Meat transfers follow social ties in the multi-level society of Guinea baboons but are not related to male reproductive success

Author list

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Abstract

In human foraging societies, hunting skill is a male quality signal closely tied to reproductive success, because it serves to provision the family, connected households, and the wider community. However, the relationship between catching or sharing prey and male reproductive success remains largely unexplored in other primate taxa. Using the multi-level society of Guinea baboons as a parallel for human foraging societies, we combined records of 109 meat-eating events with nine years of behavioural data to test whether males who acquire and share meat more frequently have more females in their social units and for longer than other males. We further tested the hypothesis that the type of meat transfer varies with social ties. We found no evidence that females preferred to join or remain longer in the units of males who acquired or shared meat more frequently. Thus, hunting skills do not appear to signal male quality. However, meat transfers were more likely to occur along stronger social relationships, as in human foraging societies. Tolerant forms of transfer were most common

at society's base, decreasing in tolerance at upper social levels. Our results demonstrate the cross-taxa influence of social organisation on the movement of sharable resources.

Introduction

In human hunter-gatherer societies, successfully catching prey signals a male's quality as a provider, and sharing the hunt's spoils broadcasts that signal throughout his community (Gurven & Von Rueden, 2006; Jaeggi & Gurven, 2013, 2018). In such societies, meat is a rare and highly prized food that arrives in quantities larger than a single individual or household can consume. Thus, the cost of sharing is small, but the benefit of receiving is large (Hawkes et al., 1991; Hill et al., 1993; Jaeggi & Gurven, 2013). As a result, meat is shared more widely than other foods (Kaplan & Hill, 1985). In the nested multi-level societies of most hunter-gatherers, meat typically flows from the household of the successful hunter, along social ties to an intermediate level of closely associated households, often linked by kinship, and then to the broader camp (Dombrowski et al., 2013; Kishigami, 2000; Ready & Power, 2018). Men who share more meat more often provide their immediate family with difficult-to-acquire nutrients, are sought after as extra pair mating partners, and experience increased reputation within their community (Gurven, 2004; Gurven & Von Rueden, 2006; Hill et al., 1993; Wiessner, 1996). As a result, frequent meat providers experience higher reproductive success in most hunter-gatherer societies (Smith, 2004; Wiessner, 1996).

While the extent of human food sharing is unique, acquiring and sharing food as a signal of male quality has deeper evolutionary roots. Food sharing is a male signal in some insect (Vahed, 1998) and bird species (*Corvus corax*, Heinrich, 1988; *Corvus monedula*: De Kort et al., 2006; *Corvus frugilegus*, Emery et al., 2007; *Turdoides squamiceps*, Kalishov et al., 2005) where males provision prospective mates to signal their quality as a provider (Amat, 2000; Snowberg & Benkman, 2009). However, in our closest living relatives, the nonhuman primates, there is little evidence of a relationship between food sharing and reproductive success (Jaeggi & Van Schaik, 2011). Chimpanzees, capuchins, and baboons are the three taxa in which meat-eating has been most often observed (Watts, 2020). Much research has been devoted to chimpanzees (*Pan troglodytes*) as the only taxon that hunts cooperatively and actively shares meat (Boesch & Boesch, 1989; Watts, 2020). So far, the results are mixed: following meat-sharing, male chimpanzee hunters have been reported to receive copulation opportunities immediately (Stanford, 1998), delayed (Achorn et al., 2023;

Gomes & Boesch, 2009), or not at all (Mitani & Watts, 2001). Both capuchins (Perry & Rose, 1994) and baboons (Allan et al., 2022; Goffe & Fischer, 2016; Schreier et al., 2019; Strum, 1975) passively share meat with select individuals (tolerated theft, Stevens & Gilby, 2004). Yet, no study has investigated whether meat sharing serves as a male quality signal in these species (Jaeggi & Gurven, 2013; Watts, 2020). Baboons, in particular, offer a valuable analogy for human hunter-gatherer diet and food practices given their shared ecological history, parallel evolution with early hominids, and, in some species, shared nested multi-level social organisation (Codron et al., 2008; DeVore & Washburn, 2017; Fischer et al., 2019; Patzelt et al., 2014).

In this study, we investigated Guinea baboons (*Papio papio*) as a possible system in which males' ability to acquire and share meat might signal their quality to females and impact their reproductive outcomes. We also examined patterns of meat transfers in Guinea baboons' multi-level society and compared them to the rules that govern meat sharing in human hunter-gatherer communities. Specifically, we asked whether meat transfer followed social relationships and ascended along societal levels.

At the base of Guinea baboon's multilevel society are stable 'units' comprised of a single reproductive male and one to several females with their young (Dal Pesco et al., 2022; Goffe et al., 2016). Male-female relationships are variable – some lasting weeks, others years (Goffe et al., 2016). Females show high mate fidelity, with males siring 91.7% of offspring in their units (Dal Pesco et al., 2022). Units are nested within 'parties', and parties are nested within 'gangs' (Fischer et al., 2017; Goffe et al., 2016). Within parties, males form enduring social bonds with other males (Dal Pesco et al., 2021), who often share a higher degree of relatedness (Dal Pesco et al., 2021). Like other baboons, Guinea baboons are highly opportunistic, eclectic omnivores (Zinner et al., 2021). Their diet consists of a wide range of woody and herbaceous plants, fruits, invertebrates, and occasionally birds and small mammals (Zinner et al., 2021). Guinea baboons opportunistically chase and catch prey (Goffe & Fischer, 2016; Watts, 2020), primarily young bushbuck (*Tragelaphus scriptus*), representing a relatively large prey item for the baboons (young bushbuck: 10 – 14 kg, adult Guinea baboon: 10 – 26kg). In this study, we use the phrase "acquiring meat" rather than "hunting" because Guinea baboons do not actively seek out prey; instead, they opportunistically catch prey animals they detect nearby.

A previous study that examined a small number of meat-eating events (Goffe & Fischer, 2016) reported that Guinea baboons did not perform active (possessor-initiated) but passive (recipient-initiated) sharing or "tolerated theft" (Boesch & Boesch, 1989). It also

reported that males preferentially shared meat with females in their units, and females did not catch prey themselves but ate 10-40% of the meat their males acquired. Lastly, males and females in possession of a carcass were not harassed by others – only transferring meat when satiated (see supplements for description and example of "queuing" behaviour).

While Guinea baboons do not actively share meat, they still exhibit a tolerant, socially mediated form of meat transfer that cannot be explained by harassment avoidance (Jaeggi & Gurven, 2018). Given their shared societal organization with human foragers its possible meat may transfer along similar patterns in both societies. Specifically we predicted that meat would transfer through the Guinea baboon society along strong social relationships and flow upward from the base of the multi-level society similar to human hunter-gatherer societies. Specifically, we predicted that meat would transfer through the Guinea baboon society along strong social relationships and flow upward from the base of the multi-level society similar to human hunter-gatherer societies. Additionally, female access to meat appears to be determined by her male's ability to catch prey or his motivation to acquire meat from prey caught by others (Goffe & Fischer, 2016). Female Guinea baboons display relatively high degrees of mate choice, but the criteria by which they choose their unit remains uncertain (Dal Pesco et al., 2022; Fischer et al., 2017). Thus, it is plausible that, as in humans, meat acquisition and sharing in Guinea baboons could signal a male's quality and influence females to join or remain in his unit. We predicted that if females consider meat acquisition success and meat sharing frequency as features of male quality, males who excel at these behaviours should have more associated females. The females should also stay with them longer.

Methods

Field site and study subjects

Field work for this study was based at the field station "Centre de Recherche de Primatologie (CRP) Simenti" (13°01'34" N, 13°17'41" W), in the Niokolo-Koba National Park, Senegal. The site lies next to the Gambia River, where multiple seasonal wetlands (Mare) occur in depressions alongside the river. The climate is highly seasonal, with a dry season from November until May and a rainy season from June until October (Fischer et al. 2017). The home ranges of the parties covered, on average, 30.3 km^2 of largely overlapping territories (Kernel density estimations 95%) (Zinner et al. 2021). Between April 2014 and June 2023, we entered 465 individually identified animals into our database, including adults,

subadults, juveniles, and infants of our core focal parties; some identified animals resided in adjacent parties. Baboons in the focal parties were fully habituated and individually identified by natural markings, body shape and size, and radio collars.

Observational data collection

Demographic, observational, and meat-eating data were recorded by researchers from April 2014 to June 2023. We performed behavioural observations of adults and subadults in our eight focal parties by conducting 20-minute focal follows (Altmann, 1974) balanced between subjects and time of day for an average of six protocols per individual and month. During protocols, we continuously recorded focal animal activity (i.e., moving, feeding, resting, and socialising) and all occurrences of social behaviours such as approaching within one meter, grooming, contact-sit and greeting (Dal Pesco & Fischer, 2024). Observers recorded all behavioural observations on electronic forms created using the software Pendragon (Pendragon Software Corporation, USA) running on cellular phones (Samsung Note 2 and Gigaset GX290).

During each observation day, we recorded census information about demographic changes (i.e., births, deaths, dispersal, and presence/absence), health status and female reproductive state and which other parties were nearby (Dal Pesco & Fischer, 2024).

We monitored female-male associations and unit composition daily by collecting data on female-male interactions (i.e., frequency of copulations, grooming bouts, contact-sit bouts, greetings, aggression events, and duration of grooming and contact-sit bouts). We used female-male interaction rates to verify daily unit composition within each study party using established methodologies (Dal Pesco et al., 2021; Dal Pesco & Fischer, 2018) based on previous findings that female Guinea baboons interact with their primary male at significantly higher rates and mated almost exclusively with him (Goffe et al., 2016).

Meat eating event data collection

Prey capture and meat-eating events were observed opportunistically and, when possible, were recorded with video cameras (handheld Panasonic HC-X909 and GoPro Hero8). At the same time, the observer verbally described the unfolding scenario and recorded the audience composition. Individuals who caught the prey and were first to possess the carcass were identified and recorded. Individuals who possessed a carcass or from whom meat was transferred were labelled ‘possessors’, while the individuals receiving meat were

labelled ‘recipients’. Only adults and subadults were recorded as possessors or recipients of meat. Individuals who did not catch the prey themselves could acquire meat through four transfer types: ‘passive sharing’, ‘scavenging’, ‘supplanting’, or ‘stealing’ (Table 1), in line with previous descriptions of meat eating in Guinea baboons (Goffe & Fischer, 2016). Passive meat sharing (Boesch & Boesch, 1989) was characterised as the tolerated transfer of a defensible item by food-motivated individuals (Feistner & McGrew, 1989). We described all transfers as passive meat sharing when a recipient took meat from the carcass or from the ground just around the carcass (< 2m) while the owner was still feeding in the absence of aggression and submission by either individual. ‘Scavenging’ occurred when recipients acquired pieces of the meat that had been left behind (>2m) when the possessor moved the carcass. ‘Supplanting’ occurred when a recipient moved into the feeding position recently vacated by the owner. ‘Stealing’ occurred when the recipient forcefully took possession of the carcass despite resistance by the owner. Transfers were labelled ‘unknown’ when meat passed from possessor to recipient, but the transfer type could not be observed (e.g., the subject was filmed from the back).

Data analysis

Model 1: Male meat acquisition and unit size

In the first set of models, we sought to measure how the frequency with which males acquired and shared meat affected their reproductive success regarding the number of associated females in their unit and the duration of their association with each unit female. Our first question was, “Do males who acquire more meat have more females?” To answer this question we used a generalised linear mixed model (GLMM) with a Poisson error distribution where the response was the mode male unit size for each year fit with the R package lme4 (lme4 version 1.1-21; (Bates et al., 2015). The model had two predictors measuring males’ meat acquisition abilities: ‘prey caught’ and ‘meat acquisition’. Prey caught was the number of times a male caught prey each year. This term was included to test whether females prefer males who actively find and capture prey. Meat acquisition was the total number of times a male possessed a carcass each year. This term was a more general measure of a male’s motivation and ability to acquire meat from his physical and social environment. The numbers of prey caught and meat acquisitions were divided by the number of meat-eating events in each male’s party in the given year. Thus, the predictors can be

understood as the number of times males caught prey or acquired a carcass, given the number of opportunities they had to access meat each year. The two predictors were z-transformed to ease model convergence and interpretation (Schielzeth, 2010). We also included the categorical variable 'mode male age category per year' (for age categories definitions, see CRP Simenti work manual (Dal Pesco & Fischer, 2024)) as a fixed effect in the model to account for a known bias that prime-aged males have larger unit sizes (Dal Pesco et al., 2022). We included Male- and Party-ID as random intercepts to account for repeated observations of the same individuals and parties. Lastly, we included random slopes of prey caught and meat acquisition within Male- and Party-ID into the model (Barr et al., 2013; Forstmeier & Schielzeth, 2011).

Model 2: Male meat acquisition and female tenure

To answer our second question, "Do females stay longer with males who share meat with them more often?" we used a survival model (cox proportional hazard model) fit with coxme version 2.2-20 (Therneau, 2018) because it allowed us to include all male-female associations and to censor those that were still ongoing. Also, by measuring how the time to an event was affected by a set of variables, a survival model allowed us to ask a slightly more causal form of our question: "Is the amount of time until a female leaves her primary male affected by the frequency with which he acquires meat or shares meat with her?". The response in the model was the duration from start to finish of each female-male association, measured in months, and indicating if the association was ongoing (i.e., right censored). Some female-male dyads were already associated when data collection started in 2014 (i.e., left-censored), so we regarded all associations as "minimum unit tenures" as we do not know the full extent of associations before 2014. The main predictors were 'meat possessions' i.e., the frequency with which each primary male possessed a carcass and 'meat shared' i.e., the frequency with which they shared meat with a female during their association. The frequency was calculated by dividing counts of meat possession and sharing by the number of days the male was observed during the male-female association. Possession and sharing frequencies were z-transformed to ease model convergence (Schielzeth, 2010). We also included whether or not a male was in a prime aged category (yes, no; see Simenti work manual for age categories: Dal Pesco & Fischer, 2024) as a fixed effect to control for the tendency of prime-aged males to have larger units. Similarly, we included mode female age as older females would necessarily have the opportunity for longer unit tenures than younger females. We also

included Female-, Male-, and Dyad-IDs as random intercepts to account for repeated observations of the same individuals in different dyads and the same dyads occurring multiple times. Random slopes were not included because they were not theoretically identifiable for any of the predictor-grouping pairs (Barr et al., 2013; Forstmeier & Schielzeth, 2011).

Model 3: Transfer tolerance and societal level

In the second set of models, we sought to measure how meat moved through the multi-level society of Guinea baboons. Our third question was: "How is the degree of tolerance – reflected by different meat transfer types – related to the level of the society at which the transfer occurs and the sex of the possessor or the recipient?". To answer this question, we fit an ordinal (i.e. cumulative logit-link) mixed model (Agresi, 2002) using the function clmm of the package ordinal version 2023.12-4 (Christensen, 2019) which allowed us to include meat transfer type as an ordinal response variable measuring three different types of transfers from least to most tolerant (steal < scavenge/supplant < share). We combined 'scavenge' and 'supplant' into one category because both are neutral transfer types that occur without direct interaction with the meat possessor. In contrast, 'stealing' is a transfer type that occurs in the face of opposition from the possessor, while 'passive sharing' only happens with the possessor's tolerance. The primary predictor of the model was 'social level', a categorical variable with three levels (same unit/same party, different unit/same party, different unit/different party), which described three types of social-level-based relationships individuals could share within the Guinea baboon society (unit, party, gang). We also included the sex of the possessor, the sex of the recipient, and their interaction as categorical predictors with the expectation that males transferring tolerantly with females would be most frequent. Finally, we included Possessor-, Recipient-, Dyad-, and Event-IDs as random intercepts to account for repeated observations. Random slopes were not included because they were not theoretically identifiable for any of the predictor-grouping pairs (Barr et al., 2013; Forstmeier & Schielzeth, 2011).. We also ran a reduced version of the model (see Supplements) without the interaction between the possessor and recipient sex to draw inferences about their effects on their own (Aiken & West, 1991).

Model Validation (Models 1-3)

Before fitting our first three models, we inspected all quantitative predictors for roughly symmetric distributions. After fitting the models as an overall test of our main predictors and to avoid "cryptic multiple testing", we conducted full-null model comparisons (Forstmeier & Schielzeth, 2011), wherein the null model lacked the primary predictors but was otherwise identical to the full model. The comparison was based on a likelihood ratio test (Dobson, 2002). After fitting the Poisson model, we checked the mean-variance assumption by ensuring dispersion parameters did not deviate much from one (0.621). We determined Variance Inflation Factors (VIF) using the function vif of the package car (version 3.0-3; Fox & Weisberg, 2011). Assessment of Variance Inflation Factors did not reveal any collinearity issues (max VIF: 1.25) (Quinn & Keough, 2002). We assessed model stability on the level of the estimated coefficients by excluding levels of the random effects one at a time using a function provided by RM (Nieuwenhuis, 2012). The models were all revealed to be of acceptable stability. We determined 95% confidence intervals of model estimates and fitted values using a parametric bootstrap (N=1.000 bootstraps) using the function bootMer of the package lme4 except for the survival model. We fitted the models in R (version 4.2.0; R Core Team 2022).

Model 4: Transfer probability and relationship strength

Our fourth question was: "Are close social associates of meat possessors more likely to receive meat transfers?". To answer this question, we built a custom Bayesian model fitted using Stan (v. 2.35.0;Stan Development Team, 2024) and its R interface cmdstanr (v. 0.8.1.9000, Gabry et al., 2024). In brief, we first estimated dyadic affinity from behavioural data (Neumann and Fischer 2023), representing the relationship strength for a pair of individuals. We then modelled the probability of an individual obtaining the meat given their affinity with its current possessor. Below, we describe this approach in more detail (see supplements for formal model specifications).

In the first step, we estimated two sociality components: individual 'gregariousness', defined as an individual's general tendency to interact with any group member regardless of their identity, and dyadic 'affinity', defined as the preference of two individuals to interact specifically with one another. We used data from three behaviours (approaches, grooming, and contact sitting) to estimate the two sociality dimensions separately for the 90 days preceding each meat-eating event. To avoid redundancies with the other behaviours,

approaches were only included if no social behaviours (positive or negative) took place in the following ten seconds.

The second step consisted of three sub-models: one primary model and two control models (see supplement for description of control sub-models). Each sub-model concerned a different feature of meat transfers (i.e. audience size, audience composition, dyadic affinity of audience members), with either gregariousness or affinity as the primary predictor. We used the full posterior of either gregariousness or affinity for all sub-models as a predictor, i.e., we propagated the uncertainty in estimating these sociality features downstream into the models of meat transfer. The final sample for the sub-models included 232 meat transfers. We removed 48 steal transfers from the initial sample of 314 because we expected that relationship strength would not affect intolerant transfer types. We removed 34 other transfers for which we could not calculate affinity: 15 because they occurred between cross-party dyads and 19 because we lacked focal observations in the party for 90 days before the meat-eating event.

The primary sub-model quantified the relationship between the dyadic affinity of all audience members with the meat possessor and the probability that one of the audience members would receive meat from the possessor. We pruned the data for this model, limiting it to events with at least two individuals in the audience, resulting in 148 transfers. The response came from a multinomial distribution and was a vector of one 1 with a varying number of 0s given audience size for each transfer. We derived the probability vector for the multinomial likelihood from a linear predictor, i.e., the dyadic affinity values of all audience members with the possessor. This linear predictor was then multiplied by the slope parameter of interest. If that slope were positive, it would indicate that larger affinities were associated with higher probabilities of obtaining meat (see supplement figure S1). The length of the linear predictor varied from event to event to reflect the different audience sizes (see below). For instance, if we had an event with an audience of three, the linear predictor would consist of three affinities and the response of a vector of a one and two zeros (one individual obtained the meat, two did not). In this model, we also included a parameter for partner sex and a varying intercept for the partner's ID. This last term reflects the possibility that individuals differed in their propensity to receive meat irrespective of their dyadic affinity with the meat possessor.

Results

Between April 2014 and June 2023, we recorded 109 meat-eating events in which 111 individuals from 13 parties (eight focal, five non-focal) participated as possessors or recipients. We recorded a median of ten events per year (Q1:8, Q3:12.5, range: 4-22). Within these 109 meat-eating events, we recorded 319 meat transfers, with a median value of two transfers per event (Q1:1, Q3:5, range: 1-17). In 57 of the 64 instances where the prey-catcher was identified, the prey was caught by males (89.1%). In the remaining seven cases, the prey was caught by females (10.9%). In transfers to female recipients, the meat originated from the females' primary male in only 59.3% (83/140) of cases (see Figure 1 a for a breakdown of transfers by sex). In 22 events, the individual who caught the prey consumed the entire prey and did not transfer any meat. In all these cases, the prey were small birds (Table S1). The breakdown showing the frequency of each transfer type among transfers can be seen in Figure 1 b. Of the transfers between adults for which we knew the unit membership of both possessor and recipient (N=299), most transfers occurred between members of the same party but belonging to different units (N=155). Ninety-nine transfers occurred between members of the same unit, and 38 occurred between members of other parties.

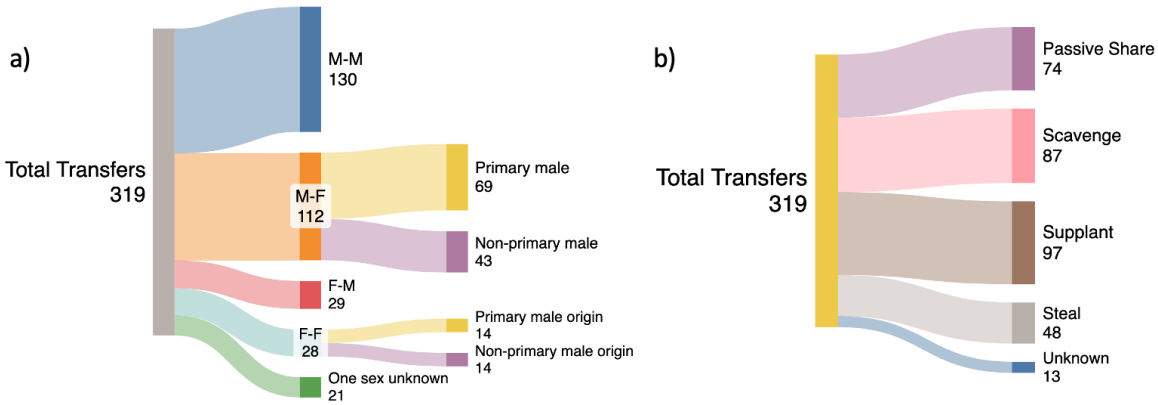

Figure 1. *Sankey diagrams of meat transfers split by a) sex and b) transfer type.*

1 Male meat acquisition and unit size

The model to assess the link between male meat acquisition and unit size included 235 observations of 54 males across 8 parties with a median unit size of one (Q1:0, Q3:3, range: 0-7). The median prey caught per male and year was 0 (Q1:0, Q3:0, range: 0-3), and the median meat acquired was 0 (Q1:0, Q3:1, range: 0-8). The full-null model comparison was not significant ($\chi^2 = 0$, df = 1, $P = 1$). Thus, we found no significant relationship between the

number of associated females in a male's unit and the number of times a male caught prey (Estimate = -0.232, SE = 0.072, $P = 0.747$) or possessed a carcass (Estimate = 0.113, SE = 0.074, $P = 0.129$; Table S2). In other words, males who caught prey or acquired meat more often did not have larger unit sizes than males who caught prey or pursued meat less frequently (Figure 1). The largest effect size of factors in the model was male age, with early and mid-prime males likely to have higher numbers of associated females in their units than sub-adult males, late-prime males, and old males (Table S2).

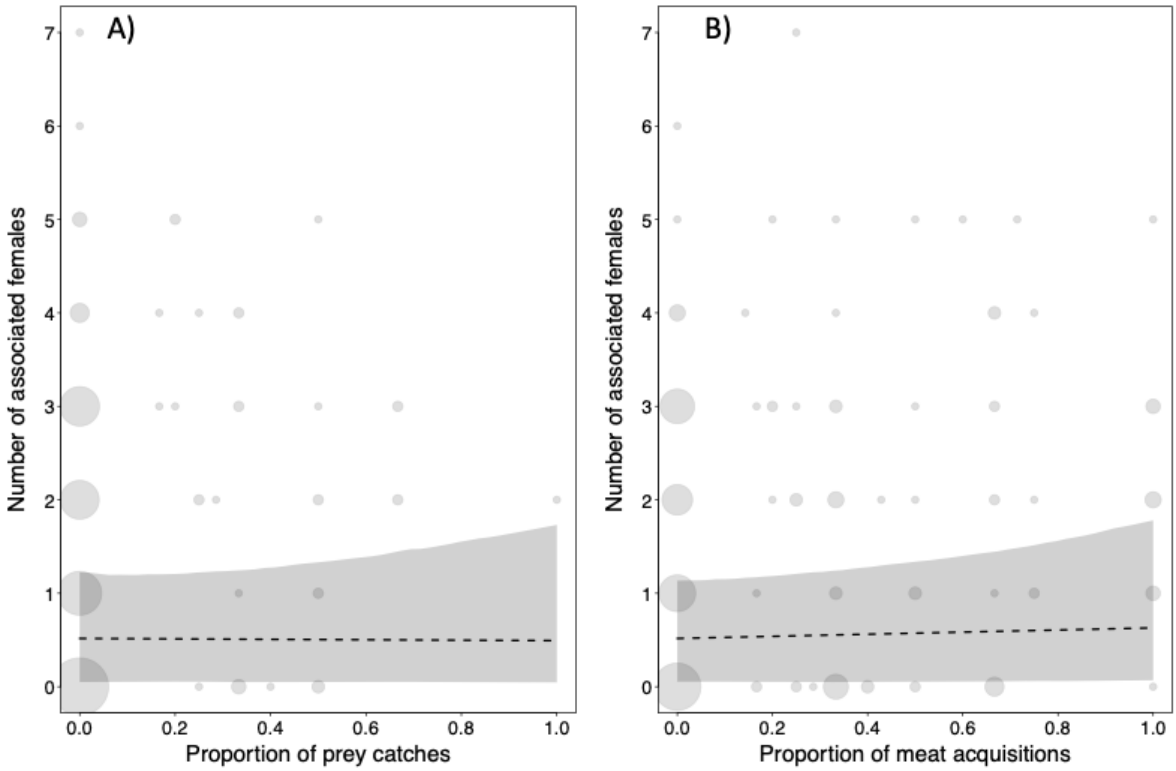

Figure 2. Relationship between the number of associated females (mode per year) and A) the proportion of times males acquired meat or B) captured the prey item from all the meat-eating events in their party each year. There was no evidence of a relationship between meat acquisition (GLMM: n = 235, p = 0.129) or prey captures (GLMM: n = 235, p = 0.747) and the number of associated females. Points represent the males in a given year (2014-2023), and the area of the points shows the number of males that have the same yearly value [range: A) 1-43, B) 1-64]. The dashed line depicts the fitted model and the grey polygon with the bootstrapped 95% confidence intervals, with all other predictors being centred.

2 Male meat acquisition and female tenure

The model on the link between male meat acquisition and female tenure contained 236 dyads formed by 99 females and 54 males with a median association duration of 269 days (Q1: 80, Q3: 704; range: 1-2967 days). Males possessed a median of 0 carcasses (Q1: 0, Q3: 0; range: 0-12) and shared a median value of 0 carcasses (Q1: 0, Q3: 0; range: 0-12). The full-null model comparison was not significant ($\chi 2 = 3.0827$, df = 2, $P = 0.2141$). Consequently, we found no significant relationship between the length of a female's tenure and the number of

times her male possessed meat (Estimate = -0.103, SE = 0.186, $P = 0.577$) or shared meat with her (Estimate = -0.157, SE = 0.195, $P = 0.419$; Table S3; Figure 2). As in the above unit size model, we found that prime-aged males were more successful in maintaining a unit, as females associated with them longer than non-prime-aged males (Estimate = 2.971, standard error = 1.152). We also found that subadult females had slightly longer unit tenures than mature adult females (Estimate = 1.152, standard error = 0.499).

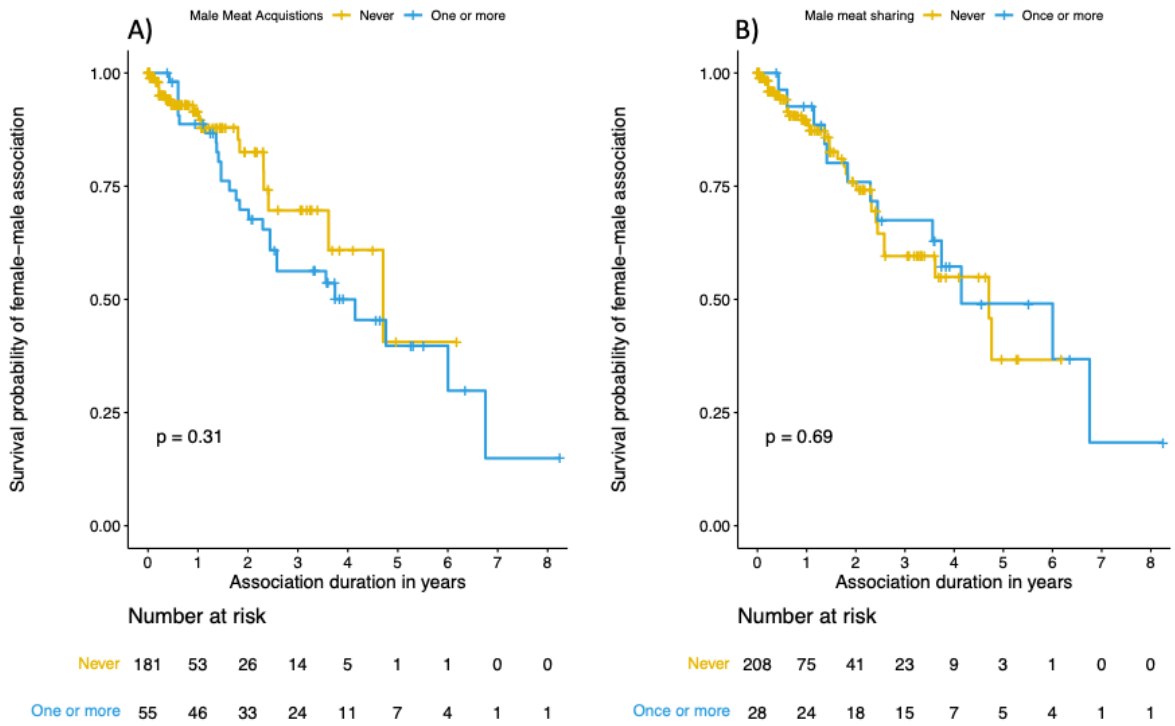

Figure 3 Kaplan-Meier survival curves for the effects of males A) acquiring meat and B) sharing meat with their female on the "survival" of the male-female association. Separate lines are for males who never acquired or shared meat (blue) and males who acquired or shared meat at least once (yellow). This figure is a simplified to illustrate the result. The model included all possible values of meat acquisition and sharing. Risk tables beneath the plots give the number of female-male associations that "survived" to each yearly increment.

3 Transfer tolerance and societal level

The model regarding the link between transfer tolerance along social levels contained 283 transfers between 65 possessors and 79 recipients in 152 dyads and 62 meat-eating events. The full-null model comparison was significant ($\chi 2 = 33.624$, df = 4, $P < 0.001$). More tolerant transfer types (passive sharing > scavenge/supplant > steal) occurred more frequently at the unit level (same unit/same party) compared to the party level (different unit/same party level: Estimate = 2.345, SE = 0.539, $P = < 0.001$) and more tolerant at the party level (different unit/same party level) compared to the gang level (different unit/different party: Estimate = 1.224, SE = 0.438, $P = 0.005$; Table S4). In other words, more tolerant types of

meat transfers were more common at the base level of the society and decreased at higher social levels (Figure 3). We found no significant effect of the interaction of possessor and recipient sex (Estimate = 0.738, SE = 0.657, $P = 0.260$; Table S4). However, in a reduced model lacking the interaction of possessor and recipient sex, males were also slightly more likely to transfer more tolerantly than females (Estimate = 0.711, SE = 0.365, $P = 0.051$; Table S5), and recipient sex was not related to the tolerance of the transfer type (Estimate = -0.428, SE = 0.377, $P = 0.246$; Table S5).

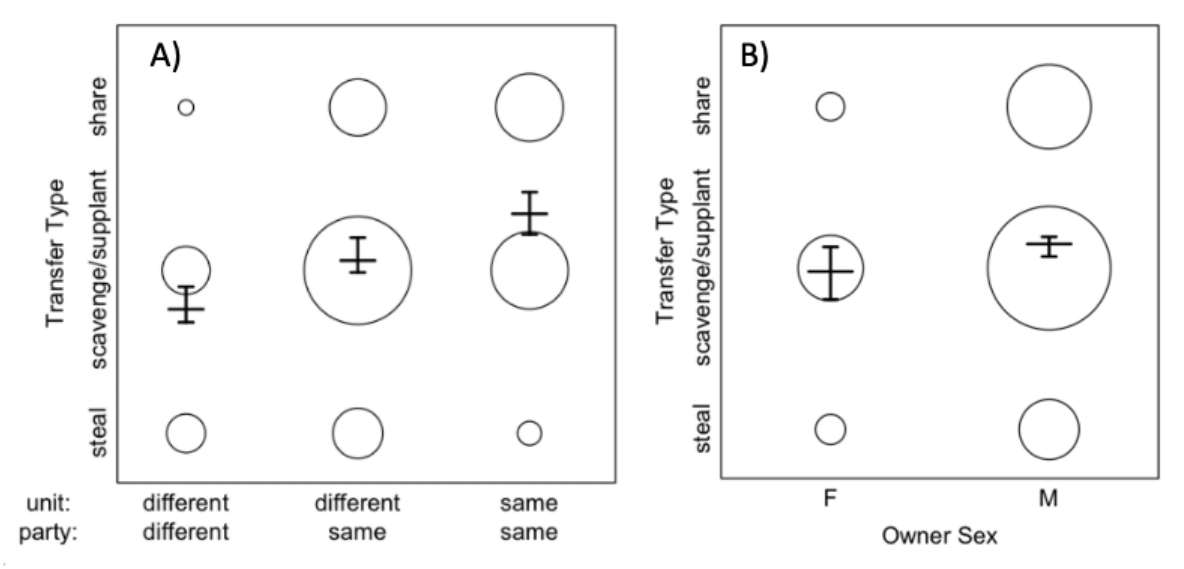

Figure 4 Transfer types of increasing tolerance (steal -> scavenge/supplant -> share) and how their frequency varies depending on A) the shared social levels of meat possessor and recipient and B) possessor sex. The area of the bubbles shows the relative frequency of transfer types [range: A) 2-101, 7-135]. Vertical lines with error bars depict the fitted model and its confidence limits (with all other predictors being centred).

4 Transfer probability and relationship strength

The final sample for the sub-models on transfer probability and bond strength included 232 meat transfers and contained individuals from eight parties, including 59 possessors, 68 recipients, and 83 audience members. The median audience size was two (Q1: 1, Q3: 3, range: 1-6).

With regard to our primary sub-model, we found an overall positive relationship between affinity and an individual's probability to receive meat (posterior median = 0.28, 89% credible interval = 0.07 – 0.56), Figure 5, and see the supplement for the result of control sub-models). To illustrate this result and its effect size, we present two scenarios. If there is a meat-eating audience of two individuals with affinities to the possessor of -1.0 and 1.0, i.e., slightly above and below average. All else being equal, the estimated probabilities of each individual receiving meat with a slope estimate of 0.30 would be 0.36 and 0.64,

respectively (Figure 5a). With an audience of three individuals with affinities of -1.0, 1.0, and 1.0, the resulting probabilities of getting meat would be 0.25, 0.32, and 0.43 (Figure 5b). From these examples, one can see the probability of getting meat increased with greater affinity to the possessor and is modulated by audience size.

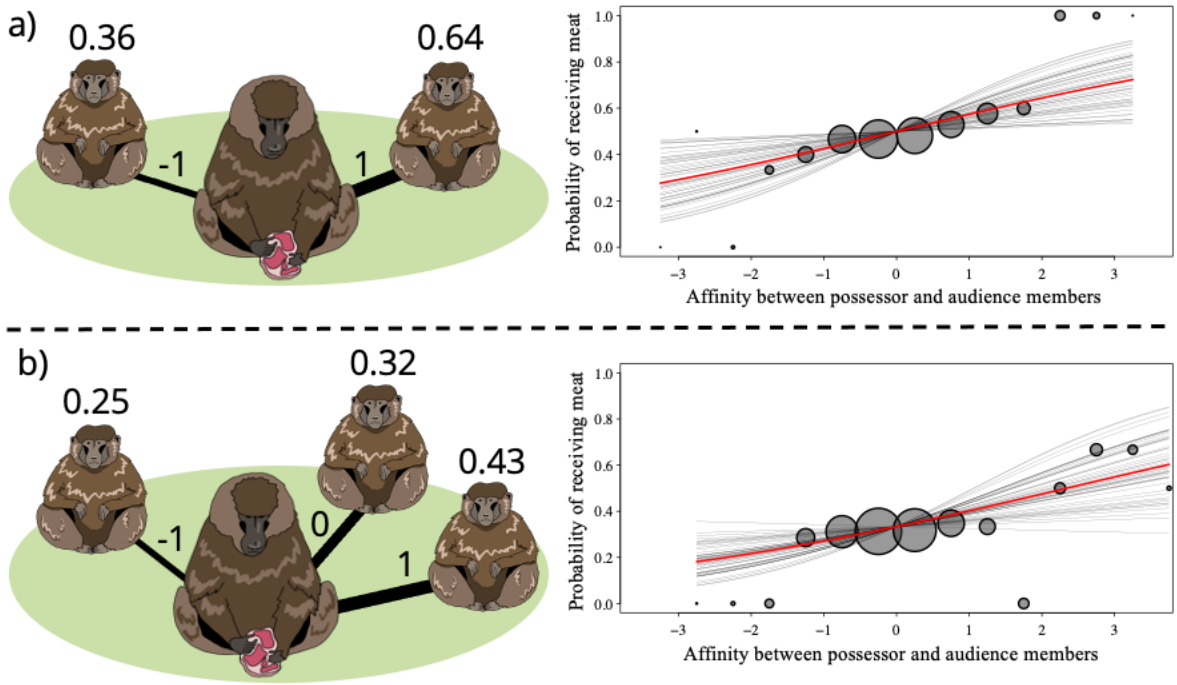

Figure 5 Social relationships and probability of receiving food. The probability of each audience member obtaining the meat is calculated using the softmax function, which creates a vector of multinomial probabilities that sum to one based on the unconstrained linear predictor, i.e., the dyadic affinity values of the audience members with the possessor. a) softmax(0.30 × [−1.0, 1.0]) = [0.36, 0.64], b) softmax(0.30 × [−1.0, 0, 1.0]) = [0.25, 0.32, 0.43]. Drawings by Maggie Slowinska.

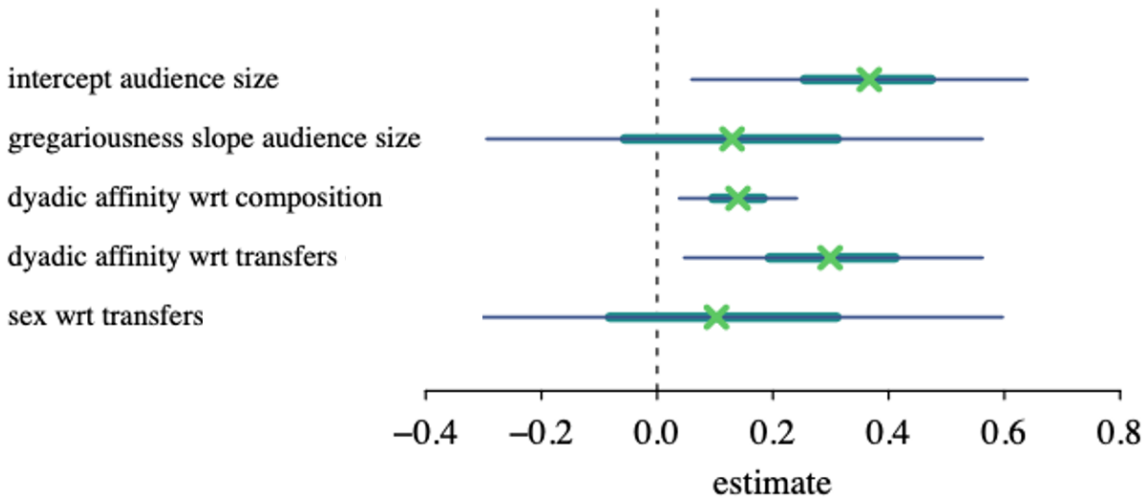

Figure 6. A visual summary of posterior distributions of the key parameters of model 4 Transfer probability and relationship strength. Shown are medians (crosses), 50% intervals (thick lines) and 89% intervals (thin lines) of the posteriors.,

Discussion

We found no evidence that female Guinea baboons preferred to join or remain in the units of males who acquired or shared meat more often. Thus, acquiring or sharing meat is unlikely to signal male quality in Guinea baboons. However, we found that the types of meat transfers varied according to societal level. While the most tolerant transfer type (passive sharing) occurred most frequently between members of the same unit, transfers between members of different units and parties were increasingly less tolerant. The greater the distance in social level, the more likely supplanting and stealing were to occur. Lastly, a higher dyadic affinity (preference of two individuals to interact with one another in an affiliative fashion) between audience members and meat possessors increased the likelihood that the audience member would be next to receive meat. Together, these results show that meat transfer occurs along existing social relationships and follows the multi-level social organisation of the society.

The simplest explanation for why female Guinea baboons do not respond to male meat acquisition as a quality signal is that meat-eating events are relatively rare in Guinea baboons. Rates of prey capture in Guinea baboons (1.12 prey per month, 2.79 prey per 100 hours) are comparable to other baboon species (*Papio anubis*: 4.54 prey per 100 h; *Papio ursinus*, 1.27 prey event per 100 h; *Papio hamadryas*: 0.1 – 2.8 prey per 100 h; *Papio cynocephalus*: 1.78 prey per 100 hours, Hausfater, 1976; Kummer, 1968; Schreier et al., 2019; Watts, 2020), and capuchins (*Cebus capucinus*: 5.35 prey per 100 h; *Sapajus libidinosus*: 0.3 prey per 100 h, Watts, 2020). However, they are generally lower than what we see in chimpanzees (Kanyawara – Ngogo: 0.8 – 7.6 per month, Watts, 2020) and far below the weekly hunts of many human hunter-gatherer societies (Hill et al., 1993; Kishigami, 2000; Naylor et al., 2021). Due to this infrequency, a male's ability to acquire meat is unlikely to impact their females' fitness as much as other features, which females might use as a criterion when choosing a unit. Male behavioural tendencies such as willingness to provide care for offspring (Rosenbaum et al., 2018), general tolerance (Goffe et al., 2016), or general attentiveness likely outweigh the impact of meat provisioning, as they might more consistently and directly impact females' fitness and reproductive output. In addition, non-male features of the unit, like the number and identities of other females, may also affect female unit choice and tenure.

Another reason male meat acquisition may not impact female partner preference is that females have more paths to meat access than was previously reported (Goffe & Fischer, 2016). In our nine years of meat-eating events, males are still the most important source of meat for their females (59%), but 41% of female's meat comes from individuals other than their primary male. Additionally, we report the first observations of female prey capture in this species. Together, these findings indicate that females are less dependent on males for the nutritional benefits of meat than was previously thought. This finding is consistent with observations of meat eating in other baboon species where males and females both catch and eat vertebrate prey (Allan et al., 2022; Schreier et al., 2019; Strum, 1975). Both sexes participating in prey capture may contribute to the value of baboons as a parallel model of hominin evolution, as research continues to reveal that female hunting is more prevalent in hunter-gatherer groups than was previously recognized (Lacy & Face, 2023).

The pattern of meat sharing we found in Guinea baboons is similar to what has been recorded in the Agta and Mbendjle hunter-gatherer communities, where sharing is most common at the lowest of three levels and decreases in frequency with each upper level (Dyble et al., 2016). In both societies, the lowest level comprises a male and one or more paired females with their offspring (unit, household), and the second level is composed of three to four units or households linked by male social bonds and kinship (Dal Pesco et al., 2021; Dyble et al., 2016). The third level is a related collection of individuals less connected by social ties or kinship (Dyble et al., 2016; Fischer et al., 2017; Kishigami, 2000). In Guinea baboons, like in humans, meat transfers appear to primarily flow from males to females at the lowest level, and then between socially connected males at the secondary level (Dombrowski et al., 2013; Dyble et al., 2016; Naylor et al., 2021). These parallels demonstrate the commonality of multi-level organisation. While humans and Guinea baboons may have evolved toward a multi-level society for separate reasons (Grueter et al., 2020; Swedell & Plummer, 2012), and human food-sharing traditions are more sophisticated than those of baboons, the influence of the society's shape on the movement of a sharable resource is nevertheless the same. Meat brought into the society by one individual diffuses along gradients of familiarity and social predictability, whether actively through human sharing or passively through tolerated theft.

Closer associates having greater access to meat is both intuitive and consistent with what occurs in other primate taxa (Jaeggi & Van Schaik, 2011; Perry & Rose, 1994; Watts, 2020). However, the size of the effect is not overwhelming, nor is the pattern a result of strategic dispensation like the chimpanzee begging circle where the possessor hands out meat

based on a preference for relationship quality or potential for future coalitions (Nishida et al., 1992; Stanford, 2014). Instead, we see audience members sitting a short distance away from a meat possessor (see supplements for more detail), neither begging or harassing. Their behaviour is reminiscent of the "respect of possession" described by Kummer, 1973. Individuals in the queue with higher affinity receive more tolerance when they sit closer, take pieces from the carcass, take pieces from the ground when the meat is moved, or take over the carcass when the possessor leaves. In this way, tolerance for close associates gives them more opportunities to acquire meat. However, audience composition matters. If there are multiple individuals in the audience with high affinity, if differences in affinity are minor, or if the audience is large, then the effect of affinity is diluted, and all audience members have similar chances of getting meat. Meat transfers then are affected, but not determined by social relationships.

In conclusion, meat acquisition and sharing does not appear to be a male-quality signal in Guinea baboons. However, meat transfers follow social relationships along social levels in the multi-level society of Guinea baboons. Our results highlight the value of Guinea baboons as a comparative model for hominin evolution, demonstrate that acquiring and sharing rare food sources need not be a quality signal, and show that shared social organization leads to the same patterns of resource exchanges despite broad differences in cultural complexity.

Ethics Declaration

This research was conducted within the regulations set by Senegalese authorities and the guidelines for the ethical treatment of nonhuman animals set down by the Association for the Study of Animal Behaviour (ASAB Ethical Committee/ABS Animal Care Committee, 2023).

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Author contributions

W.O., F.D.P., and J.F. developed the study's concept and design; W.O. extracted data from the meat-eating event records; F.D.P. curated and extracted the demographic and behavioural data, and assisted with data preparation; W.O., F.D.P., C.N., and R.M. designed and conducted the analysis with supervision from J.F.; W.O. drafted the manuscript; and W.O., F.D.P., C.N., R.M., and J.F. reviewed the manuscript and provided final approval of the submitted version.

Data availability statement

The data and code associated with the analysis of this project can be found at https://osf.io/n64ep/?view_only=f1d57b6ae2e94e009f747ec0abd1586e

Competing interests

The authors declare no competing interests.

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