



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

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Abstract. Meat sharing in non-human 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 hypothesise 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.

1 Introduction

Food sharing among non-kin 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 the 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 non-kin 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 with each other, regardless of the oestrous phase of the female and one male units (OMUs) that 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 together 12 % of the time or greater are in the same gang (Patzelt et al., 2014). As non-kin 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.

2 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 to August 2012 and December 2012 to 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 recorded all behavioural observations on electronic forms created using Pendragon 5.1.2 software (Pendragon Software Corporation, USA) and run on HP Tungsten E2 handheld devices (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 denotes detumescence; C1 denotes small tumescence; C2 denotes medium tumescence; C3 denotes large tumescence; Goffe et al., 2016). Social interactions and close spatial proximity (2 m) 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 7 m was maintained in order to not strongly influence foraging behaviours and group dynamics. Carcass weight was estimated based on juvenile and adult body weights (Skinner and Chimimba, 2005) and the amount an individual obtained was gauged 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 5 × 5 cm tissue, weighing 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, defined here as the acquisition of meat after it had been left behind (greater than 2 m) 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 (0–2 m) 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

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

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 non-human primates set down by the International Primatological Society.

3 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 5 m 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 2 kg (hare) and from 10 to 14 kg (antelope). During 14 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 as those 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 min resulted in the eventual theft of the carcass. 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, Fig. 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 shar-

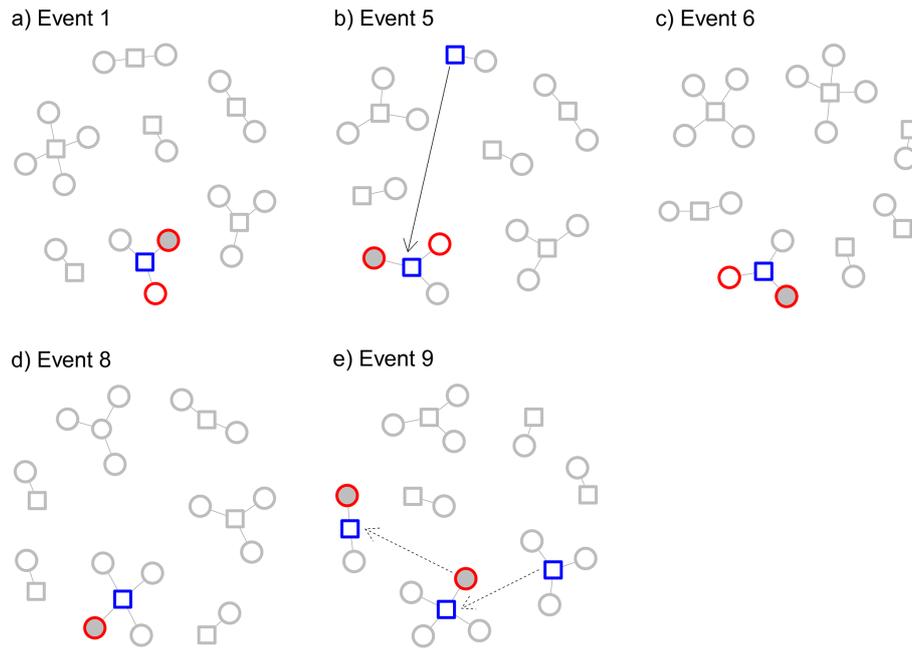


Figure 1. Five schematics (a–e) of the movement of meat between and within one male units. Node shape denotes sex (females = ○, males = □), colour indicates meat consumption (non-meat eaters are denoted by grey, male meat eaters are denoted by blue, female meat eaters are denoted by red). The arrows 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.

ing was observed between primary males and associated females (Fig. 1a–e). These adult and subadult females were allowed to approach, maintain close proximity (0–2 m) and feed on scraps while the male was feeding and also acquired the carcass when he was apparently satiated (Fig. 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 4 months to over 2 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



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

during the course of the group’s daily foraging march. Any male who subsequently gained access to a carcass after a female had left acquired the carcass through scavenging (one case), rather than through aggression or theft.

4 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 Wilkin-

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 OSM	JLA KTA	L L	300 100	JLA	5	4
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 OSM	JLA KTA	S1 P	100 50	JLA	2	1
6	antelope (sp. indet)	OSM 10		OSM	OSM	JLA KTA	P P	nr nr	JLA	4	2
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 HLN	5 4	~1 ~1
					DTM	RXN	S0	50	DTM RXN	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 denotes female reproductive state; * unsuccessful hunt/prey not captured; n/a denotes not applicable; nr denotes no record.

son, 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, 2015).

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 had 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

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

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 also eat 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.

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