S1), not all females were observed to groom with secondary males during focal observation.

Supplementary information – Chapter 4

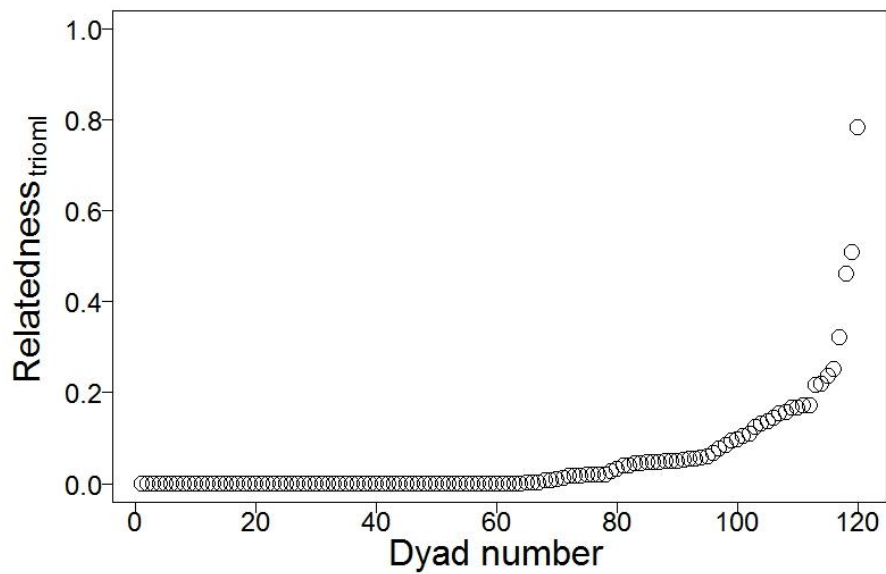


Figure S1. A plot of female-female relatedness values as determined by the triadic likelihood estimator. Dyads are represented by circles and are ordered from lowest to highest.

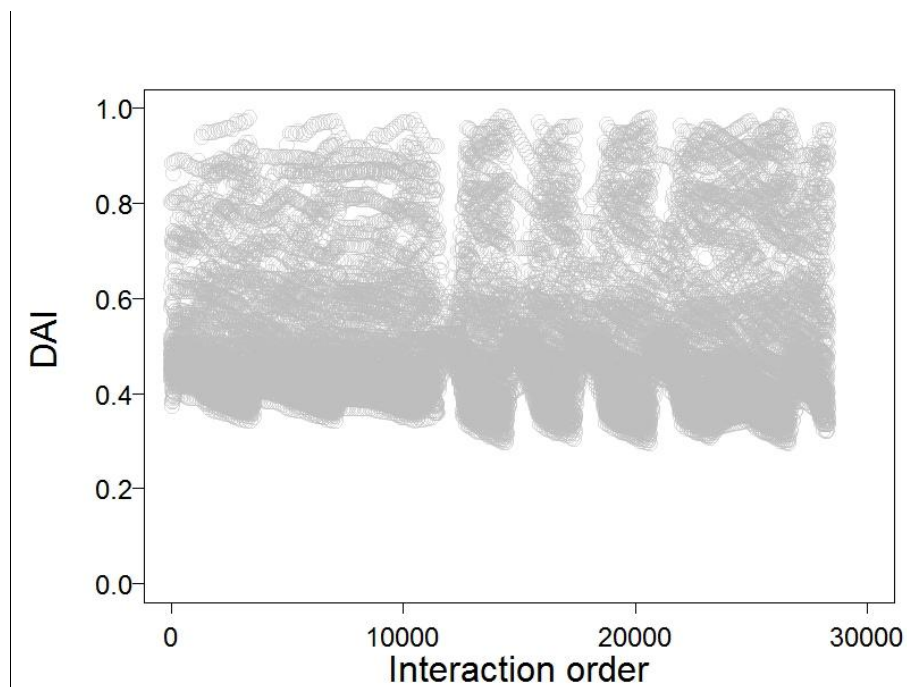


Figure S2. Dynamic association index (DAI) scores used in the model. The x-axis indicates the order in which interactions occurred. Each circle represents a score for a particular dyad.

Table S1. Description of the 25 autosomal microsatellite loci used to estimate relatedness.

Locus	Allele range	No. Alleles	Heterozygosity			HWE			NAFE	
			F_{is}	H_E	H_O	Chi ²	df	P (exact)	Brookfield	Chakraborty
D6s264	94-96	2	0.333	0.482	0.813	7.490	1	0.015	0.482	0.482
D7s503	152-166	5	0.059	0.619	0.750	27.411	10	0.003	0.773	0.773
D12s375	163-181	8	0.065	0.531	0.563	56	28	0.147	0.773	0.773
D3s1766	194-202	2	-0.015	0.404	0.438	1.254	1	0.546	0.342	0.342
D13s765	201-205	3	-0.034	0.703	0.875	16.000	3	0.061	0.525	0.525
D14s306	169-177	3	-0.010	0.588	0.813	3.232	3	0.556	0.570	0.570
D1s533	191-199	3	0.075	0.404	0.438	5.672	3	0.171	0.568	0.568
D2s1329	208-228	8	-0.007	0.549	0.688	17.721	28	0.797	0.771	0.771
D2s1326	251-259	3	-0.046	0.342	0.438	3.306	3	0.314	0.447	0.447
D10s611	133-141	3	0.020	0.676	0.938	7.779	3	0.091	0.645	0.645
D8s1106	148-156	3	0.043	0.732	0.938	0.360	3	1	0.531	0.531
D17s791	166-168	2	-0.025	0.773	0.750	0.108	1	1	0.404	0.404
D6s501	176-192	5	0.002	0.611	0.438	13.244	10	0.234	0.703	0.703
D17s1290	194-206	4	0.036	0.744	0.813	7.490	6	0.356	0.588	0.588
D6s311	228-230	2	-0.042	0.525	0.750	0.108	1	1	0.430	0.430
D5s1457	121-133	4	-0.021	0.688	0.938	4.114	6	0.589	0.549	0.549

D8s505	147-151	2	-0.042	0.730	0.813	1.254	1	0.535	0.342	0.342
D10s1432	157-167	5	-0.077	0.607	0.875	10.726	10	0.343	0.682	0.682
D5s820	178-194	5	-0.056	0.773	0.750	13.778	10	0.202	0.723	0.723
D3s1768	197-209	5	-0.038	0.342	0.438	9.941	10	0.125	0.611	0.611
D7s2204	228-244	5	0.049	0.525	0.438	11.823	10	0.456	0.744	0.744
D1s207	131-135	3	-0.012	0.570	0.625	4.874	3	0.124	0.525	0.525
D4s243	147-163	5	0.031	0.568	0.500	27.346	10	0.004	0.688	0.688
D1s548	188-208	6	0.041	0.775	0.750	14.177	15	0.345	0.730	0.730
D21s1142	230-242	4	-0.028	0.447	0.625	7.474	6	0.166	0.643	0.643

F_{is} =inbreeding coefficient according to Nei (1987); H_E =expected heterozygosity; H_O =observed heterozygosity; HWE=Hardy-Weinberg equilibrium; NAFE=null allele frequency estimations based Brookfield (1996) and Chakraborty et al. (1992).

Table S2. Summary of three covariates included in the DAI and DPI models in relation to the respective indices. Values shown are the median index score (interquartile range) for relatedness (unrelated, unclassified and related) and lactation (none, one and both) in relation to residency (non-resident and co-resident).

	OMU membership			
	non-resident		co-resident	
DAI				
unrelated	0.44	(0.40-0.49)	0.54	(0.47-0.80)
unclassified	0.46	(0.46-0.53)	0.64	(0.55-0.87)
related	0.49	(0.44-0.57)	0.64	(0.59-0.78)
none	0.46	(0.41-0.50)	0.57	(0.51-0.63)
one	0.46	(0.40-0.52)	0.59	(0.47-0.81)
both	0.45	(0.41-0.50)	0.75	(0.59-0.87)
DPI				
unrelated	0.39	(0.32-0.53)	0.85	(0.79-0.90)
unclassified	0.40	(0.31-0.58)	0.88	(0.83-0.91)
related	0.56	(0.41-0.71)	0.87	(0.83-0.89)
none	0.42	(0.36-0.58)	0.84	(0.74-0.91)
one	0.40	(0.32-0.59)	0.87	(0.81-0.91)
both	0.39	(0.31-0.59)	0.88	(0.84-0.90)

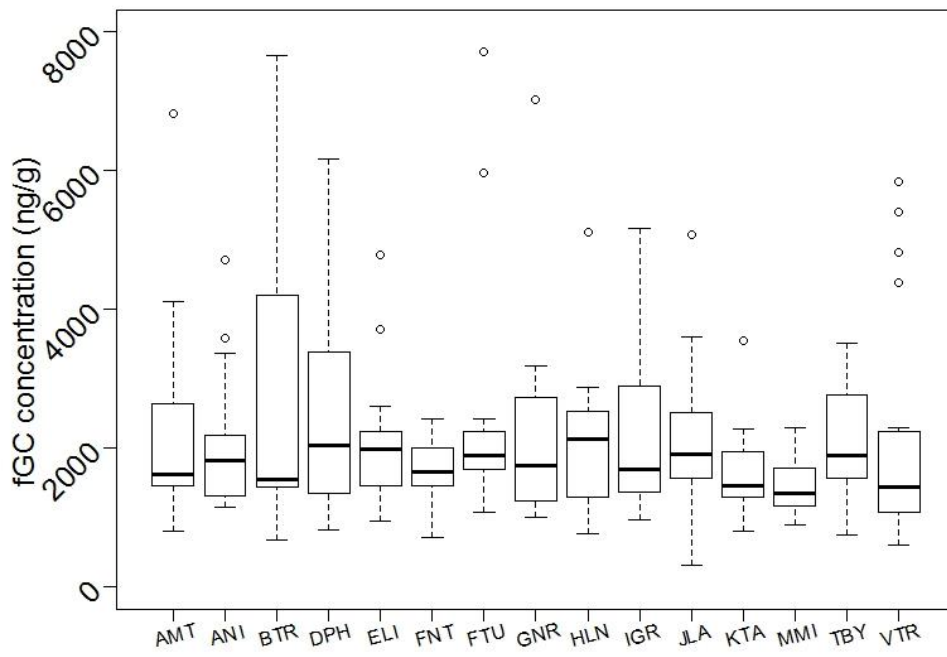


Figure S3. Faecal glucocorticoid concentrations per female.

Methods

Interactions between gangs

The vast majority of female-female interactions occurred within the gang, for example only 0.47% of greetings and 0.40% of infant handlings occurring with females from other gangs; focal females were never observed to contact sit or groom with females from other gangs during focal observations. However, females were observed to engage in inter-gang grooming bouts on two occasions during ad libitum observations. Dyadic agonistic interactions between females of different gangs were not observed, but females from the Mare gang would occasionally participate in group-level agonistic events involving males and females from other gangs. Due to the minimal number of social interactions which occurred between females of different gangs, we excluded non-gang females in the analyses.

Validation and calculation of dynamic sociality indices

Comparative sociality indices (CSIs) have been used to measure the extent to which a dyad's social tendencies deviates from the average group level of sociality (Silk et al., 2006a). However, such matrix based methods are limited by demographic changes and can also not detect short term changes in relationship dynamics (Kulik and Mundry, in prep). Female Guinea baboons are serially monogamous (Goffe et al., 2016), yet field observations indicated that the one male unit (OMU), consisting of a primary male and one or more adult females, is not a closed social group. Close proximity (2 m) and social interactions occur between females of different OMUs and parties within the same gang (Goffe unpublished data).

In order to assess the efficacy of the dynamic index method proposed by (Kulik and Mundry, in prep) we used a similar methodology to that used for calculating the CSI (Silk et al., 2006a). To start, we assessed the inclusion of the frequency and duration of grooming and contact sitting, and the frequency of greeting and infant handling with using the mantel test in the R-package *vegan* (Oksanen et al., 2016). Spearman correlations of the 15 matrices revealed that all r values indicated a strong positive correlation between the behaviours (mean \pm standard deviation (range) = 0.712 ± 0.235 (0.424-1)).

We then calculated the CSIs for 15 females during a two month period when no females changed OMU membership and there were no obvious shifts in male party or gang affiliation.

$$CSI = \frac{\left(\frac{FG_{ij}}{FG_{ave}}\right) + \left(\frac{FS_{ij}}{FS_{ave}}\right) + \left(\frac{FT_{ij}}{FT_{ave}}\right) + \left(\frac{FH_{ij}}{FH_{ave}}\right) + \left(\frac{DG_{ij}}{DG_{ave}}\right) + \left(\frac{DS_{ij}}{DS_{ave}}\right)}{6}$$

Where the three terms, FG_{ij} , FS_{ij} , FT_{ij} and FH_{ij} , representing the hourly frequency at which grooming, contact sitting, greeting and infant handling occurred within a dyad, are divided by their respective average hourly frequency across all dyads FG_{ave} , FS_{ave} , FT_{ave} and FH_{ave} . The two terms DG_{ij} and DS_{ij} represent durations of grooming and contact sitting within a dyad and divided by their respective durations across all dyads DG_{ave} and DS_{ave} . The sum of these terms is then divided by the number of behaviours included, 6. This calculation automatically centres the group mean at one; dyads with CSI scores which are above the group mean are those which have strong social relationships.

Using the same variables included in the CSI calculation we then calculated the dynamic association index (DAI) for the same female dyads. The DAI was calculated so that, in a group consisting of individuals A, B, C and D, a grooming bout between A & B results in an increase in their DAI value, a corresponding decrease in the DAI values of dyads A-C, A-D, B-C and B-D, but no change in the DAI value of dyad C-D. The gain factor for each interaction was set at 0.05 (range=0 to 1, inclusive) and the interactions were unweighted. The initial burn-in phase was determined by comparing the cross-correlation coefficients of DAI values at two-week intervals. As there are initial “start-up” costs to this method, we assessed the burn-in phase using cross-correlations and excluded the first month of data collection as values from this period were highly influenced by the artificial starting values. In addition, a dynamic proximity index (DPI) was calculated in a similar manner, with the exception that we used weighted proximity distances (as specified in the main text). DAI and DPI scores were extrapolated for all dyads on days when an interaction was not observed to occur.

Hormone assay validation

We performed a comparison of three faecal glucocorticoid (fGC) assays commonly used in other mammalian species in order to determine which assay was the most sensitive

for assessing adrenocortical activity in female Guinea baboons. The annual capture of individuals for biological sample collection and changing GPS and radio collars was used as an experimental “stressor”. For each of the 12 females assessed, 2 fGC samples were available in the pre-capture period (baseline) and 1-2 fGC samples (mean=1.67) were available during the capture period. The 11-oxoetiocholanolone assay (range=800-4,783 ng/g) showed a higher level of variability than both 11 β -hydroxyetiocholanolone (range=450-1,982 ng/g) and cortisol (range=25-319 ng/g) assays (Mann-Whitney U Test: $W=384$, $P<0.005$) when pre- and during capture fGC levels were analysed. Values for 11-oxoetiocholanolone assay in the pre-capture phase were lower (median=1336, IQR=1020-1571) than in the capture phase (median=2058, IQR=1459-2353). (Kruskall-Wallis Test: $\chi^2=9.02$, $df=1$, $P<0.005$).

REFERENCES

- Abbott, D.H., Saltzman, W., Schultz-Darken, N.J., and Smith, T.E. (1997). Specific neuroendocrine mechanisms not involving generalized stress mediate social regulation of female reproduction in cooperatively breeding marmoset monkeys. *Ann. N. Y. Acad. Sci.* *807*, 219–238.
- Abbott, D.H., Keverne, E.B., Bercovitch, F.B., Shively, C.A., Mendoza, S.P., Saltzman, W., Snowdon, C.T., Ziegler, T.E., Banjevic, M., Garland, T., et al. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Horm. Behav.* *43*, 67–82.
- Ajrouch, K.J., Blandon, A.Y., and Antonucci, T.C. (2005). Social networks among men and women: The effects of age and socioeconomic status. *J. Gerontol. B. Psychol. Sci. Soc. Sci.* *60*, S311–S317.
- Albers, P.C.H., and de Vries, H. (2001). Elo-rating as a tool in the sequential estimation of dominance strengths. *Anim. Behav.* *61*, 489–495.
- Albert, S.C., and Altmann, J. (1995). Preparation and activation: determinants of age at reproductive maturity in male baboons. *Behav. Ecol. Sociobiol.* *36*, 397–406.
- Alberts, S.C., Altmann, J., and Wilson, M.L. (1996). Mate guarding constrains foraging activity of male baboons. *Anim. Behav.* *51*, 1269–1277.
- Alerstam, T., and Lindström, A.A. (1990). Optimal bird migration: the relative importance of time, energy, and safety. In *Bird Migration*, (Springer), pp. 331–351.
- Altmann, J. (1974). Observational Study of Behavior: sampling methods. *Behaviour* *49*, 227–267.
- Altmann, J. (1990). Primate males go where the females are. *Anim. Behav.* *39*, 193–195.
- Altmann, J. (1997). Mate choice and intrasexual reproductive competition: contributions to reproduction that go beyond acquiring more mates. In *Feminism and Evolutionary Biology*, P.A. Gowaty, ed. (New York: Chapman and Hall), pp. 320–333.
- Anderson, J.R., and McGrew, W.C. (1984). Guinea baboons (*Papio papio*) at a sleeping site. *Am. J. Primatol.* *6*, 1–14.
- Andersson, M.B. (1994). *Sexual Selection* (Princeton University Press).
- Appleby, M.C. (1983). The probability of linearity in hierarchies. *Anim. Behav.* *31*, 600–608.
- Archie, E.A. (2013). Wound healing in the wild: stress, sociality, and energetic costs affect wound healing in natural populations. *Parasite Immunol.* *35*, 374–385.
- Archie, E.A., Moss, C.J., and Alberts, S.C. (2011). Friends and relations: Kinship and the nature of female elephant social relationships. *Amboseli Elephants Long-Term Perspect. Long-Lived Mamma Ed Moss CJ Croze H* 238–245.
- Asa, C.S., and Porton, I.J. (2010). Contraception as a management tool for controlling surplus animals. In *Wild Mammals in Captivity: Principles and Techniques for Zoo Management*, D.G. Kleiman, K.V. Thompson, and C.K. Baer, eds. (University of Chicago Press), pp. 469–482.

- Asher, M., De Oliveira, E.S., and Sachser, N. (2004). Social system and spatial organization of wild guinea pigs (*Cavia aperea*) in a natural population. *J. Mammal.* *85*, 788–796.
- Baayen, R.H., Davidson, D.J., and Bates, D.M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *J. Mem. Lang.* *59*, 390–412.
- Bădescu, I., Sicotte, P., Ting, N., and Wikberg, E.C. (2015). Female parity, maternal kinship, infant age and sex influence natal attraction and infant handling in a wild colobine (*Colobus vellerosus*). *Am. J. Primatol.* *77*, 376–387.
- Barber, I., Nairn, D., and Huntingford, F.A. (2001). Nests as ornaments: revealing construction by male sticklebacks. *Behav. Ecol.* *12*, 390–396.
- Barton, R.A., and Whiten, A. (1993). Feeding competition among female olive baboons, *Papio anubis*. *Anim. Behav.* *46*, 777–789.
- Bateman, A.J. (1948). Intrasexual-selection in *Drosophila*. *Heredity* *2*, 349–368.
- Bates, D., Maechler, M., Bolker, B.M., and Walker, S. (2013). lme4: linear mixed-effects models using Eigen and S4.
- Beaulieu, M., Mboumba, S., Willaume, E., Kappeler, P.M., and Charpentier, M.J.E. (2014). The oxidative cost of unstable social dominance. *J. Exp. Biol.* *217*, 2629–2632.
- Beehner, J.C. (2003). Female Behavior and Reproductive Success in a Hybrid Baboon Group. Doctoral dissertation. Washington University.
- Begg, C.M., Begg, K.S., Du Toit, J.T., and Mills, M.G.L. (2006). Spatial organization of the honey badger *Mellivora capensis* in the southern Kalahari: home-range size and movement patterns. *J. Zool.* *265*, 23–35.
- Benenson, J.F. (2013). The development of human female competition: allies and adversaries. *Philos. Trans. R. Soc. B Biol. Sci.* *368*, 20130079.
- Bensch, S., and Hasselquist, D. (1992). Evidence for active female choice in a polygynous warbler. *Anim. Behav.* *44*, 301–311.
- Bergman, T.J., and Beehner, J.C. (2004). Social system of a hybrid baboon group (*Papio anubis* X *P. hamadryas*). *Int. J. Primatol.* *25*, 1313–1330.
- Best, E.C., Dwyer, R.G., Seddon, J.M., and Goldizen, A.W. (2014). Associations are more strongly correlated with space use than kinship in female eastern grey kangaroos. *Anim. Behav.* *89*, 1–10.
- Blaustein, A.R. (1983). Kin recognition mechanisms: phenotypic matching or recognition alleles? *Am. Nat.* *121*, 749–754.
- Blouin, M.S. (2003). DNA-based methods for pedigree reconstruction and kinship analysis in natural populations. *Trends Ecol. Evol.* *18*, 503–511.
- Blouin, M.S., Parsons, M., Lacaille, V., and Lotz, S. (1996). Use of microsatellite loci to classify individuals by relatedness. *Mol. Ecol.* *5*, 393–401.
- Boese, G.K. (1973). Behavior and social organization of the Guinea baboon (*Papio papio*). Doctoral dissertation. The Johns Hopkins University.

- Boese, G.K. (1975). Social behavior and ecological considerations of West African baboons (*Papio papio*). In *Socioecology and Psychology of Primates*, R.H. Tuttle, ed. (The Hague: Mouton), pp. 205–230.
- Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., et al. (2012). Costs of dispersal. *Biol. Rev.* *87*, 290–312.
- Borgia, G. (1986). Sexual selection in bowerbirds. *Sci. Am.* *254*, 92–100.
- Borgia, G., Pruett-Jones, S.G., and Pruett-Jones, M.A. (1985). The Evolution of Bower-building and the Assessment of Male Quality. *Z Tierpsychol* *67*, 225–236.
- Bowler, D.E., and Benton, T.G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.* *80*, 205–225.
- Bradley, B.J., Doran-Sheehy, D.M., and Vigilant, L. (2007). Potential for female kin associations in wild western gorillas despite female dispersal. *Proc. R. Soc. B Biol. Sci.* *274*, 2179–2185.
- Breed, M.D. (2014). Kin and nestmate recognition: the influence of W. D. Hamilton on 50 years of research. *Anim. Behav.* *92*, 271–279.
- Breed, G.A., Bowen, W., McMillan, J., and Leonard, M. (2006). Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proc. R. Soc. B Biol. Sci.* *273*, 2319–2326.
- Butynski, T.M. (1982). Vertebrate predation by primates: a review of hunting patterns and prey. *J. Hum. Evol.* *11*, 421–430.
- Byrne, R.W., Whiten, A., and Henzi, S.P. (1987). One-male groups and intergroup interactions of mountain baboons. *Int. J. Primatol.* *8*, 615–633.
- Cameron, E.Z., Setsaas, T.H., and Linklater, W.L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proc. Natl. Acad. Sci.* *106*, 13850–13853.
- Campbell, A. (2013). The evolutionary psychology of women's aggression. *Philos. Trans. R. Soc. B Biol. Sci.* *368*, 20130078.
- Cantarero, A., López-Arrabé, J., Palma, A., Redondo, A.J., and Moreno, J. (2014). Males respond to female begging signals of need: a handicapping experiment in the pied flycatcher, *Ficedula hypoleuca*. *Anim. Behav.* *94*, 167–173.
- Carter, G.G., and Wilkinson, G.S. (2013). Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proc. R. Soc. Lond. B Biol. Sci.* *280*, 20122573.
- Castles, M., Heinsohn, R., Marshall, H.H., Lee, A.E.G., Cowlshaw, G., and Carter, A.J. (2014). Social networks created with different techniques are not comparable. *Anim. Behav.* *96*, 59–67.
- Chang, Z., Yang, B., Vigilant, L., Liu, Z., Ren, B., Yang, J., Xiang, Z., Garber, P.A., and Li, M. (2014). Evidence of male-biased dispersal in the endangered Sichuan snub-nosed monkey (*Rhinopithecus roxellana*): Dispersal Pattern of *R. roxellana*. *Am. J. Primatol.* *76*, 72–83.
- Chapais, B. (2001). Primate nepotism: what is the explanatory value of kin selection? *Int. J. Primatol.* *22*, 203–229.
- Chapais, B. (2006). Kinship, competence and cooperation in primates. In *Cooperation in Primates and Humans*, (Springer), pp. 47–64.

- Chapais, B. (2013). Monogamy, strongly bonded groups, and the evolution of human social structure. *Evol. Anthropol. Issues News Rev.* 22, 52–65.
- Chapais, B., Savard, L., and Gauthier, C. (2001). Kin selection and the distribution of altruism in relation to degree of kinship in Japanese macaques (*Macaca fuscata*). *Behav. Ecol. Sociobiol.* 49, 493–502.
- Charif, R.A., Ramey, R.R., Langbauer, W.R., Payne, K.B., Martin, R.B., and Brown, L.M. (2005). Spatial relationships and matrilineal kinship in African savanna elephant (*Loxodonta africana*) clans. *Behav. Ecol. Sociobiol.* 57, 327–338.
- Cheney, D.L. (1978). Interactions of immature male and female baboons with adult females. *Anim. Behav.* 26, 389–408.
- Cheney, D.L., Seyfarth, R.M., and Silk, J.B. (1995). The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: evidence for causal reasoning? *J. Comp. Psychol.* 109, 134–141.
- Cheney, D.L., Silk, J.B., and Seyfarth, R.M. (2012). Evidence for intrasexual selection in wild female baboons. *Anim. Behav.* 84, 21–27.
- Chowdhury, S., Pines, M., Saunders, J., and Swedell, L. (2015). The adaptive value of secondary males in the polygynous multi-level society of hamadryas baboons. *Am. J. Phys. Anthropol.* 158, 501–513.
- Chung, S., Son, G.H., and Kim, K. (2011). Circadian rhythm of adrenal glucocorticoid: Its regulation and clinical implications. *Biochim. Biophys. Acta BBA - Mol. Basis Dis.* 1812, 581–591.
- Clark, T.S., and Linzer, D.A. (2015). Should I Use Fixed or Random Effects? *Polit. Sci. Res. Methods* 3, 399–408.
- Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S., and Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* 12, 197–209.
- Clutton-Brock, T. (2009). Sexual selection in females. *Anim. Behav.* 77, 3–11.
- Clutton-Brock, T.H. (1989a). Mammalian mating systems. *Proc. R. Soc. Lond. B Biol. Sci.* 236, 339–372.
- Clutton-Brock, T.H. (1989b). Female transfer and inbreeding avoidance in social mammals. *Nature* 337, 70–72.
- Clutton-Brock, T.H. (1991). *The Evolution of Parental Care* (Princeton University Press).
- Clutton-Brock, T., and Huchard, E. (2013). Social competition and its consequences in female mammals: female reproductive competition in mammals. *J. Zool.* 289, 151–171.
- Clutton-Brock, T., and McAuliffe, K. (2009). Female Mate Choice in Mammals. *Q. Rev. Biol.* 84, 3–27.
- Clutton-Brock, T.H., and Lukas, D. (2012). The evolution of social philopatry and dispersal in female mammals: PHILOPATRY AND DISPERSAL IN FEMALE MAMMALS. *Mol. Ecol.* 21, 472–492.

- Clutton-Brock, T.H., Hodge, S.J., Spong, G., Russell, A.F., Jordan, N.R., Bennett, N.C., Sharpe, L.L., and Manser, M.B. (2006). Intrasexual competition and sexual selection in cooperative mammals. *Nature* *444*, 1065–1068.
- Cohas, A., and Allainé, D. (2009). Social structure influences extra-pair paternity in socially monogamous mammals. *Biol. Lett.* *5*, 313–316.
- Cohas, A., Yoccoz, N.G., Da Silva, A., Goossens, B., and Allainé, D. (2006). Extra-pair paternity in the monogamous alpine marmot (*Marmota marmota*): the roles of social setting and female mate choice. *Behav. Ecol. Sociobiol.* *59*, 597–605.
- Cohen, S., and McKay, G. (1984). Social Support, Stress and the Buffering Hypothesis: A Theoretical Analysis. In *Handbook of Psychology and Health*, (Hillsdal, New Jersey), pp. 253–367.
- Cohen, S., and Willis, T.A. (1985). Stress, Social Support, and the Buffering Hypothesis. *Psychol. Bull.* *98*, 310–357.
- Cohen, S., Gottlieb, B.H., and Underwood, L.G. (2000). Social Relationships and Health. In *Social Support Measurement and Intervention. A Guide for Health and Social Scientists.*, (New York: Oxford University Press, USA), pp. 3–25.
- Colquhoun, D. (2014). An investigation of the false discovery rate and the misinterpretation of p-values. *R. Soc. Open Sci.* *1*, 140216.
- Conde, D.A., Colchero, F., Zarza, H., Christensen, N.L., Sexton, J.O., Manterola, C., Chávez, C., Rivera, A., Azuara, D., and Ceballos, G. (2010). Sex matters: Modeling male and female habitat differences for jaguar conservation. *Biol. Conserv.* *143*, 1980–1988.
- Couzin, I.D. (2006). Behavioral ecology: social organization in fission–fusion societies. *Curr. Biol.* *16*, R169–R171.
- Crockford, C., Wittig, R.M., Whitten, P.L., Seyfarth, R.M., and Cheney, D.L. (2008). Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Horm. Behav.* *53*, 254–265.
- Crockford, C., Wittig, R.M., Langergraber, K., Ziegler, T.E., Zuberbuhler, K., and Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proc. R. Soc. B Biol. Sci.* *280*, 20122765.
- Csárdi, G., and Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal Complex Syst.* *1695*, 1–9.
- Dal Pesco, F. (2013). Greeting behaviour in wild Guinea baboons (*Papio papio*) in Niokolo-Koba National Park, Senegal. Freie Universität Berlin.
- D’Amato, F.R., Troisi, A., Scucchi, S., and Fuccillo, R. (1982). Mating season influence on allogrooming in a confined group of Japanese macaques: a quantitative analysis. *Primates* *23*, 220–232.
- Darwin, C. (1871). *The Descent of Man*.
- Davies, N.B., and Lundberg, A. (1984). Food Distribution and a Variable Mating System in the Dunnock, *Prunella modularis*. *J. Anim. Ecol.* *53*, 895–912.
- De Waal, F.B.M. (1997). The chimpanzee’s service economy: food for grooming. *Evol. Hum. Behav.* *18*, 375–386.

- Delson, E. (1993). *Theropithecus* fossils from Africa and India and the taxonomy of the genus. In *Theropithecus: The Rise and Fall of a Primate Genus*, Nina G. Jablonski, ed. (Cambridge: Cambridge University Press), pp. 157–189.
- Demšar, J. (2006). Statistical comparisons of classifiers over multiple data sets. *J. Mach. Learn. Res.* 7, 1–30.
- DeVries, A.C., Gasper, E.R., and Detillion, C.E. (2003). Social modulation of stress responses. *Physiol. Behav.* 79, 399–407.
- Di Fiore, A., and Rendall, D. (1994). Evolution of social organization: A reappraisal for primates by using phylogenetic methods. *Proc. Natl. Acad. Sci. U. S. A.* 91, 9941–9945.
- Dobson, F.S. (1982). Competition for mates and predominant juvenile male dispersal in mammals. *Anim. Behav.* 30, 1183–1192.
- Dobson, F.S. (2013). The enduring question of sex-biased dispersal: Paul J. Greenwood's (1980) seminal contribution. *Anim. Behav.* 85, 299–304.
- Domb, L.G., and Pagel, M. (2001). Sexual swellings advertise female quality in wild baboons. *Nature* 410, 204–205.
- Doran, D.M., Jungers, W.L., Sugiyama, Y., Fleagle, J.G., and Heesy, C.P. (2002). Multivariate and phylogenetic approaches to understanding chimpanzee and bonobo behavioral diversity. In *Sex-Biased Dispersal and Inbreeding Avoidance in Birds and Mammals*, C. Boesch, G. Hohmann, and L.F. Marchant, eds. (United Kingdom: Cambridge University Press), pp. 14–34.
- Drea, C.M. (2005). Bateman revisited: The reproductive tactics of female primates. *Integr. Comp. Biol.* 45, 915–923.
- Dunbar, R.I.M. (1983). Structure of gelada baboon reproductive units II. Social relationships between reproductive females. *Anim. Behav.* 31, 556–564.
- Dunbar, R.I.M. (1984). *Reproductive decisions: An economic analysis of gelada baboon social strategies* (Princeton, New Jersey: Princeton University Press).
- Dunbar, R.I.M. (1991). Functional Significance of Social Grooming in Primates. *Folia Primatol. (Basel)* 57, 121–131.
- Dunbar, R.I.M. (1992). A model of the gelada socio-ecological system. *Primates* 33, 69–83.
- Dunbar, R.I.M., and Dunbar, P. (1975a). *Social dynamics of gelada baboons* (Basel: S. Karger).
- Dunbar, R.I.M., and Dunbar, P. (1975b). III. Structure and Dynamics of Reproductive Units. In *Social Dynamics of Gelada Baboons*, pp. 31–58.
- Dunbar, R.I.M., and Nathan, M.F. (1972). Social Organization of the Guinea Baboon, *Papio papio*. *Folia Primatol. (Basel)* 17, 321–334.
- Eens, M., and Pinxten, R. (2000). Sex-role reversal in vertebrates: behavioural and endocrinological accounts. *Behav. Processes* 51, 135–147.
- Efron, B., and Tibshirani, R. (1998). *An introduction to the bootstrap* (New York: Chapman & Hall).
- Emlen, S.T., and Oring, L.W. (1977). Ecology, Sexual Selection, and the Evolution of Mating Systems. *Science* 197, 215–223.

- Engelhard, G.H., Brasseur, S.M.J.M., Hall, A.J., Burton, H.R., and Reijnders, P.J.H. (2002). Adrenocortical responsiveness in southern elephant seal mothers and pups during lactation and the effect of scientific handling. *J. Comp. Physiol. [B]* 172, 315–328.
- von Engelhard, N., Kappeler, P.M., and Heistermann, M. (2000). Androgen levels and female social dominance in *Lemur catta*. *Proc. R. Soc. B Biol. Sci.* 267, 1533–1539.
- Engh, A.L., Beehner, J.C., Bergman, T.J., Whitten, P.L., Hoffmeier, R.R., Seyfarth, R.M., and Cheney, D.L. (2006a). Female hierarchy instability, male immigration and infanticide increase glucocorticoid levels in female chacma baboons. *Anim. Behav.* 71, 1227–1237.
- Engh, A.L., Beehner, J.C., Bergman, T.J., Whitten, P.L., Hoffmeier, R.R., Seyfarth, R.M., and Cheney, D.L. (2006b). Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proc. R. Soc. Lond. B Biol. Sci.* 273, 707.
- Epple, G. (1978). Lack of effects of castration on scent marking, displays, and aggression in a South American primate (*Saguinus fuscicollis*). *Horm. Behav.* 11, 139–150.
- Fabiani, A. (2004). Extreme polygyny among southern elephant seals on Sea Lion Island, Falkland Islands. *Behav. Ecol.* 15, 961–969.
- Fagiolo, G., Reyes, J., and Schiavo, S. (2008). On the topological properties of the world trade web: a weighted network analysis. *Phys. A* 387, 3868–3873.
- Feh, C. (1999). Alliances and reproductive success in Camargue stallions. *Anim. Behav.* 57, 705–713.
- Feistner, A.T.C., and McGrew, W.C. (1989). Food sharing primates: a critical review. In *Perspectives in Primate Biology*, (New Delhi, India: Today & Tomorrow Printers and Publishers), pp. 21–36.
- Fernandes, W.P.A., Ibbotson, A.T., Griffiths, S.W., Maxwell, D.L., Davison, P.I., and Riley, W.D. (2015). Does relatedness influence migratory timing and behaviour in Atlantic salmon smolts? *Anim. Behav.* 106, 191–199.
- Fernando, P., and Lande, R. (2000). Molecular genetic and behavioral analysis of social organization in the Asian elephant (*Elephas maximus*). *Behav. Ecol. Sociobiol.* 48, 84–91.
- Ferreira da Silva, M.J., Casanova, C., and Godinho, R. (2013). On the western fringe of baboon distribution: mitochondrial D-loop diversity of Guinea Baboons (*Papio papio* Desmarest, 1820) (Primates: *Cercopithecidae*) in Coastal Guinea-Bissau, western Africa. *J. Threat. Taxa* 5, 4441–4450.
- Fickenscher, G. (2010). Genetic Population Structure of Free-Ranging Guinea Baboons (*Papio papio*) in the Niokolo-Koba Nationalpark, Senegal. Diploma thesis. Georg-August-Universität.
- Fickenscher, G., Ferreira da Silva, M.J., Patzelt, A., Roos, C., Fischer, J., and Zinner, D. (2011). Genetic Evidence for Male Philopatry in Guinea Baboons. *Folia Primatol. (Basel)* 82, 365.
- Field, A.P. (2009). *Discovering statistics using SPSS* (Los Angeles: SAGE).
- Fitzpatrick, J.L., Desjardins, J.K., Milligan, N., Stiver, K.A., Montgomerie, R., and Balshine, S. (2008). Female-mediated causes and consequences of status change in a social fish. *Proc. R. Soc. B Biol. Sci.* 275, 929–936.
- Folstad, I., and Karter, A.J. (1992). Parasites, bright males, and the Immunocompetence Handicap. *Am. Nat.* 139, 603–622.

- Frank, E.M. (2015). The role of infants in mediating social interactions in wild Guinea baboons (*Papio papio*) in the Niokolo Koba National Park, Senegal. Diploma thesis. Johannes Gutenberg University.
- Frank, R., and Silk, J. (2009). Grooming exchange between mothers and non-mothers: the price of natal attraction in wild baboons (*Papio anubis*). *Behaviour* 146, 889–906.
- Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N., and Skalski, G.T. (2001). Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *Am. Nat.* 158, 124–135.
- Friedman, M. (1940). A comparison of alternative tests of significance for the problem of m rankings. *Ann. Math. Stat.* 11, 86–92.
- Fruchterman, T.M., and Reingold, E.M. (1991). Graph drawing by force-directed placement. *Softw. Pract. Exp.* 21, 1129–1164.
- Furuichi, T. (1989). Social interactions and the life history of female *Pan paniscus* in Wamba, Zaire. *Int. J. Primatol.* 10, 173–197.
- Furuichi, T. (2011). Female contributions to the peaceful nature of bonobo society. *Evol. Anthropol. Issues News Rev.* 20, 131–142.
- Galat-Luong, A., Galat, G., and Hagell, S. (2006). The Social and Ecological Flexibility of Guinea Baboons: Implications for Guinea Baboon Social Organization and Male Strategies. In *Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives*, L. Swedell, and S.R. Leigh, eds. (Springer New York), pp. 105–121.
- Ganswindt, A., Palme, R., Heistermann, M., Borragan, S., and Hodges, J.K. (2003). Non-invasive assessment of adrenocortical function in the male African elephant (*Loxodonta africana*) and its relation to musth. *Gen. Comp. Endocrinol.* 134, 156–166.
- Gardner, A., and West, S.A. (2007). Social evolution: the decline and fall of genetic kin recognition. *Curr. Biol.* 17, R810–R812.
- Gauthier, C.-A. (1999). Reproductive Parameters and Paracallosal Skin Color Changes in Captive Female Guinea Baboons, *Papio papio*. *Am. J. Primatol.* 47, 67–74.
- Getz, W.M., and Smith, K.B. (1983). Genetic kin recognition: honey bees discriminate between full and half sisters. *Nature* 302, 147–148.
- Gilby, I.C. (2006). Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Anim. Behav.* 71, 953–963.
- Gilby, I.C., Eberly, L.E., and Wrangham, R.W. (2008). Economic profitability of social predation among wild chimpanzees: individual variation promotes cooperation. *Anim. Behav.* 75, 351–360.
- Gilby, I.C., Brent, L.J.N., Wroblewski, E.E., Rudicell, R.S., Hahn, B.H., Goodall, J., and Pusey, A.E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behav. Ecol. Sociobiol.* 67, 373–381.
- Gilchrist, J.S. (2006). Female eviction, abortion, and infanticide in banded mongooses (*Mungos mungo*): implications for social control of reproduction and synchronized parturition. *Behav. Ecol.* 17, 664–669.
- Gillman, J. (1940). The effect of multiple injections of progesterone on the turgescence of the perineum of the baboon (*Papio papio*). *Endocrinology* 26, 1072–1077.

- Girard-Buttoz, C., Heistermann, M., Rahmi, E., Agil, M., Fauzan, P.A., and Engelhardt, A. (2014a). Costs of and Investment in Mate-Guarding in Wild Long-Tailed Macaques (*Macaca fascicularis*): Influences of Female Characteristics and Male–Female Social Bonds. *Int. J. Primatol.* *35*, 701–724.
- Girard-Buttoz, C., Heistermann, M., Rahmi, E., Agil, M., Ahmad Fauzan, P., and Engelhardt, A. (2014b). Costs of mate-guarding in wild male long-tailed macaques (*Macaca fascicularis*): Physiological stress and aggression. *Horm. Behav.* *66*, 637–648.
- Girard-Buttoz, C., Heistermann, M., Rahmi, E., Marzec, A., Agil, M., Fauzan, P.A., and Engelhardt, A. (2014c). Mate-guarding constrains feeding activity but not energetic status of wild male long-tailed macaques (*Macaca fascicularis*). *Behav. Ecol. Sociobiol.* *68*, 583–595.
- Goffe, A.S., and Fischer, J. (2016). Meat sharing between male and female Guinea baboons (*Papio papio*). *Primate Biol.* *3*, 1–8.
- Goffe, A.S., Zinner, D., and Fischer, J. (2016). Sex and friendship in a multilevel society: behavioural patterns and associations between female and male Guinea baboons. *Behav. Ecol. Sociobiol.* *70*, 323–336.
- Goldizen, A.W. (1987). Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behav. Ecol. Sociobiol.* *20*, 99–109.
- Gomes, C.M., and Boesch, C. (2009). Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS ONE* *4*, 5116.
- González-Solís, J., Croxall, J.P., and Wood, A.G. (2000). Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. *Oikos* *90*, 390–398.
- Goubault, M., Cortesero, A.M., Poinso, D., Wajnberg, E., and Boivin, G. (2007). Does Host Value Influence Female Aggressiveness, Contest Outcome and Fitness Gain in Parasitoids? *Ethology* *113*, 334–343.
- Goudet, J., and Jombard, T. (2015). Estimation and Tests of Hierarchical F-Statistics.
- Goymann, W. (2012). On the use of non-invasive hormone research in uncontrolled, natural environments: the problem with sex, diet, metabolic rate and the individual: Non-invasive hormone research. *Methods Ecol. Evol.* *3*, 757–765.
- Goymann, W., East, M.L., and Hofer, H. (2001). Androgens and the Role of Female “Hyperaggressiveness” in Spotted Hyenas (*Crocuta crocuta*). *Horm. Behav.* *39*, 83–92.
- Greenwood, P.J. (1980). Mating Systems, Philopatry and Dispersal in Birds and Mammals. *Anim. Behav.* *28*, 1140–1162.
- Gruber, B., and Adamack, A. (2014). PopGenReport: simplifying basic population genetic analyses in R. *Methods Ecol. Evol.* *5*, 384–387.
- Grueter, C.C., and van Schaik, C.P. (2009). Evolutionary determinants of modular societies in colobines. *Behav. Ecol.* *21*, 63–71.
- Grueter, C.C., Chapais, B., and Zinner, D. (2012). Evolution of Multilevel Social Systems in Nonhuman Primates and Humans. *Int. J. Primatol.* *33*, 1002–1037.
- Grüter, C.C., and Zinner, D. (2004). Nested Societies: Convergent Adaptation of Baboons and Snub-nosed Monkeys? *Primate Rep.* *70*, 1–98.

- Guo, S., Huang, K., Ji, W., Garber, P.A., and Li, B. (2014). The role of kinship in the formation of a primate multilevel society: Kinship In a Primate Multilevel Society. *Am. J. Phys. Anthropol.* 606–613.
- Halliday, T. (1997). Study of mate choice. In *Mate Choice*, P. Bateson, ed. (Cambridge: Cambridge University Press), pp. 3–32.
- Halsey, L.G., Curran-Everett, D., Vowler, S.L., and Drummond, G.B. (2015). The fickle P value generates irreproducible results. *Nat. Methods* 12, 179–185.
- Hämäläinen, A., Heistermann, M., Fenosa, Z.S.E., and Kraus, C. (2014). Evaluating capture stress in wild gray mouse lemurs via repeated fecal sampling: Method validation and the influence of prior experience and handling protocols on stress responses. *Gen. Comp. Endocrinol.* 195, 68–79.
- Hamilton, I.M. (2004). A commitment model of reproductive inhibition in cooperatively breeding groups. *Behav. Ecol.* 15, 585–591.
- Hamilton, W.D. (1964). The genetical evolution of social behaviour. I. *J. Theor. Biol.* 7, 1–16.
- Hamilton, W.J., and Busse, C. (1982). Social dominance and predatory behavior of chacma baboons. *J. Hum. Evol.* 11, 567–573.
- Hammond, R.L., Lawson Handley, L.J., Winney, B.J., Bruford, M.W., and Perrin, N. (2006). Genetic evidence for female-biased dispersal and gene flow in a polygynous primate. *Proc. R. Soc. Lond. B Biol. Sci.* 273, 479–484.
- Hans Kummer (1990). The social system of *Hamadryas* baboons and its presumable evolution. In *Selected Proceedings of the XIIth Congress of the International Primatological Society*, M. Thiago de Mello, A. Whiten, and R.W. Byrne, eds. (Brasil), pp. 43–60.
- Harrison, F., Barta, Z., Cuthill, I., and Székely, T. (2009). How is sexual conflict over parental care resolved? A meta-analysis. *J. Evol. Biol.* 22, 1800–1812.
- Hastie, T., Tibshirani, R., and Friedman, J. (2001). *The elements of statistical learning* (Berlin: Springer).
- Haunhorst, C.B., Heistermann, M., Fürtbauer, I., Schülke, O., and Ostner, J. (in prep). Female competition for “power” and “commitment” in male partners--comparative data from macaques. *J. Hum. Evol.*
- Haunhorst, C.B., Heesen, M., Ostner, J., and Schülke, O. (under review). Social bonds with males lower costs of food competition for wild female Assamese macaques. *Behav. Ecol.*
- Heesen, M., Rogahn, S., Macdonald, S., Ostner, J., and Schülke, O. (2014). Predictors of food-related aggression in wild Assamese macaques and the role of conflict avoidance. *Behav. Ecol. Sociobiol.* 68, 1829–1841.
- Heistermann, M., Palme, R., and Ganswindt, A. (2006). Comparison of different enzymeimmunoassays for assessment of adrenocortical activity in primates based on fecal analysis. *Am. J. Primatol.* 68, 257–273.
- Henzi, S.P., and Barrett, L. (2002). Infants as a commodity in a baboon market. *Anim. Behav.* 63, 915–921.
- Henzi, S.P., Dyson, M.L., and Deenik, A. (1990). The relationship between altitude and group size in mountain baboons (*Papio cynocephalus ursinus*). *Int. J. Primatol.* 11, 319–325.

- Higham, J.P., MacLarnon, A.M., Ross, C., Heistermann, M., and Semple, S. (2008). Baboon sexual swellings: Information content of size and color. *Horm. Behav.* *53*, 452–462.
- Higham, J.P., Semple, S., MacLarnon, A., Heistermann, M., and Ross, C. (2009). Female reproductive signaling, and male mating behavior, in the olive baboon. *Horm. Behav.* *55*, 60–67.
- Hill, W.G., and Weir, B.S. (2011). Variation in actual relationship as a consequence of Mendelian sampling and linkage. *Genet. Res.* *93*, 47–64.
- Hill, R.A., Bentley, R.A., and Dunbar, R.I.M. (2008). Network scaling reveals consistent pattern in hierarchical mammalian societies. *Biol. Lett.* *4*, 748–751.
- Hinde, R.A. (1977). On assessing the bases of partner preferences. *Behaviour* *62*, 1–9.
- Hinde, R.A., and Atkinson, S. (1970). Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in rhesus monkeys. *Anim. Behav.* *18*, 169–176.
- Hirsch, B.T., Prange, S., Hauver, S.A., and Gehrt, S.D. (2013). Genetic relatedness does not predict racoon social network structure. *Anim. Behav.* *85*, 463–470.
- Hoffman, J.I., and Amos, W. (2005). Microsatellite genotyping errors: detection approaches, common sources and consequences for paternal exclusion. *Mol. Ecol.* *14*, 599–612.
- Hoffman, J.I., Forcada, J., Trathan, P.N., and Amos, W. (2007). Female fur seals show active choice for males that are heterozygous and unrelated. *Nature* *445*, 912–914.
- Holdo, R.M., Holt, R.D., and Fryxell, J.M. (2009). Opposing Rainfall and Plant Nutritional Gradients Best Explain the Wildebeest Migration in the Serengeti. *Am. Nat.* *173*, 431–445.
- Hosken, D.J., and Stockley, P. (2005). Sexual conflict. *Curr. Biol.* *15*, R535–R536.
- Huchard, E., Alvergne, A., Féjan, D., Knapp, L.A., Cowlshaw, G., and Raymond, M. (2009). More than friends? Behavioural and genetic aspects of heterosexual associations in wild chacma baboons. *Behav. Ecol. Sociobiol.* *64*, 769–781.
- Imamura, K. (2015). Life History and Sexual Relationships of Female Kalahari Hunter-Gatherers. In *Dispersing Primate Females*, T. Furuichi, J. Yamagiwa, and F. Aureli, eds. (Tokyo: Springer Japan), pp. 185–211.
- Isbell, L.A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behav. Ecol.* *2*, 143–155.
- Isbell, L.A., and Van Vuren, D. (1996). Differential costs of locational and social dispersal and their consequences for female group-living primates. *Behaviour* *133*, 1–36.
- Isbell, L.A., and Young, T.P. (2002). Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. *Behaviour* *139*, 177–202.
- Jaeggi, A.V., and Gurven, M. (2013). Natural cooperators: food sharing in humans and other primates. *Evol. Anthropol.* *22*, 186–195.
- Jaeggi, A.V., and van Schaik, C.P. (2011). The evolution of food sharing in primates. *Behav. Ecol. Sociobiol.* *65*, 2125–2140.
- Jarman, P. (1974). The social organisation of antelope in relation to their ecology. *Behaviour* *48*, 215–267.

- Jennings, D.J., Gammell, M.P., Carlin, C.M., and Hayden, T.J. (2004). Effect of body weight, antler length, resource value and experience on fight duration and intensity in fallow deer. *Anim. Behav.* *68*, 213–221.
- Jiang, Y., Bolnick, D.I., and Kirkpatrick, M. (2013). Assortative Mating in Animals. *Am. Nat.* *181*, E125–E138.
- Johnson, M.L., and Gaines, M.S. (1990). Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annu. Rev. Ecol. Syst.* *449–480*.
- Jolly, C.J. (2009). Fifty Years of Looking at Human Evolution: Backward, Forward, and Sideways. *Curr. Anthropol.* *50*, 187–199.
- Jolly, C.J., and Phillips-Conroy, J.E. (2003). Testicular size, mating system, and maturation schedules in wild anubis and hamadryas baboons. *Int. J. Primatol.* *24*, 125–142.
- Jolly, C.J., and Phillips-Conroy, J.E. (2006). Testicular Size, Developmental Trajectories, and Male Life History Strategies in Four Baboon Taxa. In *Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives*, L. Swedell, and S.R. Leigh, eds. (US: Springer Science & Business Media), pp. 257–275.
- Jones, A.G., and Ratterman, N.L. (2009). Mate choice and sexual selection: what have we learned since Darwin? *Proc. Natl. Acad. Sci.* *106*, 10001–10008.
- Jowett, B. (2006). *Symposium and Phaedrus (Echo Library)*.
- Kahlenberg, S.M., Emery Thompson, M., and Wrangham, R.W. (2008a). Female Competition over Core Areas in Pan troglodytes schweinfurthii, Kibale National Park, Uganda. *Int. J. Primatol.* *29*, 931–947.
- Kahlenberg, S.M., Thompson, M.E., Muller, M.N., and Wrangham, R.W. (2008b). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Anim. Behav.* *76*, 1497–1509.
- Kalbitz, J., Ostner, J., and Schülke, O. (2016). Strong, equitable and long-term social bonds in the dispersing sex in Assamese macaques. *Anim. Behav.* *113*, 13–22.
- Kalbitzer, U., Heistermann, M., Cheney, D., Seyfarth, R., and Fischer, J. (2015). Variation in aggressiveness and spatial tolerance between male chacma and Guinea baboons in relation to testosterone and glucocorticoid levels. *Horm. Behav.* *100–110*.
- Kanitz, E., Hameister, T., Tuchscherer, M., Tuchscherer, A., and Puppe, B. (2014). Social support attenuates the adverse consequences of social deprivation stress in domestic piglets. *Horm. Behav.* *65*, 203–210.
- Kano, T. (1992). *The last ape: pygmy chimpanzee behavior and ecology* (Stanford, California: Stanford University Press).
- Kappeler, P.M., and Fichtel, C. (2012). Female reproductive competition in *Eulemur rufifrons*: eviction and reproductive restraint in a plurally breeding Malagasy primate. *Mol. Ecol.* *21*, 685–698.
- Kappeler, P.M., and Schaik, C. van (2004). *Sexual selection in primates new and comparative perspectives* (Cambridge, UK; New York: Cambridge University Press).
- Kappeler, P.M., and van Schaik, C.P. (2002). Evolution of primate social systems. *Int. J. Primatol.* *23*, 707–740.

- Kapsalis, E., and Berman, C. (1996). Models of affiliative relationships among free-ranging macaque monkeys (*Macaca mulatta*) I. Criteria for kinship. *Behaviour* 133, 1209–1234.
- Kaseda, Y., and Khalil, A.M. (1996). Harem size and reproductive success of stallions in Misaki feral horses. *Appl. Anim. Behav. Sci.* 47, 163–173.
- Kasper, C., and Voelkl, B. (2009). A social network analysis of primate groups. *Primates* 50, 343–356.
- Kawai, M., and Mori, U. (1979). Spacing within units and unit integrity. In *Ecological and Sociological Studies of Gelada Baboons*, M. Kawai, ed. (Karger), pp. 199–217.
- Kerth, G., Perony, N., and Schweitzer, F. (2011). Bats are able to maintain long-term social relationships despite the high fission-fusion dynamics of their groups. *Proc. R. Soc. Lond. B Biol. Sci.* 278, 2761–2767.
- King, A.J., Isaac, N.J.B., and Cowlishaw, G. (2009). Ecological, social, and reproductive factors shape producer-scrounger dynamics in baboons. *Behav. Ecol.* 20, 1039–1049.
- Kirkpatrick, R.C., and Grueter, C.C. (2010). Snub-nosed monkeys: Multilevel societies across varied environments. *Evol. Anthropol. Issues News Rev.* 19, 98–113.
- Kirkpatrick, R.C., Long, Y.C., Zhong, T., and Xiao, L. (1998). Social organization and range use in the Yunnan snub-nosed monkey *Rhinopithecus bieti*. *Int. J. Primatol.* 19, 13–51.
- Kitchen, D.M., Beehner, J.C., Bergman, T.J., Cheney, D.L., Crockford, C., Engh, A.L., Fischer, J., Seyfarth, R.M., and Wittig, R. (2009). The causes and consequences of male aggression directed at female chacma baboons. In *Sexual Coercion in Primates and Humans: An Evolutionary Perspective on Male Aggression against Females*, (Cambridge, MA: Harvard University Press), pp. 128–156.
- Kleindorfer, S., and Wasser, S.K. (2004). Infant handling and mortality in yellow baboons (*Papio cynocephalus*): evidence for female reproductive competition? *Behav. Ecol. Sociobiol.* 56, 328–337.
- Knol, B.W., and Egberink-Alink, S.T. (1989). Androgens, progestagens and agonistic behaviour: A review. *Vet. Q.* 11, 94–101.
- Koch, F., Signer, J., Kappeler, P.M., and Fichtel, C. (2016). Intergroup encounters in Verreaux's sifakas (*Propithecus verreauxi*): who fights and why? *Behav. Ecol. Sociobiol.* 70, 797–808.
- Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *Int. J. Primatol.* 23, 759–783.
- Kokko, H., and Jennions, M.D. (2014). The Relationship between Sexual Selection and Sexual Conflict. *Cold Spring Harb. Perspect. Biol.* 6, a017517.
- Kokko, H., Brooks, R., McNamara, J.M., and Houston, A.I. (2002). The sexual selection continuum. *Proc. R. Soc. Lond. B Biol. Sci.* 269, 1331–1340.
- Kokko, H., Brooks, R., Jennions, M.D., and Morley, J. (2003). The evolution of mate choice and mating biases. *Proc. R. Soc. Lond. B Biol. Sci.* 270, 653–664.
- Kopp, G.H., Ferreira da Silva, M.J., Fischer, J., Brito, J.C., Regnaut, S., Roos, C., and Zinner, D. (2014). The influence of social systems on patterns of mitochondrial DNA variation in baboons. *Int. J. Primatol.* 35, 210–225.

- Kopp, G.H., Fischer, J., Patzelt, A., Roos, C., and Zinner, D. (2015). Population genetic insights into the social organization of Guinea baboons (*Papio papio*): evidence for female-biased dispersal. *Am. J. Primatol.* *77*, 878–889.
- Korstjens, A.H., and Schippers, E.P. (2003). Dispersal patterns among olive colobus in Tai National Park. *Int. J. Primatol.* *24*, 515–539.
- Kreft, I., and de Leeuw, J. (1998). *Introducing Multilevel Modeling* (London: Sage).
- Kuester, J., and Paul, A. (1992). Influence of male competition and female mate choice on male mating success in Barbary macaques (*Macaca sylvanus*). *Behaviour* *120*, 192–216.
- Kulik, L., and Mundry, R. (in prep). A dynamic measure of social relationships.
- Kummer, H. (1968). *Social Organization of Hamadryas Baboons, A field study* (Chicago: University of Chicago Press).
- Kvarnemo, C., and Ahnesjö, I. (1996). The dynamics of operational sex ratios and competition for mates. *TREE* *11*, 404–408.
- Kyle, C.J., Karels, T.J., Davis, C.S., Mebs, S., Clark, B., Strobeck, C., and Hik, D.S. (2007). Social structure and facultative mating systems of hoary marmots (*Marmota caligata*). *Mol. Ecol.* *16*, 1245–1255.
- Langergraber, K.E., Mitani, J.C., and Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proc. Natl. Acad. Sci.* *104*, 7786–7790.
- Lawson Handley, L.J., and Perrin, N. (2007). Advances in our understanding of mammalian sex-biased dispersal. *Mol. Ecol.* *16*, 1559–1578.
- Lee, P.C., and Strier, K.B. (2015). Complexities of Understanding Female Dispersal in Primates. In *Dispersing Primate Females*, T. Furuichi, J. Yamagiwa, and F. Aureli, eds. (Tokyo: Springer Japan), pp. 215–230.
- Lehtonen, J., Parker, G.A., and Schärer, L. (2016). Why anisogamy drives ancestral sex roles. *Evolution* *70*, 1129–1135.
- Leigh, S.R., and Shea, B.T. (1995). Ontogeny and the evolution of adult body size dimorphism in apes. *Am. J. Primatol.* *36*, 37–60.
- Lemasson, A., Palombit, R.A., and Jubin, R. (2008). Friendships between males and lactating females in a free-ranging group of olive baboons (*Papio hamadryas anubis*): evidence from playback experiments. *Behav. Ecol. Sociobiol.* *62*, 1027–1035.
- Lewis, S.M., Cratsley, C.K., and Rooney, J.A. (2004). Nuptial gifts and sexual selection in *Photinus* fireflies. *Integr. Comp. Biol.* *44*, 234–237.
- Li, C.C., Weeks, D.E., and Chakravarti, A. (1993). Similarity of DNA fingerprints due to chance and relatedness. *Hum. Hered.* *43*, 45–52.
- Liedigk, R., Roos, C., Brameier, M., and Zinner, D. (2014). Mitogenomics of the Old World monkey tribe Papionini. *BMC Evol. Biol.* *14*, 176.
- Linklater, W.L. (2000). Adaptive explanation in socio-ecology: lessons from the Equidae. *Biol. Rev. Camb. Philos. Soc.* *75*, 1–20.

- Linklater, W.L., Cameron, E.Z., Minot, E.O., and Stafford, K.J. (1999). Stallion harassment and the mating system of horses. *Anim. Behav.* *58*, 295–306.
- Lloyd, P.H., and Rasa, O.A.E. (1989). Status, reproductive success and fitness in Cape mountain zebra (*Equus zebra zebra*). *Behav. Ecol. Sociobiol.* *25*, 411–420.
- Lukas, D., and Clutton-Brock, T.H. (2011). Group structure, kinship, inbreeding risk and habitual female dispersal in plural-breeding mammals. *J. Evol. Biol.* *24*, 2624–2630.
- Lukas, D., Reynolds, V., Boesch, C., and Vigilant, L. (2005). To what extent does living in a group mean living with kin? *Mol. Ecol.* *14*, 2181–2196.
- Lusseau, D. (2003). The emergent properties of a dolphin social network. *Proc. R. Soc. Lond. B Biol. Sci.* *270*, S186–S188.
- Lynch, M., and Ritland, K. (1999). Estimation of pairwise relatedness with molecular markers. *Genetics* *152*, 1753–1766.
- Lyon, B.E., and Montgomerie, R. (2012). Sexual selection is a form of social selection. *Philos. Trans. R. Soc. B Biol. Sci.* *367*, 2266–2273.
- Mabry, K.E., Shelley, E.L., Davis, K.E., Blumstein, D.T., and Van Vuren, D.H. (2013). Social Mating System and Sex-Biased Dispersal in Mammals and Birds: A Phylogenetic Analysis. *PLoS ONE* *8*, e57980.
- Mac Carron, P., and Dunbar, R.I.M. (2016). Identifying natural grouping structure in gelada baboons: a network approach. *Anim. Behav.* *114*, 119–128.
- Maciej, P. (2013). Vocal communication in a tolerant multi-level society: insights from signallers and receivers in Guinea baboons. Doctoral dissertation. Georg-August-Universität Göttingen.
- Maciej, P., Patzelt, A., Ndao, I., Hammerschmidt, K., and Fischer, J. (2012). Social monitoring in a multilevel society: a playback study with male Guinea baboons. *Behav. Ecol. Sociobiol.* *67*, 61–68.
- Maestriperi, D., Leoni, M., Raza, S.S., Hirsch, E.J., and Whitham, J.C. (2005). Female copulation calls in Guinea baboons: evidence for postcopulatory female choice? *Int. J. Primatol.* *26*, 737–758.
- Maestriperi, D., Mayhew, J., Carlson, C.L., Hoffman, C.L., and Radtke, J.M. (2007). One-male harems and female social dynamics in Guinea baboons. *Folia Primatol. (Basel)* *78*, 56–68.
- Mann, J., and Smuts, B.B. (1998). Natal attraction: allomaternal care and mother–infant separations in wild bottlenose dolphins. *Anim. Behav.* *55*, 1097–1113.
- Markham, A.C., Geschiere, L.R., Alberts, S.C., and Altmann, J. (2015). Optimal group size in a highly social mammal. *Proc. Natl. Acad. Sci.* 201517794.
- Marlowe, F. (2001). Male Contribution to Diet and Female Reproductive Success among Foragers. *Curr. Anthropol.* *42*, 755–760.
- Marlowe, F.W. (2003). A critical period for provisioning by Hadza men. *Evol. Hum. Behav.* *24*, 217–229.
- Marlowe, F.W., and Berbesque, J.C. (2012). The human operational sex ratio: Effects of marriage, concealed ovulation, and menopause on mate competition. *J. Hum. Evol.* *63*, 834–842.
- Marty, P. (2015). Male migration and alpha male takeovers in crested macaques, *Macaca nigra*. Georg-August-Universität Göttingen.

- Marty, P., Hodges, K., Agil, M., and Engelhardt, A. (accepted). Determinants of immigration strategies in male crested macaques (*Macaca nigra*). *Sci. Rep.*
- Matsuura, N. (2015). Human Female Dispersal and Social Organization: A Case of Central African Hunter-Gatherers. In *Dispersing Primate Females*, T. Furuichi, J. Yamagiwa, and F. Aureli, eds. (Tokyo: Springer Japan), pp. 165–183.
- Matthysen, E. (2005). Density-dependent dispersal in birds and mammals. *Ecography* 28, 403–416.
- Mays, H.L., and Hill, G.E. (2004). Choosing mates: good genes versus genes that are a good fit. *Trends Ecol. Evol.* 19, 554–559.
- McFarland, R., and Majolo, B. (2011). Exploring the Components, Asymmetry and Distribution of Relationship Quality in Wild Barbary Macaques (*Macaca sylvanus*). *PLoS ONE* 6, e28826.
- McGlothlin, J.W., Moore, A.J., Wolf, J.B., and Brodie III, E.D. (2010). Interacting phenotypes and the evolutionary process. III. Social evolution. *Evolution* 64, 2558–2574.
- McPherson, M., Smith-Lovin, L., and Cook, J.M. (2001). Birds of a feather: Homophily in social networks. *Annu. Rev. Sociol.* 415–444.
- Milligan, B.G. (2003). Maximum-likelihood estimation of relatedness. *Genetics* 163, 1153–1167.
- Milton, K., Nolin, D.A., Ellis, K., Lozier, J., Sandel, B., and Lacey, E.A. (2016). Genetic, spatial, and social relationships among adults in a group of howler monkeys (*Alouatta palliata*) from Barro Colorado Island, Panama. *Primates* 57, 253–265.
- Mitani, J.C. (1990). Experimental Field Studies of Asian Ape Social Systems. *Int. J. Primatol.* 11, 103–126.
- Mitani, J.C., Gros-Louis, J., and Richards, A.F. (1996). Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. *Am. Nat.* 147, 996–980.
- Mitani, J.C., Merriwether, D.A., and Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Anim. Behav.* 59, 885–893.
- Mitani, J.C., Watts, D.P., and Muller, M.N. (2002). Recent developments in the study of wild chimpanzee behavior. *Evol. Anthropol. Issues News Rev.* 11, 9–25.
- Modig, A.O. (1996). Effects of body size and harem size on male reproductive behaviour in the southern elephant seal. *Anim. Behav.* 51, 1295–1306.
- Möhle, U., Heistermann, M., Palme, R., and Hodges, J.K. (2002). Characterization of urinary and fecal metabolites of testosterone and their measurement for assessing gonadal endocrine function in male nonhuman primates. *Gen. Comp. Endocrinol.* 129, 135–145.
- Møller, A.P., and Thornhill, R. (1998). Male parental care, differential parental investment by females and sexual selection. *Anim. Behav.* 55, 1507–1515.
- Molnar, P.K., Derocher, A.E., Lewis, M.A., and Taylor, M.K. (2008). Modelling the mating system of polar bears: a mechanistic approach to the Allee effect. *Proc. R. Soc. Lond. B Biol. Sci.* 275, 217–226.
- Monard, A.-M., and Duncan, P. (1996). Consequences of natal dispersal in female horses. *Anim. Behav.* 52, 565–579.
- Moore, T. (1984). Female Transfer in Primates. *Int. J. Primatol.* 5, 537–589.

- Moore, A.J., Brodie, E.D., and Wolf, J.B. (1997). Interacting Phenotypes and the Evolutionary Process: I. Direct and Indirect Genetic Effects of Social Interactions. *Evolution* 51, 1352.
- Mori, U. (1979a). Individual relationships within a unit. In *Ecological and Sociological Studies of Gelada Baboons*, M. Kawai, ed. (Karger), pp. 93–124.
- Mori, U. (1979b). Inter-unit relationships. In *Ecological and Sociological Studies of Gelada Baboons*, M. Kawai, ed. (Karger), pp. 83–92.
- Möstl, E., Maggs, J.L., Schrötter, G., Besenfelder, U., and Palme, R. (2002). Measurement of cortisol metabolites in faeces of ruminants. *Vet. Res. Commun.* 26, 127–139.
- Muller, M.N., Kahlenberg, S.M., Thompson, E.M., and Wrangham, R.W. (2007). Male coercion and the costs of promiscuous mating for female chimpanzees. *Proc. R. Soc. Lond. B Biol. Sci.* 274, 1009–1014.
- Nei, M. (1987). *Molecular evolutionary genetics* (New York: Columbia University Press).
- Neumann, C., and Kulik, L. (2015). *Animal Dominance Hierarchies by Elo Rating*.
- Neumann, C., Dubocq, J., Dubuc, C., Ginting, A., Irwan, A.M., Agil, M., Widdig, A., and Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Anim. Behav.* 82, 911–921.
- Newman, M.E.J., and Girvan, M. (2004). Finding and evaluating community structure in networks. *Phys. Rev. E* 69, 26113.
- Newman, T.K., Jolly, C.J., and Rogers, J. (2004). Mitochondrial phylogeny and systematics of baboons (*Papio*). *Am. J. Phys. Anthropol.* 124, 17–27.
- Newton-Fisher, N.E. (2006). Female Coalitions Against Male Aggression in Wild Chimpanzees of the Budongo Forest. *Int. J. Primatol.* 27, 1589–1599.
- Nitsch, F., Stueckle, S., Stahl, D., and Zinner, D. (2011). Copulation patterns in captive hamadryas baboons: a quantitative analysis. *Primates* 52, 373–383.
- van Noordwijk, M.A., and van Schaik, C.P. (2009). Intersexual food transfer among orangutans: do females test males for coercive tendency? *Behav. Ecol. Sociobiol.* 63, 883–890.
- Nsubuga, A.M., Robbins, M.M., Roeder, A.D., Morin, P.A., Boesch, C., and Vigilant, L. (2004). Factors affecting the amount of genomic DNA extracted from ape faeces and the identification of an improved sample storage method. *Mol. Ecol.* 13, 2089–2094.
- Nunn, C.L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Anim. Behav.* 58, 229–246.
- Oates, J.F., Gippoliti, S., and Groves, C.P. (2008). *Papio papio* (The IUCN Red List of Threatened Species).
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., and Wagner, H. (2016). *vegan: Community ecology package*.
- Orians, G.H. (1969). On the Evolution of Mating Systems in Birds and Mammals. *Am. Nat.* 103, 589–603.
- Packer, C., and Pusey, A.E. (1983). Adaptations of female lions to infanticide. *Am. Nat.* 121, 716–728.

- Packer, C., Scheel, D., and Pusey, A.E. (1990). Why lions form groups food is not enough. *Am. Nat.* *136*, 1–19.
- Packer, C., Pusey, A.E., and Eberly, L.E. (2001). Egalitarianism in female African lions. *Science* *293*, 690–693.
- Pagès, V., and Fuchs, R.P. (2003). Uncoupling of leading-and lagging-strand DNA replication during lesion bypass in vivo. *Science* *300*, 1300–1303.
- Palombit, R. (2009). “Friendship” with males: a female counterstrategy to infanticide in chacma baboons of the Okavango Delta. In *Sexual Coercion in Primates and Humans*, M.N. Muller, and R.W. Wrangham, eds. (Cambridge, MA: Harvard University Press), pp. 377–409.
- Palombit, R.A., Cheney, D.L., and Seyfarth, R.M. (2001). Female–female competition for male “friends” in wild chacma baboons (*Papio cynocephalus ursinus*). *Anim. Behav.* *61*, 1159–1171.
- Pappano, D.J., Snyder-Mackler, N., Bergman, T.J., and Beehner, J.C. (2012). Social “predators” within a multilevel primate society. *Anim. Behav.* *84*, 653–658.
- Paradis, E. (2010). pegas: an R package for population genetics with an integrated-modular approach. *Bioinformatics* *26*, 419–420.
- Parish, A.R. (1996). Female Relationships in Bonobos (*Pan paniscus*). *Hum. Nat.* *7*, 61–96.
- Parker, G.A. (2006). Sexual conflict over mating and fertilization: an overview. *Philos. Trans. R. Soc. B Biol. Sci.* *361*, 235–259.
- Parker, G.A., Baker, R.R., and Smith, V.G.F. (1972). Origin and evolution of gamete dimorphism and male–female phenomenon. *J. Theor. Biol.* *36*, 529–553.
- Patzelt, A. (2013). The social system of Guinea baboons (*Papio papio*) with a focus on male-male relationships. Doctoral dissertation. Georg-August-Universität Göttingen.
- Patzelt, A., Zinner, D., Fickenscher, G., Diedhiou, S., Camara, B., Stahl, D., and Fischer, J. (2011). Group Composition of Guinea Baboons (*Papio papio*) at a Water Place Suggests a Fluid Social Organization. *Int. J. Primatol.* *32*, 652–668.
- Patzelt, A., Kopp, G.H., Ndao, I., Kalbitzer, U., Zinner, D., and Fischer, J. (2014). Male tolerance and male-male bonds in a multilevel primate society. *Proc. Natl. Acad. Sci.* *111*, 14740–14745.
- Penn, D.J., and Frommen, J.G. (2010). Kin recognition: an overview of conceptual issues, mechanisms and evolutionary theory. In *Animal Behaviour: Evolution and Mechanisms*, P. Kappeler, ed. (Berlin, Heidelberg: Springer Berlin Heidelberg), pp. 55–85.
- Penn, D.J., and Smith, K.R. (2007). Differential fitness costs of reproduction between the sexes. *Proc. Natl. Acad. Sci.* *104*, 553–558.
- Perry, S. (1996). Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *Am. J. Primatol.* *40*, 167–182.
- Perry, S. (1997). Male-female social relationships in wild white-faced capuchins (*Cebus capucinus*). *Behaviour* *134*, 477–510.
- Persson, J. (2005). Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. *Can. J. Zool.* *83*, 1453–1459.

- Petrie, M. (1983). Mate choice in role-reversed species. In *Mate Choice*, P. Bateson, ed. (Cambridge: Cambridge University Press), pp. 167–180.
- Pew, J., Wang, J., Muir, P., and Frasier, T. (2015). *related*: an R package for analyzing pairwise relatedness data based on codominant molecular markers.
- Phillips, B.L., Brown, G.P., and Shine, R. (2010). Life-history evolution in range-shifting populations. *Ecology* *91*, 1617–1627.
- Pines, M., Saunders, J., and Swedell, L. (2011). Alternative routes to the leader male role in a multi-level society: follower vs. solitary male strategies and outcomes in hamadryas baboons. *Am. J. Primatol.* *73*, 679–691.
- Platt, A. (1912). The generation of animals. In *The Oxford Translation of Aristotle*, W.D. Ross, ed. (Oxford: Clarendon Press), pp. 2009–2204.
- Pohlert, T. (2014). The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR).
- Polansky, L., and Robbins, M.M. (2013). Generalized additive mixed models for disentangling long-term trends, local anomalies, and seasonality in fruit tree phenology. *Ecol. Evol.* *3*, 3141–3151.
- Pons, P., and Latapy, M. (2005). Computing communities in large networks using random walks. In *Computer and Information Sciences-ISCIS 2005*, (Springer Berlin Heidelberg), pp. 284–293.
- Pride, R.E. (2005). Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behav. Ecol.* *16*, 550–560.
- Prokop, Z.M., Michalczyk, L., Drobniak, S.M., Herdegen, M., and Radwan, J. (2012). Meta-Analysis Suggests Choosy Females Get Sexy Sons More than “Good Genes.” *Evolution* *66*, 2665–2673.
- Pusey, A.E. (1987). Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol. Evol.* *2*, 295–299.
- Pusey, A.E., and Schroepfer-Walker, K. (2013). Female competition in chimpanzees. *Philos. Trans. R. Soc. B Biol. Sci.* *368*, 20130077–20130077.
- Pusey, A., Murray, C., Wallauer, W., Wilson, M., Wroblewski, E., and Goodall, J. (2008). Severe Aggression Among Female Pan troglodytes schweinfurthii at Gombe National Park, Tanzania. *Int. J. Primatol.* *29*, 949–973.
- Qi, X.-G., Garber, P.A., Ji, W., Huang, Z.-P., Huang, K., Zhang, P., Guo, S.-T., Wang, X.-W., He, G., Zhang, P., et al. (2014). Satellite telemetry and social modeling offer new insights into the origin of primate multilevel societies. *Nat. Commun.* *5*, 5296.
- Queller, D.C., and Goodnight, K.F. (1989). Estimating relatedness using genetic markers. *Evolution* *43*, 258–275.
- Raum, R.L., Sterner, K.N., Noviello, C.M., Stewart, C.-B., and Disotell, T.R. (2005). Catarrhine primate divergence dates estimated from complete mitochondrial genomes: concordance with fossil and nuclear DNA evidence. *J. Hum. Evol.* *48*, 237–257.
- R Core Team (2014). *R: A language and environment for statistical computing* (Vienna, Austria: R Foundation for Statistical Computing).
- Randall, J.A. (2005). Flexible social structure of a desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints. *Behav. Ecol.* *16*, 961–973.

- Réale, D., Gallant, B.Y., Leblanc, M., and Festa-Bianchet, M. (2000). Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Anim. Behav.* *60*, 589–597.
- Reichardt, J., and Bornholdt, S. (2006). Statistical mechanics of community detection. *Phys. Rev. E* *74*, 16110.
- Rendall, D. (2004). “Recognizing” kin: Mechanisms, media, minds, modules, and muddles. In *Kinship and Behavior in Primates*, B. Chapais, and C.M. Berman, eds. pp. 295–316.
- Rhys Roberts, W. (1912). Rhetoric. In *The Oxford Translation of Aristotle*, W.D. Ross, ed. (Oxford: Clarendon Press), pp. 3132–3307.
- Ridley, M. (1986). The number of males in a primate troop. *Anim. Behav.* *34*, 1848–1858.
- Riehl, C. (2013). Evolutionary routes to non-kin cooperative breeding in birds. *Proc. R. Soc. B Biol. Sci.* *280*, 20132245.
- Rigby, R.A., and Stasinopoulos, D.M. (2005). Generalized additive models for location, scale and shape (with discussion). *Appl. Stat.* *54*, 507–554.
- Rimbach, R., Link, A., Heistermann, M., Gomez-Posada, C., Galvis, N., and Heymann, E.W. (2013). Effects of logging, hunting, and forest fragment size on physiological stress levels of two sympatric ateline primates in Colombia. *Conserv. Physiol.* *1*, cot031.
- Ritland, K. (1996). Estimators for pairwise relatedness and inbreeding coefficients. *Genet. Res.* *67*, 175–186.
- Roeder, A.D., Archer, F.I., Poinar, H.N., and Morin, P.A. (2004). A novel method for collection and preservation of faeces for genetic studies. *Mol. Ecol. Notes* *4*, 761–764.
- Rosvall, K.A. (2008). Sexual selection on aggressiveness in females: evidence from an experimental test with tree swallows. *Anim. Behav.* *75*, 1603–1610.
- Rosvall, K.A. (2011). Intrasexual competition in females: evidence for sexual selection? *Behav. Ecol.* *22*, 1131–1140.
- le Roux, A., and Bergman, T.J. (2012). Indirect rival assessment in a social primate, *Theropithecus gelada*. *Anim. Behav.* *83*, 249–255.
- le Roux, A., Beehner, J.C., and Bergman, T.J. (2011). Female philopatry and dominance patterns in wild geladas. *Am. J. Primatol.* *73*, 422–430.
- RStudio (2012). RStudio: integrated development environment for R (Boston, Massachusetts: RStudio Inc).
- Rubenstein, D.I. (1978). On predation, competition, and the advantages of group living. In *Social Behavior*, (Springer US), pp. 205–231.
- Rubenstein, D.I. (1986). Ecology and Sociality in Horses and zebras. In *Ecological Aspects of Social Evolution*, D.I. Rubenstein, and R.W. Wrangham, eds. (Princeton, New Jersey: Princeton University Press), pp. 282–302.
- Rubenstein, D.I. (1994). The ecology of Female Social Behaviour in Horses, Zebras and Asses. In *Animal Societies: Individuals, Interactions, and Organization*, P. Jarman, and A. Rossiter, eds. (Kyoto, Japan: Kyoto University Press), pp. 13–28.

- Rubenstein, D.I., and Hack, M. (2004). Natural and sexual selection and the evolution of multi-level societies: insights from zebras with comparisons to primates. In *Sexual Selection in Primates: New and Comparative Perspectives*, P.M. Kappeler, and C.P. van Schaik, eds. (Cambridge University Press), pp. 266–279.
- Rubenstein, D.I., Sundaesan, S., Fischhoff, I., and Saltz, D. (2007). Social networks in wild asses: comparing patterns and processes among populations. *Explor. Biol. Resour. Mong.* *10*, 159–176.
- Safi, K., König, B., and Kerth, G. (2007). Sex differences in population genetics, home range size and habitat use of the parti-colored bat (*Vespertilio murinus*, Linnaeus 1758) in Switzerland and their consequences for conservation. *Biol. Conserv.* *137*, 28–36.
- Sakamaki, T., Behncke, I., Laporte, M., Mulavwa, M., Ryu, H., Takemoto, H., Tokuyama, N., Yamamoto, S., and Furuichi, T. (2015). Intergroup Transfer of Females and Social Relationships Between Immigrants and Residents in Bonobo (*Pan paniscus*) Societies. In *Dispersing Primate Females*, T. Furuichi, J. Yamagiwa, and F. Aureli, eds. (Tokyo: Springer Japan), pp. 127–164.
- Sapolsky, R.M. (1992). Cortisol concentrations and the social significance of rank instability among wild baboons. *Psychoneuroendocrinology* *17*, 701–709.
- Sapolsky, R.M. (2004). Social status and health in humans and other animals. *Annu. Rev. Anthropol.* *33*, 393–418.
- Sapolsky, R.M. (2005). The Influence of Social Hierarchy on Primate Health. *Science* *308*, 648–652.
- Scelza, B.A. (2011). Female choice and extra-pair paternity in a traditional human population. *Biol. Lett.* *7*, 889–891.
- Schaid, D.J. (2004). Linkage disequilibrium testing when linkage phase is unknown. *Genetics* *166*, 505–512.
- Schärer, L., Rowe, L., and Arnqvist, G. (2012). Anisogamy, chance and the evolution of sex roles. *Trends Ecol. Evol.* *27*, 260–264.
- Schauber, E.M., Connors, M.J., Goodwin, B.J., Jones, C.G., and Ostfeld, R.S. (2009). Quantifying a dynamic risk landscape: heterogeneous predator activity and implications for prey persistence. *Ecology* *90*, 240–251.
- Schneider, T.C. (2016). Social organisation of the narrow-striped mongoose (*Mungotictis decemlineata*) in Kirindy Forest CNFEREF, Madagascar. Doctoral dissertation. Göttingen, Georg-August Universität.
- Schreier, A.L., and Swedell, L. (2009). The fourth level of social structure in a multi-level society: ecological and social functions of clans in hamadryas baboons. *Am. J. Primatol.* *71*, 948–955.
- Schreier, A.L., and Swedell, L. (2011). The socioecology of network scaling ratios in the multilevel society of hamadryas baboons (*Papio hamadryas hamadryas*). *Int. J. Primatol.* *33*, 1069–1080.
- Schreier, A.L., and Swedell, L. (2012). Ecology and sociality in a multilevel society: Ecological determinants of spatial cohesion in hamadryas baboons. *Am. J. Phys. Anthropol.* *148*, 580–588.
- Scott, N.M. (2014). *Female Intrasexual Competition in Primates: Why Humans Aren't as Progressive as We Think* (Oxford University Press).
- Simple, S., McComb, K., Alberts, S., and Altmann, J. (2002). Information content of female copulation calls in yellow baboons. *Am. J. Primatol.* *56*, 43–56.

- Seyfarth, R.M., and Cheney, D.L. (2012). The Evolutionary Origins of Friendship. *Annu. Rev. Psychol.* *63*, 153–177.
- Seyfarth, R.M., Silk, J.B., and Cheney, D.L. (2014). Social bonds in female baboons: the interaction between personality, kinship and rank. *Anim. Behav.* *87*, 23–29.
- Shackelford, T., and Goetz, A. (2009). Sexual conflict in humans: evolutionary consequences of asymmetric parental investment and paternity uncertainty. *Anim. Biol.* *59*, 449–456.
- Sharman, M.J. (1982). Feeding, ranging and social organisation of the Guinea baboon. Doctoral dissertation. University of St Andrews.
- Shuker, D.M. (2010). Sexual selection: endless forms or tangled bank? *Anim. Behav.* *79*, e11–e17.
- Sigg, H., Stolba, A., Abegglen, J.-J., and Dasser, V. (1982). Life history of hamadryas baboons: physical development, infant mortality, reproductive parameters and family relationships. *Primates* *23*, 473–487.
- Sigurjonsdottir, H., Thorhallsdottir, A.G., Hafthorsdottir, H.M., and Granquist, S.M. (2012). The Behaviour of Stallions in a Semiferal Herd in Iceland: Time Budgets, Home Ranges, and Interactions. *Int. J. Zool.* *2012*, 1–7.
- Sih, A., Bell, A., and Johnson, J.C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* *19*, 372–378.
- Silk, J.B. (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Anim. Behav.* *57*, 1021–1032.
- Silk, J.B. (2002). Using the 'F' word in primatology. *Behaviour* *139*, 421.
- Silk, J.B. (2007). The adaptive value of sociality in mammalian groups. *Philos. Trans. R. Soc. B Biol. Sci.* *362*, 539–559.
- Silk, J.B. (2009). Nepotistic cooperation in non-human primate groups. *Philos. Trans. R. Soc. B Biol. Sci.* *364*, 3243–3254.
- Silk, J.B., Alberts, S.C., and Altmann, J. (2003a). Social bonds of female baboons enhance infant survival. *Science* *302*, 1231.
- Silk, J.B., Rendall, D., Cheney, D.L., and Seyfarth, R.M. (2003b). Natal attraction in adult female baboons (*Papio cynocephalus ursinus*) in the Moremi Reserve, Botswana. *Ethology* *109*, 627–644.
- Silk, J.B., Alberts, S.C., and Altmann, J. (2004). Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Anim. Behav.* *67*, 573–582.
- Silk, J.B., Alberts, S.C., and Altmann, J. (2006a). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behav. Ecol. Sociobiol.* *61*, 197–204.
- Silk, J.B., Altmann, J., and Alberts, S.C. (2006b). Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behav. Ecol. Sociobiol.* *61*, 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., and Cheney, D.L. (2009). The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proc. R. Soc. Lond. B Biol. Sci.* *276*, 3099–3104.

- Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., and Cheney, D.L. (2010a). Strong and consistent social bonds enhance the longevity of female baboons. *Curr. Biol.* *20*, 1359–1361.
- Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., and Cheney, D.L. (2010b). Female chacma baboons form strong, equitable, and enduring social bonds. *Behav. Ecol. Sociobiol.* *64*, 1733–1747.
- Silk, J.B., Brosnan, S.F., Henrich, J., Lambeth, S.P., and Shapiro, S. (2013). Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. *Anim. Behav.* *85*, 941–947.
- de Silva, S., and Wittemyer, G. (2012). A Comparison of Social Organization in Asian Elephants and African Savannah Elephants. *Int. J. Primatol.* *33*, 1125–1141.
- de Silva, S., Ranjeewa, A., and Kryazhimskiy, S. (2011). The dynamics of social networks among female Asian elephants. *BMC Ecol.* *11*, 17.
- Skinner, J.D., and Chimimba, C.T. (2005). *The mammals of the southern African sub-region* (Cambridge University Press).
- Slagsvold, T., and Lifjeld, J.T. (1994). Polygyny in Birds: The Role of Competition between Females for Male Parental Care. *Am. Nat.* *143*, 59–94.
- Small, M.F. (1990). Promiscuity in Barbary macaques (*Macaca sylvanus*). *Am. J. Primatol.* *20*, 267–282.
- Small, M.F. (1993). *Female Choices: Sexual Behavior of Female Primates* (Cornell University Press).
- Smith, K., Alberts, S.C., and Altmann, J. (2003). Wild female baboons bias their social behaviour towards paternal half-sisters. *Proc. R. Soc. Lond. B Biol. Sci.* *270*, 503–510.
- Smolker, R.A., Richards, A.F., Connor, R.C., and Pepper, J.W. (1992). Sex Differences in Patterns of Association Among Indian Ocean Bottlenose Dolphins. *Behaviour* *123*, 38–69.
- Smuts, B. (1985). *Sex and Friendship in Baboons* (New York: Aldine).
- Smuts, B.B., and Smuts, R.W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Adv. Study Behav.* *22*, 1–63.
- Snyder-Mackler, N., Beehner, J.C., and Bergman, T.J. (2012a). Defining Higher Levels in the Multilevel Societies of Geladas (*Theropithecus gelada*). *Int. J. Primatol.* *33*, 1054–1068.
- Snyder-Mackler, N., Alberts, S.C., and Bergman, T.J. (2012b). Concessions of an alpha male? Cooperative defence and shared reproduction in multi-male primate groups. *Proc. R. Soc. Lond. B Biol. Sci.* *279*, 3788–3795.
- Städle, V., Van Doren, V., Pines, M., Swedell, L., and Vigilant, L. (2015). Fine-scale genetic assessment of sex-specific dispersal patterns in a multilevel primate society. *J. Hum. Evol.* *78*, 103–113.
- Städle, V., Pines, M., Swedell, L., and Vigilant, L. (2016). The ties that bind: maternal kin bias in a multilevel primate society despite natal dispersal by both sexes. *Am. J. Primatol.* *78*, 731–744.
- Stephens, P.A., Russell, A.F., Young, A.J., Sutherland, W.J., and Clutton-Brock, T.H. (2005). Dispersal, eviction, and conflict in meerkats (*Suricata suricatta*): an evolutionarily stable strategy model. *Am. Nat.* *165*, 120–135.

- Sterck, E.H.M., Watts, D.P., and van Schaik, C.P. (1997). The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.* *41*, 291–309.
- Stevens, J.R., and Gilby, I.C. (2004). A conceptual framework for nonkin food sharing: timing and currency of benefits. *Anim. Behav.* *67*, 603–614.
- Stockley, P., and Bro-Jørgensen, J. (2011). Female competition and its evolutionary consequences in mammals. *Biol. Rev.* *86*, 341–366.
- Stokes, E.J., Parnell, R.J., and Olejniczak, C. (2003). Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behav. Ecol. Sociobiol.* *54*, 329–339.
- Stokke, S., and Toit, J.T. (2000). Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography* *23*, 70–80.
- Strier, K.B., and Ziegler, T.E. (2000). Lack of pubertal influences on female dispersal in muriqui monkeys, *Brachyteles arachnoides*. *Anim. Behav.* *59*, 849–860.
- Strum, S.C. (1981). Processes and products of change: baboon predatory behaviour at Gilgil, Kenya. In *Omnivorous Primates: Gathering and Hunting in Human Evolution*, (New York: Columbia University Press), pp. 255–302.
- Strum, S.C. (1982). Agonistic dominance in male baboons: an alternative view. *Int. J. Primatol.* *3*, 175–202.
- Sugawara, K. (1979). Sociological study of a wild group of hybrid baboons between *Papio anubis* and *P. hamadryas* in the Awash Valley, Ethiopia. *Primates* *20*, 21–56.
- Sukumar, R. (2003). *The living elephants: evolutionary ecology, behavior, and conservation* (New York: Oxford University Press).
- Sundaesan, S.R., Fischhoff, I.R., and Rubenstein, D. (2007). Male harassment influences female movements and associations in Grevy's zebra (*Equus grevyi*). *Behav. Ecol.* *18*, 860–865.
- Swedell, L. (2000). Two takeovers in wild hamadryas baboons. *Folia Primatol. (Basel)* *71*, 169–172.
- Swedell, L. (2002). Affiliation among females in wild hamadryas baboons (*Papio hamadryas hamadryas*). *Int. J. Primatol.* *23*, 1205–1226.
- Swedell, L. (2006). *Strategies of Sex and Survival Hamadryas Baboons: Through a Female Lens* (Routledge).
- Swedell, L. (2011). African Papionins: diversity of social organization and ecological flexibility. In *Primates in Perspective*, C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger, and S.K. Bearder, eds. (New York: Oxford University Press), pp. 241–277.
- Swedell, L., and Schreier, A. (2009). Male aggression towards females in hamadryas baboons: Conditioning, coercion, and control. In *Sexual Coercion in Primates and Humans: An Evolutionary Perspective on Male Aggression against Females*, M.N. Muller, and R.W. Wrangham, eds. pp. 244–268.
- Swedell, L., Hailemeskel, G., and Schreier, A. (2008). Composition and seasonality of diet in wild hamadryas baboons: preliminary findings from Filoha. *Folia Primatol. (Basel)* *79*, 476–490.
- Swedell, L., Saunders, J., Schreier, A., Davis, B., Tesfaye, T., and Pines, M. (2011). Female “dispersal” in hamadryas baboons: Transfer among social units in a multilevel society. *145*, 360–370.

- Swedell, L., Leedom, L., Saunders, J., and Pines, M. (2014). Sexual conflict in a polygynous primate: costs and benefits of a male-imposed mating system. *Behav. Ecol. Sociobiol.* *68*, 263–273.
- Székely, T., Weissing, F.J., and Komdeur, J. (2014). Adult sex ratio variation: implications for breeding system evolution. *J. Evol. Biol.* *27*, 1500–1512.
- Szykman, M., Engh, A.L., Van Horn, R.C., Boydston, E.E., Scribner, K.T., and Holekamp, K.E. (2003). Rare male aggression directed toward females in a female-dominated society: Baiting behavior in the spotted hyena. *Aggress. Behav.* *29*, 457–474.
- Szykman, M., Van Horn, R.C., Engh, A.L., Boydston, E.E., and Holekamp, K.E. (2007). Courtship and mating in free-living spotted hyenas. *Behaviour* *144*, 815–846.
- Tanaka, Y. (1996). Social Selection and the Evolution of Animal Signals. *Evolution* *50*, 512.
- Tang-Martinez, Z., and Ryder, T.B. (2005). The problem with paradigms: Bateman’s worldview as a case study. *Integr. Comp. Biol.* *45*, 821–830.
- Taylor, S.E., Klein, L.C., Lewis, B.P., Gruenewald, T.L., Gurung, R.A.R., and Updegraff, J.A. (2000). Biobehavioral responses to stress in females: tend-and-befriend, not fight-or-flight. *Psychol. Rev.* *107*, 411–429.
- Teleki, G. (1975). Primate subsistence patterns: collector-predators and gatherer-hunters. *J. Hum. Evol.* *4*, 125–184.
- Tiedemann, R., Hardy, O., Vekemans, X., and Milinkovitch, M.C. (2000). Higher impact of female than male migration on population structure in large mammals. *Mol. Ecol.* *9*, 1159–1163.
- Tinsley Johnson, E., Snyder-Mackler, N., Beehner, J.C., and Bergman, T.J. (2013). Kinship and Dominance Rank Influence the Strength of Social Bonds in Female Geladas (*Theropithecus gelada*). *Int. J. Primatol.* *35*, 288–304.
- Tobias, J.A., Montgomerie, R., and Lyon, B.E. (2012). The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Philos. Trans. R. Soc. B Biol. Sci.* *367*, 2274–2293.
- Trivers, R.L. (1972). Parental Investment and Sexual Selection. In *Sexual Selection and the Descent of Man*, (Aldine, Chicago), pp. 136–179.
- Tung, J., Archie, E.A., Altmann, J., and Alberts, S.C. (2016). Cumulative early life adversity predicts longevity in wild baboons. *Nat. Commun.* *7*, 11181.
- Vaillancourt, T. (2013). Do human females use indirect aggression as an intrasexual competition strategy? *Philos. Trans. R. Soc. B Biol. Sci.* *368*, 20130080–20130080.
- VanderWaal, K.L., Wang, H., McCowan, B., Fushing, H., and Isbell, L.A. (2014). Multilevel social organization and space use in reticulated giraffe (*Giraffa camelopardalis*). *Behav. Ecol.* *25*, 17–26.
- Wade, M.J., and Shuster, S.M. (2005). Don’t throw Bateman out with the bathwater! *Integr. Comp. Biol.* *45*, 945–951.
- Wang, J. (2002). An estimator for pairwise relatedness using molecular markers. *Genetics* *160*, 1203–1215.
- Wang, J. (2007). Triadic IBD coefficients and applications to estimating pairwise relatedness. *Genet. Res.* *89*.

- Wasser, S.K., and Barash, D.P. (1983). Reproductive suppression among female mammals: implications for biomedicine and sexual selection theory. *Q. Rev. Biol.* 513–538.
- Wasserman, S., and Faust, K. (1994). *Social Network Analysis: Methods and Applications* (Cambridge University Press).
- Wasserstein, R.L., and Lazar, N.A. (2016). The ASA’s statement on p-values: context, process, and purpose. *Am. Stat.* 129–133.
- Watts, D.P. (1994). Social relationships of immigrant and resident female mountain gorillas, II: relatedness, residence, and relationships between females. *Am. J. Primatol.* 32, 13–30.
- Watts, H.E., Tanner, J.B., Lundrigan, B.L., and Holekamp, K.E. (2009). Post-weaning maternal effects and the evolution of female dominance in the spotted hyena. *Proc. R. Soc. B Biol. Sci.* 276, 2291–2298.
- Wedell, N., Kvarnemo, C., Lessells, C.M., and Tregenza, T. (2006). Sexual conflict and life histories. *Anim. Behav.* 71, 999–1011.
- Weingrill, T., Lycett, J.E., Barrett, L., Hill, R.A., and Henzi, S.P. (2003). Male consortship behaviour in chacma baboons: the role of demographic factors and female conceptive probabilities. *Behaviour* 140, 405–427.
- Weingrill, T., Gray, D.A., Barrett, L., and Henzi, S.P. (2004). Fecal cortisol levels in free-ranging female chacma baboons: relationship to dominance, reproductive state and environmental factors. *Horm. Behav.* 45, 259–269.
- West-Eberhard, M.J. (1979). Sexual selection, social competition, and evolution. *Proc. Am. Philos. Soc.* 123, 222–234.
- West-Eberhard, M.J. (1983). Sexual selection, social competition, and speciation. *Q. Rev. Biol.* 155–183.
- Whiten, A., Byrne, R.W., and Henzi, S.P. (1987). The behavioral ecology of mountain baboons. *Int. J. Primatol.* 8, 367–388.
- Widdig, A. (2007). Paternal kin discrimination: the evidence and likely mechanisms. *Biol. Rev.* 82, 319–334.
- Wildt, D.E., Doyle, L.L., Stone, S.C., and 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.
- Wiszniewski, J., Corrigan, S., Beheregaray, L.B., and Möller, L.M. (2012). Male reproductive success increases with alliance size in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*): Reproductive success in bottlenose dolphins. *J. Anim. Ecol.* 81, 423–431.
- Wittemyer, G., Douglashamilton, I., and Getz, W. (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. *Anim. Behav.* 69, 1357–1371.
- Wittig, R.M., Crockford, C., Wikberg, E., Seyfarth, R.M., and Cheney, D.L. (2007). Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proc. R. Soc. Lond. B Biol. Sci.* 274, 1109–1115.
- Wittig, R.M., Crockford, C., Lehmann, J., Whitten, P.L., Seyfarth, R.M., and Cheney, D.L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Horm. Behav.* 54, 170–177.

- Wittig, R.M., Crockford, C., Deschner, T., Langergraber, K.E., Ziegler, T.E., and Zuberbuhler, K. (2014). Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proc. R. Soc. Lond. B Biol. Sci.* *281*, 20133096–20133096.
- Wolf, J.B., Brodie III, E.D., and Moore, A.J. (1999). Interacting Phenotypes and the Evolutionary Process. II. Selection Resulting from Social Interactions. *Am. Nat.* *153*, 254–266.
- Wolf, J.B.W., Mawdsley, D., Trillmich, F., and James, R. (2007). Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. *Anim. Behav.* *74*, 1293–1302.
- Wolff, J.O. (1993). Why Are Female Small Mammals Territorial? *Oikos* *68*, 364.
- Wolff, J.O., and Macdonald, D.W. (2004). Promiscuous females protect their offspring. *Trends Ecol. Evol.* *19*, 127–134.
- Wong, B.B.M., and Candolin, U. (2005). How is female mate choice affected by male competition? *Biol. Rev.* *80*, 559.
- Wood, S., and Scheipl, F. (2014). gamm4: Generalized additive mixed models using mgcv and lme4.
- Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. *Behaviour* *262–300*.
- Young, L.J., and Wang, Z. (2004). The neurobiology of pair bonding. *Nat. Neurosci.* *7*, 1048–1054.
- Young, C., Majolo, B., Heistermann, M., Schülke, O., and Ostner, J. (2013). Male mating behaviour in relation to female sexual swellings, socio-sexual behaviour and hormonal changes in wild Barbary macaques. *Horm. Behav.* *63*, 32–39.
- Young, C., Majolo, B., Heistermann, M., Schülke, O., and Ostner, J. (2014). Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. *Proc. Natl. Acad. Sci.* *111*, 18195–18200.
- Yue, S., Pilon, P., Phinney, B., and Cavadias, G. (2002). The influence of autocorrelation on the ability to detect trend in hydrological series. *Hydrol. Process.* *16*, 1807–1829.
- Zhang, P., Watanabe, K., and Li, B. (2008). Female social dynamics in a provisioned free-ranging band of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Qinling mountains, China. *Am. J. Primatol.* *70*, 1013–1022.
- Ziegler, A., Kentenich, H., and Uchanska-Ziegler, B. (2005). Female choice and the MHC. *Trends Immunol.* *26*, 496–502.
- Zinner, D., Krebs, E., Schrod, A., and Kaumanns, W. (2006). Early sexual maturity in male hamadryas baboons (*Papio hamadryas hamadryas*) and its reproductive implications. *Am. J. Phys. Anthropol.* *129*, 584–590.
- Zinner, D., Groeneveld, L., Keller, C., and Roos, C. (2009). Mitochondrial phylogeography of baboons (*Papio* spp.) - Indication for introgressive hybridization? *BMC Evol. Biol.* *9*, 83.
- Zinner, D., Buba, U., Nash, S., and Roos, C. (2011). Pan-African Voyagers: The Phylogeography of Baboons. In *Primates of Gashaka*, V. Sommer, and C. Ross, eds. (New York, NY: Springer New York), pp. 319–358.
- Zuckerman, S., and Parkes, A.S. (1939). Observations on secondary sexual characters in monkeys. *J. Endocrinol.* *1*, 430–439.

ACKNOWLEDGEMENTS

First, I would like to express my gratitude Julia Fischer for giving me the opportunity to join the Cognitive Ethology Lab and to work with the Guinea baboons in Senegal. I am grateful for being given the opportunity to work with such an encouraging and inspiring scientist, who was able to find the patience to deal with my near zealotry when it came to my work. Thank you, Julia for your faith in me and willingness in allowing me to join your scientific family and the diverse research environment offered by the German Primate Center.

I would like to express my appreciation to Julia Ostner and Michael Heistermann for the privilege of having them as my co-supervisors and to Julia for the time, patience and support involved in evaluating my thesis. I also extend my appreciation to Bernard Fink, Martina Gerken, Cornelia Kraus and Christian Roos for agreeing to be on my thesis committee. The research topic of my dissertation, involving research in Germany and Senegal, was made possible by the financial support of the German Primate Center and the Leakey Foundation.

Being a member of the Cognitive Ethology Lab has been a life changing experience. I would like to thank all of my fellow Coggies for the various ways in which they have offered me their support, friendship and tasty food. Thank you to Barbara, Brandon, Chris, Dietmar and Kurt for having open doors when I was so full of questions. Thanks to Annika and Peter for introducing me to the baboons and to Tanya for showing me around the genetics lab. I am especially grateful to Rasmus for lending me his pipetting skills and to Andrea for companionship and laughter in the hormone lab. I would also like to show my appreciation to Ludwig and Mechthilde for their kindness and always going above and beyond, and to express my gratitude to Holger and Roger for beguiling me with their friendship and statistical magic. Also, I wish to thank a long list of friends who have helped me to find a much-needed balance. Thanks to Andreas, Chris H., Chris M., Christof, Darja, Fede, Fili, Flavia, Fred, Josi, Julie, Katja, Laura A., Laura D., Matthis, Pascal, Philip, Rebe, Rebecca, Steffi for contributing, in your own special ways, to my happiness, and to Chris Y. and Tabby for bringing their humour and pragmatism to another shared academic journey. Cedric and Marlies, thank you for the late-night chats, forest adventures, and of course, the dancing. To

the RedHouse inhabitants, especially Anni, Barbora, Kim, Sally, Scottie and Yajie, thank you for helping me to find a home in Göttingen.

For fieldwork in Senegal would like to thank the *Diréction des Parcs Nationaux* and the *Ministère de l'Environnement et de la Protéction de la Nature de la République du Sénégal* for permission to work in the *Parc Nationale de Niokolo Koba*, as well as the conservateur of PNNK, Mamadou Sidibé, for his logistical support. I would like to show my appreciation for the Senegalese staff of the *Centre de Recherche de Primatologie Simenti*, in particular Sané, Faye, and Nyafouna for the long, hot and at times fruitless days searching for baboons, and also to Boudiang, Boudou and Diatta for their friendship and sweet tea. Thank you to my fellow researchers, Urs and Gisi for sharing my first experiences with the baboons, Fede for her openness and great care in baboon-sitting, Matze for teaching me which baboon foods I really can eat and of course to Ulli for her compassion.

I would like to express my profound appreciation to those who have offered me amazing emotional support, despite vast geographic distances. I want to thank Alice, Jojo, Loxi and Nele for their physical, emotional and in some cases culinary support throughout this long journey even without the bonds of kinship. Thank you to Anja, for all of the good times in Berlin and for reminding me that there is more. And to those with whom I have a high r estimate, Bev, James, Junior, Ricky, Shelley and Tasha, thank you for the hugs, for the chats and for just being there when I needed you. And finally, to Drae, Thelma and Tony, thank you.

CURRICULUM VITAE

Personal Information

Adeelia S. Goffe

Nationality: British and American

Education

- | | |
|-----------|--|
| 2012-2016 | PhD Biology, Georg-August-Universität Göttingen, Germany |
| 2006-2007 | MRes Primatology, Roehampton University, London, UK |
| 1999-2002 | BS Animal Science, Cornell University, USA |

Practical Experience

- | | |
|-----------|---|
| 2009-2011 | Research Assistant for the Wildlife Conservation Research Unit, University of Oxford, UK at the Robert Koch-Institute, Germany |
| 2008 | Research Assistant for the Wildlife Conservation Research Unit, University of Oxford, UK at the Budongo Forest Conservation Station, Uganda |
| 2009 | Programme Coordinator for the Primate Department of the Max Planck Institute for Evolutionary Anthropology, Germany |
| 2004-2006 | Programme Coordinator for the Office of Animal Welfare, University of Washington, USA |
| 2002-2004 | Research Assistant for Shin Nippon Biomedical Laboratories, USA |
| 2002 | Research Assistant for the Laboratory of Ornithology, Cornell University, USA at the Bonaire Research Station, Bonaire, Dutch Antilles |
| 2000-2002 | Student Researcher/Laboratory Assistant for Prof. Katherine Houpt, Department of Biomedical Sciences, College of Veterinary Medicine, Cornell University, USA |
| 1999-2000 | Student Researcher/Laboratory Assistant for the Dairy Cattle Division-Department of Animal Science, Cornell University, USA |

Publications

- submitted Fischer., J., Kopp, G. H., Dal Pesco F., Goffe A. S., Hammerschmidt, K., Kalbitzer, U., Klapproth, M., Maciej, P., Ndao, I., Patzelt, A. & Zinner, D. Charting the neglected West: the social system of Guinea baboons. *American Journal of Physical Anthropology*
- 2016 Goffe, A. S. & Fischer J. Meat sharing between male and female Guinea baboons (*Papio papio*). *Primate Biology* 3: 1-8. DOI: 10.5194/pb-3-1-2016.
- 2016 Goffe, A. S., Zinner, D. & Fischer J. Sex and friendship in a multilevel society: behavioural patterns and associations between female and male Guinea baboons. *Behavioural Ecology and Sociobiology*. 70: 323-336. DOI: 10.1007/s00265-015-2050-6.
- 2015 MacLarnon, A. M., Sommer, V., Goffe, A. S., Higham, J. P., Lodge, E., Tkaczynski, P. & Ross, C. Assessing adaptability and reactive scope: Introducing a new measure and illustrating its use through a case study of environmental stress in forest-living baboons. *General and Comparative Endocrinology*. 215: 10-24. DOI: 10.1016/j.ygcen.2014.09.022.
- 2013 Blasse, A., Calvignac-Spencer, S., Merkel, K., Goffe, A. S., Boesch, C., Mundry, R. & Leendertz, F. H. Mother-offspring transmission and age dependent accumulation of simian foamy virus in wild chimpanzees. *Journal of Virology* 87(9):5193. DOI: 10.1128/JVI.02743-12.
- 2012 Goffe, A. S., Blasse, A., Mundry, R., Leendertz, F. H. & Calvignac-Spencer, S. Detection of retroviral super-infection from non-invasive samples. *PlosOne* 7(5): e36570. DOI:10.1371/journal.pone.0036570.
- 2011 Blasse, A., Goffe, A., Mundry, R., Leendertz, F. & Calvignac-Spencer, S. Investigating retroviral super-infection in wild chimpanzees (*Pan troglodytes verus*). *Retrovirology* 8(Suppl 1): A242. DOI: 10.1371/journal.pone.0036570.
- 2010 Leendertz, S. A., Junglen, S., Hedemann, C., Goffe, A., Calvignac, S., Boesch, C. & Leendertz, F. H. High prevalence, co-infection rate and genetic diversity of retroviruses in wild red colobus monkeys (*Piliocolobus badius badius*) in Taï National Park, Côte d'Ivoire. *Journal of Virology* 84: 7427-7436. DOI: 10.1128/JVI.00697-10.
- 2010 Kaiser, M., Löwa, A., Ulrich, M., Ellerbrok, H., Goffe, A. S., Blasse, A., Zommers, Z., Couacy-Hymann, E., Babweteera, F., Zuberbühler, K., Metzger, S., Geidel, S., Boesch, C., Gillespie, T. R. & Leendertz, F. H. Wild Chimpanzees Infected with 5 *Plasmodium* Species. *Emerging Infectious Diseases* 16: 1956. doi: 10.3201/eid1612.100424.

Scientific Presentations

- 2015 Talk, Göttinger Freilandtage, Germany.
- 2015 Seminar, Primate Biology, Behaviour and Conservation Postgraduate Course, Roehampton University, UK
- 2014 Poster, Association for the Study of Animal Behaviour Winter meeting: Individuals in Groups. London, UK.
- 2014 Talk, PhD student meeting, Courant Research Centre, Germany
- 2014 Talk, The International Primatological Society, Hanoi, Vietnam.
- 2014 Poster, The International Primatological Society, Hanoi, Vietnam.
- 2013 Talk, PhD student meeting, Courant Research Centre, Germany

Grants & Awards

- 2016 Leibniz Science Campus Primate Cognition
- 2014 Stabsstelle Göttingen International, Georg-August-Universität Göttingen
- 2013 The Leakey Foundation
- 2007 L. S. B. Leakey Trust
- 2007 Chester Zoo
- 2007 Roehampton University

Professional Societies

Association for the Study of Animal Behaviour
Gesellschaft für Primatologie
International Primatological Society
Society for Conservation Biology

Journal Reviewer

American Journal of Primatology
Folia Primatologica

DECLARATION

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

_____Göttingen

Adeelia S. Goffe