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Reciprocity and beyond: Explaining meat transfers in savanna-dwelling chimpanzees at Fongoli, Senegal

Angela Achorn[1,2] | Stacy Lindshield[3] | Papa Ibnou Ndiaye[4] | Jeffrey Winking[1] | Jill D. Pruetz[5]

[1]Department of Anthropology, Texas A&M University, College Station, Texas, USA

[2]Department of Comparative Medicine, Michael E. Keeling Center for Comparative Medicine and Research, University of Texas MD Anderson Cancer Center, Bastrop, Texas, USA

[3]Department of Anthropology, Purdue University, West Lafayette, Indiana, USA

[4]Département de Biologie Animale, Université Cheikh Anta Diop de Dakar, Dakar, Senegal

[5]Department of Anthropology, Texas State University, San Marcos, Texas, USA

Correspondence
Angela Achorn, Department of Anthropology, Texas A&M University, College Station, TX, USA.
Email: amachorn@mdanderson.org; aachorn@tamu.edu

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Abstract

Objectives: To understand the function of food sharing among our early hominin ancestors, we can turn to our nonhuman primate relatives for insight. Here, we examined the function of meat sharing by Fongoli chimpanzees, a community of western chimpanzees (*Pan troglodytes verus*) in southeastern Sénégal.

Materials and Methods: We tested three non-mutually exclusive hypotheses that have been used to explain patterns of food sharing: kin selection, generalized reciprocity, and meat-for-mating opportunities. We analyzed meat sharing events ($n = 484$) resulting from hunts, along with data on copulations, age-sex class, and kinship to determine which variables predict the likelihood of meat sharing during this study period (2006–2019).

Results: We found full or partial support for kin selection, direct reciprocity, and meat-for-mating-opportunities. However, the analyses reveal that reciprocity and a mother/offspring relationship were the strongest predictors of whether or not an individual shared meat.

Conclusions: The results of this study emphasize the complexity of chimpanzee meat sharing behaviors, especially at a site where social tolerance offers increased opportunities for meat sharing by individuals other than dominant males. These findings can be placed in a referential model to inform hypotheses about the sensitivity of food sharing to environmental pressures, such as resource scarcity in savanna landscapes.

KEYWORDS
chimpanzee, food sharing, kinship, meat sharing, reciprocity

1 | INTRODUCTION

Humans form larger, more complex, and more cooperative social groups than any other vertebrate taxa, which begs the question of how this level of organization emerged (Silk et al., 2013). Food sharing is often considered to be a component of this large-scale cooperation, since it is a universal trait among foraging societies and associated with notions of fairness, generosity, reciprocity, and egalitarianism (Jaeggi & Gurven, 2018). Among foraging societies, sharing subsidizes female reproduction (Kaplan et al., 2000), supports infant, child, and adolescent development, and supplements daily food shortages throughout adulthood, such as those resulting from day-to-day variance in hunting success (Jaeggi & Gurven, 2018; Kaplan & Hill, 1985). Food sharing is of interest to anthropologists since it impacts both economic and social life (Jaeggi & Gurven, 2018).

In order to understand the function of food sharing among our early hominin ancestors and relatives—which is valuable since food sharing has been hypothesized to have played a crucial role throughout our evolutionary history—we can turn to our nonhuman primate relatives for insight. Through referential models (Moore, 1996) based on homology and analogy, chimpanzees and bonobos are often used to test hypotheses about human social organization since they are our closest living relatives. We focus on chimpanzees in this study, as they participate in a wide range of collective activities and they are the only nonhuman primates that *routinely* share food with other adult group members in the wild (Jaeggi & Van Schaik, 2011; Silk et al., 2013).

The goal of this study is to examine the function of meat sharing by Fongoli chimpanzees, a community of western chimpanzees (*Pan troglodytes verus*) in southeastern Sénégal. While most studies of chimpanzees have focused on forest-dwelling groups, the Fongoli chimpanzees inhabit a savanna landscape, which makes them a particularly useful analogous model for human evolution given that many of the earliest hominins dealt with similar environmental pressures (Pruetz et al., 2015; Pruetz & Bertolani, 2007; White et al., 2009). Additionally, only two nonhuman primate species are known to hunt with tools, chimpanzees (Pruetz et al., 2015) and tufted capuchins (*Sapajus libidinosis*; Falótico, 2023), and, within these species, the populations routinely hunting with tools also range in savanna landscapes. Lastly, in a study assessing 308 instances of hunting by Fongoli chimpanzees, females hunted significantly more than expected, being responsible for 30% of all hunts, and 47.6% of hunts involving tools (Pruetz et al., 2015). This is likely influenced by the fact that at other sites where chimpanzees hunt vertebrates, dominant males take approximately 25% of prey captured by lower-ranking individuals (Boesch & Boesch, 1989; Pickering, 2013). At some of these sites (i.e., Gombe and Kanyawara), males are reported to steal more from females than from other males (Gilby et al., 2017). Thus, there may be a lack of incentive for females and immatures to hunt if there is a good chance the prey will be taken by more dominant individuals (though it has been suggested that hunting by females at other sites is likely to have been underestimated; Gilby et al., 2017). At Fongoli, dominant males took prey from lower-ranking individuals less than 5% of the time, which could explain the increased hunting frequency of females and immatures (Pruetz et al., 2015). Increased hunting by females creates additional opportunities for meat sharing by females, which has not been explored in depth in *Pan troglodytes*.

Here, we test three major hypotheses that have been put forth to explain food sharing among humans and nonhuman primates: kin selection, direct reciprocity, and meat-for-mating-opportunities (also known as "meat-for-sex" or "food-for-sex"). These hypotheses differ in what they consider to be the primary benefits of sharing; however, they are not mutually exclusive, and it is possible that food sharing serves different functions in different contexts (Silk et al., 2013). It is also important to note that there are other major food sharing models, such as sharing-under-pressure or tolerated theft (Blurton-Jones, 1987; Gilby, 2006; Wrangham, 1975), which we have not included here since the nature of the data used in this study limited our ability to rigorously test predictions related to sharing-under-pressure.

1.1 | Kin selection

Kin selection argues that natural selection will favor behaviors that enhance the survival and reproduction of an individual's genetic relatives (i.e., group members who share a proportion of their genes; Hamilton, 1964). In the context of meat sharing, it is predicted that: (1) Sharing events are more likely to be successful (i.e., not refused) between related individuals than between unrelated individuals, and (2) Individuals share more with kin than with non-kin.

1.2 | Reciprocity

Reciprocal altruism attempts to explain altruistic acts (i.e., those that are costly to the actor but benefit the recipient) by suggesting that the actors could benefit in the long run if recipients return the favor (Trivers, 1971). A strict form of reciprocal altruism (i.e., "tit-for-tat reciprocity") assumes that exchanges are balanced, and that reciprocity occurs in the same "currency" as the initial act (e.g., food-for-food; Stevens & Gilby, 2004). However, due to differences in marginal values, food transfers between individuals do not need to be perfectly balanced—in terms of kilocalories, kilograms of food, or any other metric—as long as both individuals do slightly better than they would have if they had not shared (Gurven, 2004; Hill & Kaplan, 1993; Nolin, 2010). As long as the benefits received from an individual influence the benefits donated to that individual, the food sharing reflects a pattern of direct reciprocity. Thus, in the context of meat sharing, direct reciprocity would predict that: (1) Sharing events are more likely to be successful (i.e., not refused) with group members who have previously shared with the sharer, and (2) There is a significant association between the number of times food is shared and received within dyads (Hill & Kaplan, 1993; Nolin, 2010).

1.3 | Meat-for-mating-opportunities

The final hypothesis we test is the idea that males share food with females in order to increase their mating opportunities. This hypothesis is sometimes referred to as "meat-for-sex" or "food-for-sex" (Teleki, 1973), though to non-experts, these terms may suggest immediate transactions, which is not always the case. More concerning, if extrapolated to humans, "meat-for-sex" may be misinterpreted as an evolutionary explanation for sex work. We therefore use the term "meat-for-mating-opportunities."

This hypothesis predicts that: (1) Sharing events are more likely to be successful (i.e., not refused) between adult males and adult females than between other age/sex parings; (2) males share with adult females more than with any other age-sex class; and (3) males that share food with a female will be more likely to be observed mating with that female within some period of time in the future (Mitani & Watts, 2001). While these predictions are generally accepted, there is some debate regarding the time frame in which we should expect to see mating benefits. In chimpanzees, studies have found that males who shared food received immediate mating benefits (e.g., Stanford, 1998), though it is worth noting that the Stanford (1998) sample size is very small. Others have found that food sharing seems to enhance long-term mating prospects rather than short-term ones, suggesting delayed benefits (e.g., Gomes & Boesch, 2009). Still, others have found no evidence that food sharing accrues any form of mating benefits (e.g., Mitani & Watts, 2001; and see review by Gilby et al., 2010).

2 | MATERIALS AND METHODS

2.1 | Study site and subjects

The Fongoli chimpanzee community resides in the Kedougou region in southeastern Sénégal (12°40 N, 12°13 W). The savanna environment is described as a mosaic of bamboo, grassland, woodland, and gallery forest habitats (Pruetz, 2006). The dry season lasts more than 7 months, with maximum temperatures exceeding 40°C, and the area receives less than 100 cm of rainfall per year (Pruetz & Bertolani, 2009). Fongoli chimpanzees are sympatric with humans who grow corn and millet, but they do not crop raid (Pruetz & Lindshield, 2012).

Systematic behavioral observation began in 2005, at which point, most Fongoli community members were habituated, with the exception of some adult females who remained "semi-habituated" for several years (i.e., showed signs of nervousness around observers if adult males were not present). The Fongoli community varied annually from 29 to 36 individuals between 2005 and 2020 (Fongoli Savanna Chimpanzee Project, unpublished data).

2.2 | Categorizing kinship

Similar to other chimpanzee populations, females at Fongoli typically disperse at sexual maturity; however, approximately 30% of females at the site have stayed in their natal unit-group into adulthood. This means that adult females sometimes have adult relatives in the group, including their mothers and adult siblings. Thus, matrilineal kinship among the chimps could reflect mother-offspring, sibling-sibling, aunt/uncle-niece/nephew, cousin-cousin, or grandmother-grandchild relationships (see Figure 1).

Because we do not have data on paternity at this time, kinship was assigned based on matrilineal ties. Dyads who share a mother were marked as siblings. If we did not know the mother of one or both individuals (e.g., if the individual transferred into the group), the dyad was marked as "unknown," meaning we cannot be certain whether or not they share a mother. To determine whether sharing occurred within a mother-offspring dyad, we only needed to know the mother of the recipient. We could also exclude this status if the sharer is a male or is younger than the recipient.

We also created distant kin category comprised of grandparent-grandchild dyads and aunt/uncle-niece/nephew dyads. However,

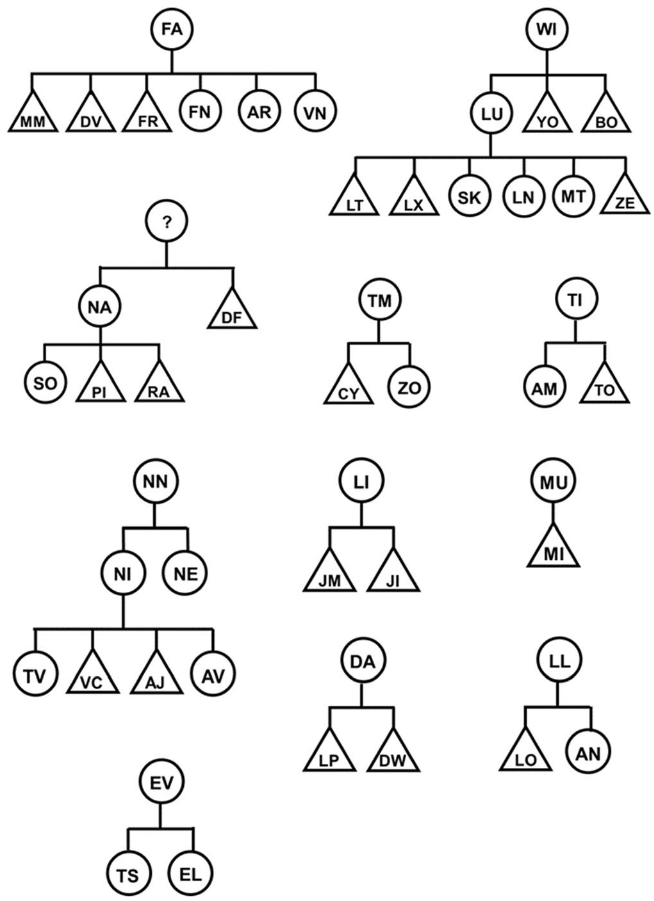

FIGURE 1 Fongoli chimpanzee matrilineal kinship diagram.

among all distant kin dyads, there were only three observed begs and none of these resulted in meat being transferred. Thus, sharing analyses in this study focus on the kinship categories of mother-offspring, offspring-mother, sibling-sibling, and unrelated.

2.3 | Data collection

The data for this study were collected by members of the Fongoli Savanna Chimpanzee Project (Pruetz and colleagues) between 2006 and 2019. At this site, age-sex classes were defined as: infants ≤4 years, juveniles 4–7 years, and adolescents ≥7 and ≤15 years for males or until age at first birth for females. Primiparous females and males ≥15 are considered adults (Baldwin, 1979; Pruetz et al., 2015). Adult males were full-day focal sampled monthly, using a predetermined order to provide at least 100 (but usually closer to 200) hours of observational data per month, uniformly sampled during daylight hours. Focal subject sampling order followed the previous month's order and varied depending on which males were available on a particular day for sampling. All males in the community were sampled before repeating the focal follow schedule, unless a male was not available the day they were scheduled for sampling, in which case the next male on the list was sampled.

Data collected at Fongoli follow the ethogram of Nishida et al. (1999) regarding basic activity and detailed social behaviors. Almost all behavioral data in the current study were collected by two observers (JDP and Michel Sadiakho, head researcher of the Fongoli Savanna Chimpanzee Project). Researchers review operational definitions of behavior annually, although systematic interobserver reliability tests were not conducted. Copulations were recorded ad libitum from May 2005 through October 2019 while focal sampling the adult males at 5-min intervals.

2.4 | Meat sharing

Data on hunting, meat eating, begging, and meat sharing for this study were collected on an all-occurrence basis between January 2006 and June 2017. Begs were defined following Gilby (2006): (1) sitting and staring at the carcass; (2) reaching toward but not touching the carcass or possessor; (3) touching the carcass or possessor; and (4) placing a hand directly over the possessor's mouth. In this study, an "unsuccessful" beg was one in which an individual engaged in one of these begging behaviors but the behavior ceased with no meat being transferred to them. We refer to completed transfers as "successful" transfers, regardless of whether they were initiated by conspicuous begging. For all observed meat transfers, the following were recorded: (1) ID of sharer; (2) ID of recipient; (3) sharing order (e.g., primary = first instance of sharing from the initial possessor to a recipient; secondary = recipient of a primary share subsequently shared with another individual, etc.); (4) type of prey shared; and (5) sharing type. Sharing type was scored according to a scale originally developed by Boesch and Boesch (1989, p. 551) and modified by Pruetz and Lindshield (2012) (Table 1).

TABLE 1 Sharing type (as per Boesch & Boesch, 1989, p. 551, modified by Pruetz & Lindshield, 2012).

Sharing type (transfer score)	Description of transfer
Theft (T1)	The receiver uses force or aggression to take a resource from the owner, and the owner protested the receiver's behavior; theft is the only obvious agonistic exchange in this classification system.
Recovery (T2)	The receiver takes an item that was dropped or placed on the ground by the owner, and the owner tolerates the receiver's actions. Pruetz and Lindshield (2012) modified this category by stipulating that the food must be within an arm's length of the owner to distinguish from scrounging of foods that have been distinctly abandoned.
Passive transfer (T3)	The receiver takes an item held by the owner, and the owner passively tolerates the receiver's behavior.
Active-passive transfer (T4)	Similar to T3 except the owner moves to facilitate the exchange.
Active Transfer (T5)	The owner actively divided the item so that the recipient could easily take a portion, or presented a portion to the recipient, but kept a majority of the item for themselves.
Giving (T6)	The owner allotted the majority of an item to the recipient.

2.5 | Statistical analyses

Because the major food sharing hypotheses evaluated in this study are not mutually exclusive, our objective was to determine which framework(s) best explain patterns of meat sharing among this chimpanzee community. We used two approaches to analyze the sharing data: a transfer approach and a dyadic approach.

2.5.1 | Transfer approach

Because chimpanzee sharing often includes conspicuous begging by potential recipients, we were able to analyze the likelihood of a transfer being successful given different conditions. For this first approach, the unit of analysis is each transfer event—which includes completed transfers and unsuccessful begging bouts. Here, we presume that all completed transfers represent "successful" transfers, regardless of whether they were initiated by conspicuous begging. Begging bouts that did not result in a transfer are coded as unsuccessful. The same predictor variables are used in as in the dyad analysis. Here, adult male-to-female status includes all cases in which the male sharer and female recipient are at least within 1 year of adulthood status (female adulthood is defined by first birth, and this 1 year allows for the gestation period). The data were analyzed using a generalized linear mixed effects regression (GLMM) with a binomial distribution and logit link function using the GLMER function in the LME4 package in R. Individual 1 and Individual 2 were included as crossed random effects.

2.5.2 | Dyadic approach

For the second approach, data were analyzed on the level of the dyad, similar to previous approaches (e.g., Jaeggi & Gurven, 2018; Silk et al., 2013). Dyads were included if the two individuals shared at least 1 year together during which both were non-infants during the observation period of 2005–2017. In/out demographic data were collected on an annual basis, and number of years together as non-infants was included as a control variable. The outcome variable was the number of successful transfers from individual 1 to individual 2. Predictor variables included the number of previous successful transfers from individual 2 to individual 1, kin status, and whether the relationship was one between a male and female who were adults at some time during the observation. The data were analyzed using a GLMM with a Poisson distribution using the GLMER function in the LME4 package in R. Individual 1 and Individual 2 were included as crossed random effects.

Mother's identity was known for 35 of 58 individuals, and the mother's identity was known for both individuals in 694 of 1781 dyads that were included in the final sample. Kin status was limited to parent/offspring and sibship status due to these limitations. To determine whether a share occurred between a mother-to-offspring dyad, we only needed to know the mother of the recipient. We could also exclude this status if the sharer is a male or is younger than the recipient. The reverse is also true for determining if the dyad is characterized by an offspring-to-mother relationship. Thus, only around 9% cases could not be classified as a mother/offspring, offspring/mother, or neither of these two. However, determining sibship status requires knowledge of both individuals' mothers, and therefore resulted in many more unknowns (61%). We therefore conducted analyses using three different approaches. In the first, we included the full sample and used a kin variable that included categories for mother/offspring, sibling, unrelated, and unknown (which was a large majority of cases). We included a "mother-focused" approach that did not include the sibling category, and therefore had a much smaller number of unknown cases. Finally, we used a "restricted" sample that only included dyads for whom both mothers were known.

2.5.3 | Copulations

For an additional test of the meat-for-sex hypothesis, we explored how meat shares were associated with the timing of subsequent copulations. We used a discrete-time events history approach where the unit of analysis was each month that a dyad was present together and the outcome variable was the number of copulations in that month. The predictor variable was the number of shares going from the Individual 1 (male) to Individual 2 (female) within a defined window that included that month plus some amount of time into the past (different windows were used in different models, as the salient window for the exchange of meat for sex is not theoretically well-defined). Dyad months were included if both members were present that year and each member was within 1 year of becoming an adult. Since in/out data were recorded on a yearly basis, dyads were included for full years when both individuals were present.

Individuals were excluded if they were known to be siblings or mother and son. However, in the final sample, mothers' identities were known for both individuals for only 26 of the 212 dyads. The data were analyzed using a GLMM with a Poisson distribution using the GLMER function in the LME4 package in R. Individual 1 and Individual 2 were included as crossed random effects. We planned to include female sexual swelling score as one of the predictor variables to control for sexual receptivity; however, not every female's swelling score was recorded every day. Consequently, the sample size of meat transfers from adult males to adult females that occurred on days when swelling scores were reported for the female recipients was quite limited, so we decided not to include swelling scores in the model.

TABLE 2 Successful and unsuccessful transfers.

	N	Successful
All transfers	466	287 (61.6%)
Transfers excluding infants	419	261 (62.3)
Kin		
All strong kin categories		
Mother → offspring	22	17 (77.3)
Offspring → mother	7	7 (100.0)
Sib → Sib	13	8 (61.5)
Unrelated	95	56 (58.9)
Unknown	282	173 (61.3)
Only mother-offspring categories		
Mother → offspring	22	17 (77.3)
Offspring → mother	7	7 (100.0)
Non-mother/offspring	345	208 (60.3)
Unknown	45	29 (64.4)
Age and sex categories		
Adult male → adult female	62	39 (62.9)
Adult female → adult male	19	9 (47.3)
Adult male → adult male	195	132 (67.6)
Adult female → adult female	12	9 (75.0)
Other age/sex categories	131	72 (54.9)
Share type categories		
Recovery	82	82 (100.0)
Passive sharing	83	83 (100.0)
Active-passive sharing	9	9 (100.0)
Active sharing	22	22 (100.0)
Gift	0	0 (N/A)
Unknown successful	65	65 (100.0)
Unsuccessful	158	0 (0.0)

3 | RESULTS

Over the course of the study, 58 chimpanzees were observed, including 29 females and 29 males. The oldest observed age classification was adult for 31 individuals, adolescent for 13, juvenile for 8, and infant for 6. The number of years a given chimpanzee was observed ranged from 1 to 15 years, with an average of 9.74 years.

3.1 | Successful shares

Table 2 presents the descriptive frequencies for the sharing events (successful shares and unsuccessful begging bouts) that occurred between non infants. Nearly two thirds (62.3%) of events not involving infants were successful. The vast majority of observed shares were between individuals who were either unrelated or for whom relatedness was unknown. Within the sample of individuals for whom both mothers' identities were known, 64% (56/88) of observed

TABLE 3 GLMM of likelihood of success by kin, age/sex status, and previous receipts.

	Model 1 (full)[a]			Model 2 (mom-focused)[b]			Model 3 (restricted)[c]		
	B	St. err	*p*	*B*	St. err	*p*	*B*	St. err	*p*
Intercept	0.429	0.278	0.123	0.2696	03178	0.130	0.409	0.511	0.424
Kinship									
Unrelated (baseline)	–	–	–	–	–	–	–	–	–
Mother/offspring[d]	0.948	0.595	0.111	1.109	0.557	0.046	1.132	0.906	0.212
Sib → Sib	0.368	0.680	0.588				−0.007	0.913	0.994
Unknown	−0.205	0.301	0.496	0.353	0.423	0.405			
Adult M to adult F = Yes	0.142	0.400	0.723	−0.310	0.42	0.460	−1.389	1.829	0.448
Prev shares from Recip	0.301	0.126	0.016	0.303	0.124	0.014	0.987	0.806	0.221

[a]$N = 419$ transfers, 28 sharers, 37 recipients. AIC = 546.9. Random effects for SharerID (variance = 0.198) and RecipientID (variance = 0.039). Inclusion criteria = All. Unrelated = both mothers are known, and dyad is not mother/offspring, offspring/mother, nor siblings.
[b]$N = 419$ transfers, 28 sharers, 37 recipients. AIC = 545.1. Random effects for SharerID (variance = 0.217) and ReceiverID (variance = 0.059). Inclusion criteria = Mother → offspring not unknown and Offspring → mother not unknown (see Section 2). Unrelated = Not mother/offspring nor offspring/mother.
[c]$N = 137$ transfers, 20 sharers, 26 recipients. AIC = 170.0. Random effects for SharerID (variance = 1.749) and RecipientID (variance = 0.353). Inclusion criteria = Both mothers are known. Unrelated = both mothers are known, and dyad is not mother/offspring, offspring/mother, nor siblings.
[d]Mother → Offspring and Offspring → Mother are combined into the category mother/offspring. Offspring → mother included only seven cases, and models including both categories separately failed to converge.

shares took place between individuals who were not maternally related. Among different age/sex classes, the plurality of shares took place between adult males. Although we were unable to test predictions of the sharing-under-pressure hypothesis, transfer type is still useful to consider since it provides qualitative descriptions of the nature of meat transfers. We observed very few instances of theft ($n = 18$ out of 484 observations), meaning that in most instances, meat possessors retained control over the carcass (thefts are excluded from all analyses here). Most transfers in this study were passive in nature, with Recovery and Passive Sharing constituting 84% of observations for which a transfer type was recorded.

When using the full sample of sharing events (excluding 18 thefts), the number of previous shares from the beggar/recipient to the sharer was positively associated with likelihood of the current begging bout being successful (Table 3a,b). Similarly, mother/offspring status appeared to increase the likelihood of shares. Shares going from adult males to adult females were no more likely to be successful than others. When using the restricted sample in which mothers' identities are known for both sharer and recipient (reducing the sample from $N = 419$ to $N = 137$), no predictors were strongly associated with likelihood of success (Table 3c).

3.2 | Shares within dyads

Table 4 presents the descriptive frequencies for all dyads for which individuals shared at least 1 year together as adults (starting 1 year prior to adulthood) as well as the number of dyads that included at least one observed share. Because kin data are limited to matrilineal relationships and mother's identity was unknown for many individuals, there were more unrelated or unknown dyads in the sample than related dyads (570 unrelated dyads and 1087 unknown dyads compared to 24 mother-offspring dyads, 25 offspring-mother dyads, when requiring that both mothers be known). A greater proportion of mother/offspring dyads had at least one share between them

TABLE 4 Dyads and sharing.

	N	*N* with ≥1 share
All possible dyads	3306	150 (4.5%)
All dyads with ≥1 year together as non-infants	1781	141 (7.9)
Kin		
All strong kin categories		
Mother → offspring	24	7 (29.2)
Offspring → mother	25	3 (12.0)
Sib → Sib	75	3 (4.0)
Unrelated	570	38 (6.7)
Unknown	1087	90 (8.3)
Only mother-offspring categories		
Mother → offspring	24	7 (29.2)
Offspring → mother	25	3 (12.0)
Non-mother/offspring	1565	122 (7.8)
Unknown	167	9 (5.3)
Age and sex categories		
Adult male → adult female	216	19 (8.8)
Adult female → adult male	216	13 (6.0)
Adult male → adult male	376	67 (17.8)
Adult female → adult female	121	7 (5.8)
Other age/sex categories	852	35 (4.1)

TABLE 5 GLMM analysis of number of receipts of meat by dyad.

	Model 1 (full)[a]			Model 2 (mom-focused)[b]			Model 3 (restricted)[c]		
	B	St. err	*p*	*B*	St. err	*p*	*B*	St. err	*p*
Intercept	−5.647	0.498	<0.001	−5.691	0.488	<0.001	−5.546	0.687	<0.001
Kinship									
Unrelated (baseline)	–	–	–	–	–	–	–	–	–
Mother → offspring	2.489	0.394	<0.001	2.511	0.357	<0.001	2.004	0.632	0.002
Offspring → mother	0.735	0.559	0.189	0.755	0.544	0.165	0.947	0.706	0.180
Sib → Sib	−0.246	0.391	0.529						
Unknown	−0.016	0.248	0.950	0.191	0.382	0.617			
Adult M to adult F = Yes	−0.811	0.319	0.011	−0.785	0.319	0.014	−2.757	1.136	0.014
Shares from recipient	0.169	0.037	<0.001	0.170	0.037	<0.001	−0.213	0.198	0.284
Years together	0.240	0.043	<0.001	0.240	0.043	<0.001	0.228	0.064	<0.001

[a]*N* = 1781 dyads, 45 sharers, 44 recipients. AIC = 1039.9. Random effects for SharerID (variance = 2.529) and RecipientID (variance = 0.763). Inclusion criteria = All Unrelated = both mothers are known, and dyad is not mother/offspring, offspring/mother, nor siblings.
[b]*N* = 1781 dyads, 45 sharers, 44 recipients. AIC = 1038.1. Random effects for SharerID (variance = 2.539) and RecipientID (variance = 0.768). Inclusion criteria = Mother → offspring not unknown and offspring → mother not unknown (see Section 2). Unrelated = not mother/offspring nor offspring/mother.
[c]*N* = 694 dyads, 35 sharers, 34 recipients. AIC = 398.5. Random effects for SharerID (variance = 2.242) and RecipientID (variance = 1.017). Inclusion criteria = Both mothers are known. Unrelated = Not mother/offspring nor offspring/mother.

(20.41% of 49 mother/offspring dyads compared to 6.67% of 570 unrelated dyads). Furthermore, dyads consisting of two adult males were more likely to have experienced at least one observed sharing event (17.82% of 376) compared to other age/sex classes.

In Table 5, the analyses of number of shares within dyads suggests similar trends as those revealed by the analyses of observed shares. Specifically, when using the full sample of shares (Table 4a,b), the number of previous shares from individual 1 to individual 2 was significantly associated with the number of shares from individual 2 to individual 1, whereby individuals who had previously shared more with the current sharer received more meat from them in return. In the restricted model (Table 5c), there was no significant association between shares from individual 1 to individual 2 and shares from individual 2 to individual 1. In all three models, mother-to-offspring shares (excluding shares to infants) occurred at a significantly higher frequency than shares to unrelated individuals. Furthermore, adult males shared with adult females significantly less often than rates observed among all other age/sex classes, likely reflecting the overall pattern of sharing occurring disproportionally among males.

3.3 | Copulations

Finally, analyses of associations between meat sharing and the timing of copulations between male and female dyads revealed that meat sharing does not increase the number of copulations within each month when testing within a 1-month window of the sharing event (Table 6). However, within 3-month and 1-year windows of sharing events, there was a significant positive association between meat sharing and subsequent copulations. Interestingly, there was no association found when using a 3-year window, and a 5-year window resulted in a significant negative effect.

4 | DISCUSSION

In this study, we evaluated three major food sharing models (i.e., kin selection, direct reciprocity, and meat-for-mating-opportunities) in order to examine the function of meat sharing in savanna chimpanzees at the Fongoli site. We will discuss the results of these analyses below.

4.1 | Kin selection

The results from this study indicate that kinship influences meat sharing; however, this effect is driven by shares from mothers to offspring. When we separated dyads by kinship type, we found that mother-to-offspring shares were significantly more likely to be successful than shares between unrelated dyads. We found no significant effect for sibling-sibling dyads, offspring-mother dyads, or dyads of unknown relatedness. We were unable to compare shares between close kin and distant kin because there were only three begs between distant kin, and none of these resulted in meat transfer. However, we anticipate that the ability to recognize more dyads of distant relatedness after obtaining patrilineal data for this community may shed light on patterns of meat sharing among kin.

TABLE 6 GLMM of number of copulations in a month by number of previous shares across various time windows.

	B	St. err	p
One month[a]			
Intercept	−3.940	0.473	<0.001
Copulations	0.169	0.185	0.362
Three months[b]			
Intercept	−3.940	0.474	<0.001
Copulations	0.226	0.111	0.042
One year[c]			
Intercept	−3.909	0.556	<0.001
Copulations	0.228	0.059	<0.001
Three years[d]			
Intercept	−4.300	0.741	<0.001
Copulations	−0.078	0.058	0.179
Five years[e]			
Intercept	−4.241	0.716	<0.001
Copulations	−0.248	0.071	<0.001

[a]$N = 17{,}738$ months, 18 males, 13 females. AIC = 7550.6. Random effects for MaleID (variance = 0.260) and FemaleID (2.596).
[b]$N = 17{,}502$ months, 18 males, 13 females. AIC = 7501.0. Random effects for MaleID (variance = 0.296) and FemaleID (2.533).
[c]$N = 16{,}440$ months, 18 males, 12 females. AIC = 7336.8. Random effects for MaleID (variance = 0.566) and FemaleID (1.825).
[d]$N = 13{,}500$ months, 16 males, 12 females. AIC = 6168.1. Random effects for MaleID (variance = 0.310) and FemaleID (2.422).
[e]$N = 10{,}692$ months, 14 males, 11 females. AIC = 4281.3. Random effects for MaleID (variance = 0.324) and FemaleID (4.952).

4.2 | Meat-for-mating-opportunities

The meat-for-mating-opportunities (i.e., "meat-for-sex" or "food-for-sex") hypothesis has received considerable attention from primatologists, having been tested in different species and in different living conditions (e.g., Gilby et al., 2010; Gomes & Boesch, 2009; Mitani & Watts, 2001; Stanford, 1998). Tests of this hypothesis in chimpanzees have reported that male food sharers received immediate mating benefits (e.g., Stanford, 1998), delayed mating benefits (e.g., Gomes & Boesch, 2009), or no apparent mating benefits (e.g., Mitani & Watts, 2001). The present study found partial support for the meat-for-mating-opportunities hypothesis. The findings that adult-male to adult-male shares were over-represented in the sample, and that an adult-male to adult-female relationship is actually predictive of *less* sharing compared to all other relationships suggests that mating opportunities may not be the primary factor driving male meat possessors to share. However, we did find a significant association between meat shares and copulations in male–female dyads during a 3-month window and a 1-year window, though this effect disappeared at a 3-year window and reversed at a 5-year window. This suggests that although adult males do not share meat with adult females more than with other age-sex classes, when sharing does occur, it may be associated with short-term mating benefits (i.e., within 3 months to 1 year), but not long-term benefits (i.e., beyond 3 years). The fact that the association between sharing and copulations becomes significantly negative using a 5-year window is peculiar and difficult to interpret. This might be due to the fact that over such a length of time, there would undoubtedly be periods during which females are not sexually receptive. Another possible explanation is that it might be due to the missing kinship data. All known mother/son dyads were excluded from the copulation analyses, but the male's mother's identity was unknown for many dyads. Through time, mother/son dyads (including ones unbeknownst to us at present) should exhibit a negative association between meat shares (higher) and copulations (absent). However, if the association between meat sharing and copulations is substantial enough in the short-term (among non-related individuals), then such an effect might swamp the missing-data kin effect resulting in the positive effect when using the 3-month and 1-year windows.

Importantly, in order to claim that a behavior enhances an individual's fitness in the context of mate choice via sexual selection, one would need to demonstrate that the behavior increases the individual's reproductive output. In the absence of this data, observed copulations are often used as a proxy for sired offspring, and thus increased copulations are interpreted as increased fitness. If additional opportunities to mate with females enhance a male's chances of siring offspring, meat sharing *may* confer fitness benefits. However, since we do not examine paternity data in this study, we do not claim that males definitively enhance their fitness by siring more offspring with the females they provisioned.

4.3 | Reciprocity

The results of this study offer strong evidence of direct reciprocity. When using the full sample of shares (excluding 18 thefts), the number of previous shares from the recipient to the sharer is positively associated with likelihood of meat being shared. Additionally, the number of previous shares from individual 1 to individual 2 is significantly associated with the number of shares from individual 2 to individual 1, meaning that individuals who have previously shared more times with the current sharer receive more meat from them in return. The only times that we do not see reciprocity having a significant effect is in the restricted models in which dyads were only included if the mother(s) of both sharer and recipient are known. However, the failure to detect a significant association in these models is likely due to the reduced sample size (i.e., 694 dyads compared to the full 1781 dyads) causing a loss of power.

4.4 | How these results compare to previous reports of meat sharing among wild chimpanzees

We found that reciprocity, specifically meat-for-meat reciprocity, was a predictor of sharing among this community. In other chimpanzee communities, reciprocal exchanges have been reported numerous

TABLE 7 Comparing this study's results to previous reports of food sharing among chimpanzees.

Population	Conditions	Resource(s) shared	Models tested	Models supported
Fongoli chimpanzees (this study)	Wild (Senegal)	Meat	Kin selection Reciprocity (food-for-food) Food-for-sex (=“meat-for-mating opportunities”)	Full or partial support for all three models
Yerkes Primate Center chimpanzees	Captive (Lawrenceville, GA, USA)	Plant foods	Reciprocity (food-for-grooming) (de Waal, 1989, 1997)	Food-for-grooming (de Waal, 1989, 1997)
Michale E. Keeling Center chimpanzees	Captive (Bastrop, TX, USA)	Frozen fruit disks	Kin selection Reciprocity (food-for-food) Sharing-under-pressure (Silk et al., 2013)	Support for several models: “Chimpanzees preferentially transfer food to kin, reciprocating partners, close associates, and perhaps to potential mates” (Silk et al., 2013)
Gombe National Park chimpanzees	Wild (Tanzania)	Meat	Sharing-under-pressure (Gilby, 2006; Wrangham, 1975) Reciprocal exchange (including “meat-for-meat,” “meat-for-sex,” and “meat-for-allies”) (Gilby, 2006) Food-for-sex (Gilby et al., 2010; Stanford, 1998)	Sharing-under-pressure (Gilby, 2006) Sharing-under-pressure (Wrangham, 1975) Food-for-sex (short-term benefits) (Stanford, 1998) (though see Gilby et al., 2010: “meat transfers in chimpanzees are rarely sexually motivated”)
Mahale mountain chimpanzees	Wild (Tanzania)	Meat	Food-for-grooming (Nishida et al., 1992)	Food-for-grooming (and possibly coalitionary support) by one alpha male; not entire population. Authors write that at Mahale, reciprocal exchange rarely occurs through the same “currency” because the alpha male typically controls access to carcasses (Nishida et al., 1992)
Ngogo chimpanzees at Kibale National Park	Wild (Uganda)	Meat	Food-for-sex Food-for-food Food-for-coalitionary support among males (Mitani & Watts, 2001)	Food-for-food reciprocity among males Food-for-coalitionary support among males (Mitani & Watts, 2001)
Tai National Park chimpanzees	Wild (Côte d'Ivoire)	Meat	Food-for-sex (Gomes & Boesch, 2009) Sharing-under-pressure Costly signaling Reciprocal altruism (Samuni et al., 2018) Reciprocity (both in-kind and exchange) Costly Signaling Sharing-under-pressure Mutualism (Gomes et al., 2019; Gomes & Boesch, 2011)	Food-for-sex (delayed benefits) (Gomes & Boesch, 2009) Food-for-grooming (described by authors as “bonding-based reciprocal altruism,” in which food possessors more likely to share with mutual long-term grooming partners, and sharing is associated with increased oxytocin levels; Samuni et al., 2018) Reciprocal exchange (i.e., meat-for-support in agonistic encounters and meat-for-sex) Partial support for mutualism (Gomes et al., 2019; Gomes & Boesch, 2011)
Bossou chimpanzees	Wild (Republic of Guinea)	Plant foods	Describing the context of sharing behaviors	Food-for-sex and food-for-grooming (for one male food sharer, at least) (Hockings et al., 2007)

times (see Table 7). However, a key difference is that in most of these studies, the reciprocated “currency” was not necessarily meat. Some studies report a food-for-grooming exchange system (e.g., de Waal, 1989, 1997; Nishida et al., 1992; Samuni et al., 2018), while others report that males exchanged meat for coalitionary support (e.g., Mitani & Watts, 2001; Nishida et al., 1992).

Boesch and Boesch (1989) report several different exchange systems including grooming for grooming, coalitionary support for coalitionary support, coalitionary support for meat, and meat for sex (Boesch & Boesch, 1989). This variation in reciprocal exchanges is perhaps related to the degree of social tolerance at a site. At most sites where chimpanzees hunt vertebrates, dominant males monopolize prey carcasses, with higher-ranking individuals seizing prey captured by lower-ranking individuals (Pickering, 2013). At some sites, it has even been stated that reciprocal exchanges rarely occur through the same "currency" because the alpha male controls access to carcasses (e.g., Nishida et al., 1992). However, at other sites (namely, Tai), meat theft occurs extremely rarely (Boesch, 2012), providing more opportunities for meat sharing to occur. Fongoli chimpanzees exhibit an exceptionally high level of social tolerance, with dominant males taking prey from lower-ranking individuals less than 4% of the time. This social tolerance allows individuals other than adult males to capture and retain control of prey, which creates additional opportunities for meat sharing by a greater number of individuals. Different levels of social tolerance following vertebrate hunting may reflect distinct cultures of hunting and meat sharing among different populations of chimpanzees. Furthermore, while most transfers in this study were passive in nature, with Recovery and Passive Sharing constituting 84% of observations for which a transfer type was recorded, this does not mean that meat possessors did not exercise choice—38% of events in this study were unsuccessful begging attempts, which suggests that meat possessors have quite a bit of agency to reject or facilitate transfers.

The fact that some studies consider food-for-sex exchanges to be a form of reciprocity (e.g., Boesch & Boesch, 1989; Gilby, 2006; Gilby et al., 2010; Gomes et al., 2019) is especially interesting, because the prediction that meat sharing will be associated with mating opportunities was the only prediction of the food-for-sex ("meat-for-mating-opportunities") hypothesis that received support in this study. We found that while adult males did not preferentially share with adult females, there *was* a significant association between the number of times a male shared food with a female and the number of times those two copulated within a short window of time (i.e., up to 1 year). These findings could suggest that while reciprocity best explains patterns of meat sharing at Fongoli, reciprocal exchanges may take the form of food-for-food *and* food-for-sex transactions, depending on the context. See Table 7 for more detail about how these results relate to those of previous food sharing studies in chimpanzees.

4.5 | Informing hypotheses about food sharing in early hominins

Savanna chimpanzees inhabit hot, dry, and open environments. Consequently, crucial resources (e.g., nesting resources, food, water, and shelter from high temperatures or predators) often occur at relatively low densities, either seasonally or year-round (Lindshield et al., 2021). A "landscape approach" (e.g., Turner, 1989) can be useful for comparing and contrasting chimpanzees that live in forested habitats with those that live in savanna habitats. Doing so reveals several key insights about how habitat type influences chimpanzee ecology and behavior. As Lindshield et al. (2021) review, there is extensive evidence that the environmental conditions of savanna landscapes can elicit behavioral, cultural, morphological, or physiological responses from chimpanzees. These include observable differences in home range size (Humle et al., 2016), population densities (Lindshield et al., 2021), group cohesiveness (Pruetz & Bertolani, 2009), the composition of plant species (e.g., Matthews et al., 2019, 2020; McGrew et al., 1988; Piel et al., 2017; Pruetz, 2006; Yoshikawa & Ogawa, 2015) and meat (Moore et al., 2017; Wessling et al., 2019) in the diet, and even the ability to regulate temperature through behavioral or physiological responses (Pruetz & Bertolani, 2009). Recent evidence suggests that the environmental conditions of savanna landscapes may elicit intriguing responses from tufted capuchins (*Sapajus libidinosis*), as well (Falótico, 2023). Like western chimpanzees, tufted capuchins living in both forest and savanna habitats have been observed to hunt vertebrate prey (Butynski, 1982; Falótico & Ottoni, 2014; Fedigan, 1990), yet it is the savanna-dwelling counterparts that have been seen engaging in tool-assisted hunting (Falótico, 2023). As more data become available, it will be interesting to see if this pattern extends to other primate populations too.

Paleoecological reconstructions indicate that some early hominins also inhabited savanna mosaic landscapes, and that environmental pressures associated with open and dry landscapes may have contributed to the evolutionary split of the *Homo* and *Pan* lineages (Cerling et al., 2011; Moore, 1992). For this reason, chimpanzees that live in open and dry environments can be used to form hypotheses about early hominin behavior and ecology through referential models (Moore, 1996). As Lindshield et al. (2021) discuss, chimpanzees are not modern-day replicas of early hominins (e.g., *Ardipithecus* and *Australopithecus* spp.), and there may be some limitations regarding the use of chimpanzees to model hominin evolution (e.g., Sayers & Lovejoy, 2008). However, studying savanna chimpanzees can reveal how great apes adapt to highly seasonal, dry, hot, and open landscapes (Moore, 1996). By comparing the behavior, morphology, and ecology of savanna and forest chimpanzees, we can test hypotheses about how early hominins may have responded to retreating African forests millions of years ago (McGrew et al., 1981; Moore, 1996; Pruetz & Bertolani, 2009; Suzuki, 1969).

4.6 | Future research

As previously discussed, the kinship analyses conducted in this study were based on matrilineal data only. We plan to reexamine the effects of kinship using maternal *and* paternal data when the latter become available. Doing so would shed light on whether maternal kin and paternal kin differ in their food sharing patterns, which can be especially interesting in male-philopatric, female-dispersing species, such as chimpanzees. Furthermore, having paternity data would allow for more specific kinship analyses by clarifying relationships between group members. With this additional data, it might become possible to fully test the second prediction of kin selection, which is that food possessors are more likely to share with close kin than with distant kin. Additionally, knowing the mothers and fathers of group members would enhance reciprocity analyses by elucidating whether the reciprocity we observed between dyads of unknown relatedness is being driven by kinship (e.g., siblings or half-siblings) or whether it is occurring between unrelated individuals. Lastly, the nature of our current data did not allow for rigorous tests of the sharing-under-pressure hypothesis. However, future meat sharing analyses will incorporate prey size, rank relationships, and detailed descriptions of the nature and duration of begging behaviors as variables.

5 | CONCLUSIONS

The findings from this study indicate that several factors explain patterns of meat sharing among this community. First, we see that kinship influences meat sharing; however, this effect is driven by shares from mothers to offspring. Mother-to-offspring shares occurred at a significantly higher frequency and begging bouts were significantly more likely to be successful than those between unrelated dyads or dyads of other kin relationships. Second, we found that meat-for-meat reciprocity was a significant predictor of sharing among this community—the number of previous shares from individual 1 to individual 2 is significantly associated with the number of shares from individual 2 to individual 1, and a begging bout is significantly more likely to be successful if the recipient has previously shared with the current meat possessor. Lastly, while adult males did not preferentially share meat with adult females, we found a significant association between the number of times a male shared food with a female and the number of times those two copulated within a limited window of time (i.e., up to 1 year).

The discovery that all three hypotheses tested in this study received full or partial support highlights the intricacy of chimpanzee behavior and further suggests that meat sharing may serve multiple different functions. It is likely that the relative importance of kinship, reciprocity, and mating opportunities will depend on the specific sharer-recipient relationship. It is also possible that Fongoli chimpanzees exhibit reciprocal networks of kin, and/or that reciprocal exchanges can take the form of food-for-food *and* food-for-sex transactions, depending on the context. Research on paternity is needed to verify these results. The results of this study emphasize the complexity of chimpanzee meat sharing behaviors, especially at a site where social tolerance offers increased opportunities for meat sharing by individuals other than dominant males. These findings can be placed in a referential model to inform hypotheses about the sensitivity of food sharing to environmental pressures, such as resource scarcity in savanna landscapes.

AUTHOR CONTRIBUTIONS

Angela Achorn: Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Stacy Lindshield:** Conceptualization (equal); data curation (equal); formal analysis (supporting); investigation (equal); supervision (equal); writing – original draft (supporting); writing – review and editing (supporting). **Papa Ibnou Ndiaye:** Investigation (equal); methodology (equal); project administration (equal); writing – review and editing (equal). **Jeffrey Winking:** Formal analysis (equal); methodology (equal); writing – review and editing (equal). **Jill D. Pruetz:** Conceptualization (equal); data curation (equal); funding acquisition (lead); investigation (equal); project administration (lead); resources (equal); supervision (equal); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

The data and R code that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Angela Achorn https://orcid.org/0000-0002-3425-2551
Stacy Lindshield https://orcid.org/0000-0002-4507-1502

REFERENCES

Baldwin, P. J. (1979). *The natural history of the chimpanzee (Pan troglodytes verus), at Mt. Assirik, Senegal* (Unpublished doctoral dissertation). University of Stirling. Stirling.

Blurton-Jones, N. (1987). Tolerated theft suggestions about the ecology and evolution of sharing, hoarding, and scrounging. *Social Science Information*, *26*, 31–54. https://doi.org/10.1177/053901887026001002

Boesch, C. (2012). *Wild cultures: A comparison between chimpanzee and human cultures*. Cambridge University Press.

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, *78*, 547–573. https://doi.org/10.1002/ajpa.1330780410

Butynski, T. M. (1982). Vertebrate predation by primates: A review of hunting patterns and prey. *Journal of Human Evolution*, *11*, 421–430. https://doi.org/10.1016/S00472484(82)80095-X

Cerling, T. E., Wynn, J. G., Andanje, S. A., Bird, M. I., Korir, D. K., Levin, N. E., MacE, W., MacHaria, A. N., Quade, J., & Remien, C. H. (2011). Woody cover and hominin environments in the past 6-million years. *Nature*, *476*, 51–56. https://doi.org/10.1038/nature10306

de Waal, F. B. M. (1989). Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution*, *18*, 433–459. https://doi.org/10.1016/0047-2484(89)90074-2 de Waal, F. B. M. (1997). The chimpanzee's service economy: Food for grooming. *Evolution and Human Behavior*, *18*, 375–386. https://doi.org/10.1016/S1090-5138(97)00085-8

Falótico, T. (2023). Vertebrate predation and tool-aided capture of prey by savannah wild capuchin monkeys (*Sapajus libidinosus*). *Int J Primatol*, *44*, 9–20. https://doi.org/10.1007/s10764-022-00320-z

Falótico, T., & Ottoni, E. B. (2014). Sexual bias in probe tool manufacture and use by wild bearded capuchin monkeys. *Behavioural Processes*, *108*, 117–122. https://doi.org/10.1016/j.beproc.2014.09.036

Fedigan, L. M. (1990). Vertebrate predation in *Cebus capucinus*: Meat eating in a neotropical monkey. *Folia Primatologica*, *54*, 196–205. https://doi.org/10.1159/000156444

Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour*, *71*, 953–963. https://doi.org/10.1016/j.anbehav.2005.09.009

Gilby, I. C., Emery Thompson, M., Ruane, J. D., & Wrangham, R. (2010). No evidence of shortterm exchange of meat for sex among chimpanzees. *Journal of Human Evolution*, *59*, 44–53. https://doi.org/10.1016/j.jhevol.2010.02.006

Gilby, I. C., Machanda, Z. P., O'Malley, R. C., Murray, C. M., Lonsdorf, E. V., Walker, K., Mjungu, D. C., Otali, E., Muller, M. N., Emery Thompson, M., Pusey, A. E., & Wrangham, R. W. (2017). Predation by female chimpanzees: Toward an understanding of sex differences in meat acquisition in the last common ancestor of pan and homo. *Journal of Human Evolution*, *110*, 82–94. https://doi.org/10.1016/j.jhevol.2017.06.015

Gomes, C., Mundry, R., & Boesch, C. (2019). Why do the chimpanzees of the Taï Forest share meat? The value of bartering, begging and hunting. In C. Crockford, L. Vigilant, T. Deschner, F. Leendertz, C. Boesch, & R. Wittig (Eds.), *The chimpanzees of the Taï Forest: 40 years of research* (pp. 316–338). Cambridge University Press. https://doi.org/10.1017/9781108674218.021

Gomes, C. M., & Boesch, C. (2009). Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS One*, *4*, 16–18. https://doi.org/10.1371/journal.pone.0005116

Gomes, C. M., & Boesch, C. (2011). Reciprocity and trades in wild west african chimpanzees. *Behavioral Ecology and Sociobiology*, *65*(11), 2183–2196. https://doi.org/10.1007/s00265011-1227-x

Gurven, M. (2004). To give and to give not: The behavioral ecology of human food transfers. *Behavioral and Brain Sciences*, *27*, 543–583. https://doi.org/10.1017/S0140525X04000123

Hamilton, W. D. (1964). The genetical evolution of social behavior. *Journal of Theoretical Biology*, *7*, 1–16. https://doi.org/10.4324/9780203790427-4

Hill, K., & Kaplan, H. (1993). On why male foragers hunt and share food. *Current Anthropology*, *34*, 701–710. https://doi.org/10.1086/204213

Hockings, K. J., Humle, T., Anderson, J. R., Biro, D., Sousa, C., Ohashi, G., & Matsuzawa, T. (2007). Chimpanzees share forbidden fruit. *PLoS ONE*, *2*(9), e886. https://doi.org/10.1371/journal.pone.0000886

Humle, T., Maisels, F., Oates, J. F., Plumptre, A., & Williamson, E. A. (2016). *Pan troglodytes* (errata version published in 2018). The IUCN Red List of Threatened Species.

Jaeggi, A. V., & Gurven, M. (2018). Food-sharing models. In C. Hilary (Ed). *The International Encyclopedia of Anthropology* (pp. 1–8). https://doi.org/10.1002/9781118924396.wbiea1655

Jaeggi, A. V., & Van Schaik, C. P. (2011). The evolution of food sharing in primates. *Behavioral Ecology and Sociobiology*, *65*, 2125–2140. https://doi.org/10.1007/s00265-011-1221-3

Kaplan, H., & Hill, K. (1985). Food sharing among ache foragers: Tests of explanatory hypotheses. *Current Anthropology*, *26*, 223–246. https://doi.org/10.1086/203251

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology*, *9*, 156–185. https://doi.org/10.1002/1520-6505(2000)9:4<156::aid-evan5>3.3.co;2-z

Lindshield, S., Hernandez-Aguilar, R. A., Korstjens, A. H., Marchant, L. F., Narat, V., Ndiaye, P. I., Ogawa, H., Piel, A. K., Pruetz, J. D., Stewart, F. A., van Leeuwen, K. L., Wessling, E. G., & Yoshikawa, M. (2021). Chimpanzees (*Pan troglodytes*) in savanna landscapes. *Evolutionary Anthropology*, *30*, 399–420. https://doi.org/10.1002/evan.21924

Matthews, J. K., Ridley, A., Kaplin, B. A., & Grueter, C. C. (2020). A comparison of fecal sampling and direct feeding observations for quantifying the diet of a frugivorous primate. *Current Zoology*, *66*, 333–343. https://doi.org/10.1093/CZ/ZOZ058

Matthews, J. K., Ridley, A., Niyigaba, P., Kaplin, B. A., & Grueter, C. C. (2019). Chimpanzee feeding ecology and fallback food use in the montane forest of Nyungwe National Park, Rwanda. *American Journal of Primatology*, *81*(4), 1–15. https://doi.org/10.1002/ajp.22971

McGrew, W. C., Baldwin, P. J., & Tutin, C. E. G. (1981). Chimpanzees in a hot, dry, and open habitat: Mt. Asserik, Senegal, West Africa. *Journal of Human Evolution*, *10*, 227–244. https://doi.org/10.1016/S0047-2484(81)80061-9

McGrew, W. C., Baldwin, P. J., & Tutin, C. E. G. (1988). Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Assirik, Senegal: I. Composition. *American Journal of Primatology*, *16*, 213–226. https://doi.org/10.1016/S0163-4453(81)91844-2

Mitani, J. C., & Watts, D. P. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour*, *61*, 915–924. https://doi.org/10.1006/anbe.2000.1681

Moore, J. (1992). "Savanna" chimpanzees. In T. Nishida, W. McGrew, P. Marler, M. Pickford, & F. de Waal (Eds.), *Topics in primatology* (Vol. I, pp. 99–118). University of Tokyo Press.

Moore, J. (1996). Savanna chimpanzees, referential models and the last common ancestor. In W. C. McGrew, L. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 275–292). Cambridge University Press.

Moore, J., Black, J., Hernandez-Aguilar, R. A., Idani, G., Piel, A., & Stewart, F. (2017). Chimpanzee vertebrate consumption: Savanna and forest chimpanzees compared. *Journal of Human Evolution*, *112*, 30–40. https://doi.org/10.1016/j.jhevol.2017.09.004

Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y., & Uehara, S. (1992). Meat-sharing as a coalition strategy by an alpha male chimpanzee? In T. Nishida, W. McGrew, P. Marler, M. Pickford, & F. de Waal (Eds.), *Topics in primatology* (Vol. I, pp. 159–174). University of Tokyo Press.

Nishida, T., Kano, T., Goodall, J., McGrew, W. C., & Nakamura, M. (1999). Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science*, *107*, 141–188. https://doi.org/10.1537/ase.107.141

Nolin, D. A. (2010). Food-sharing networks in Lamalera, Indonesia: Reciprocity, kinship, and distance. *Human Nature*, *21*, 243–268. https://doi.org/10.1007/s12110-010-9091-3.FoodSharing

Pickering, T. (2013). *Rough and tumble: Aggression, hunting, and human evolution*. University of California Press.

Piel, A. K., Strampelli, P., Greathead, E., Hernandez-Aguilar, R. A., Moore, J., & Stewart, F. A. (2017). The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*) in the Issa valley, western Tanzania. *Journal of Human Evolution*, *112*, 57–69. https://doi.org/10.1016/j.jhevol.2017.08.016

Pruetz, J. D. (2006). Feeding ecology of savanna chimpanzees. In G. Hohmann, M. M. Robbins, & C. Boesch (Eds.), *Feeding ecology of great apes and other primates* (pp. 161–182). Cambridge University Press.

Pruetz, J. D., & Bertolani, P. (2007). Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology*, *17*, 412–417. https://doi.org/10.1016/j.cub.2006.12.042

Pruetz, J. D., & Bertolani, P. (2009). Chimpanzee (*pan troglodytes verus*) behavioral responses to stresses associated with living in a savanna-mosaic environment: Implications for hominin adaptations to open habitats. *PaleoAnthropology*, 252–262. https://doi.org/10.4207/PA.2009.ART33

Pruetz, J. D., Bertolani, P., Ontl, K. B., Lindshield, S., Shelley, M., & Wessling, E. G. (2015). New evidence on the tool-assisted hunting exhibited by chimpanzees (*Pan troglodytes verus)* in a savannah habitat at Fongoli, Sénégal. *Royal Society Open Science*, *2*(4), 140507. https://doi.org/10.1098/rsos.140507

Pruetz, J. D., & Lindshield, S. (2012). Plant-food and tool transfer among savanna chimpanzees at Fongoli, Senegal. *Primates*, *53*, 133–145. https://doi.org/10.1007/s10329-011-0287-x

Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R. M., & Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1888), 20181643. https://doi.org/10.1098/rspb.2018.1643

Sayers, K., & Lovejoy, C. O. (2008). The chimpanzee has no clothes: A critical examination of *Pan troglodytes* in models of human evolution. *Current Anthropology*, *49*, 87–99. https://doi.org/10.1086/523675

Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P., & Schapiro, S. (2013). Chimpanzees share food for many reasons: The role of kinship, reciprocity, social bonds and harassment on food transfers. *Animal Behaviour*, *85*, 941–947. https://doi.org/10.1016/j.anbehav.2013.02.014

Stanford, C. (1998). *Chimpanzee and red colobus: The ecology of predator and prey*. Harvard University Press.

Stevens, J. R., & Gilby, I. C. (2004). A conceptual framework for nonkin food sharing: Timing and currency of benefits. *Animal Behaviour*, *67*, 603–614. https://doi.org/10.1016/j.anbehav.2003.04.012

Suzuki, A. (1969). An ecological study of chimpanzees in a savanna woodland. *Primates*, *10*, 103–148. https://doi.org/10.1007/BF01730979

Teleki, G. (1973). *The predatory behavior of wild chimpanzees*. Bucknell University Press.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, *46*, 35–57. https://doi.org/10.1086/406755

Turner, M. G. (1989). Landscape ecology: The effect of pattern on process. *Annual Review of Ecology and Systematics*, *20*, 171–197. https://doi.org/10.1146/annurev.es.20.110189.001131

Wessling, E. G., Oelze, V. M., Eshuis, H., Pruetz, J. D., & Kühl, H. S. (2019). Stable isotope variation in savanna chimpanzees (*Pan troglodytes verus*) indicate avoidance of energetic challenges through dietary compensation at the limits of the range. *American Journal of Physical Anthropology*, *168*, 665–675. https://doi.org/10.1002/ajpa.23782

White, T. D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C. O., Suwa, G., & WoldeGabriel, G. (2009). Ardipithecus ramidus and the paleobiology of early hominids. *Science*, *326*, 64–86. https://doi.org/10.1126/science.1175802

Wrangham, R. W. (1975). *Behavioural ecology of chimpanzees in Gombe National Park, Tanzania* (Doctoral dissertation). University of Cambridge. https://doi.org/10.17863/CAM.16415

Yoshikawa, M., & Ogawa, H. (2015). Diet of savanna chimpanzees in the Ugalla Area, Tanzania. *African Study Monographs*, *36*, 189–209. https://doi.org/10.14989/200275

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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