

EXAMINING THE FUNCTION OF MEAT SHARING IN SAVANNA-DWELLING
CHIMPANZEES AT FONGOLI, SÉNÉGAL

A Dissertation

by

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ABSTRACT

Humans form social groups that are larger, more complex, and more cooperative than those of any other vertebrate taxa, which begs the question of how this level of social organization emerged. Food sharing is often considered to be a component of this large-scale cooperation and is hypothesized to have played a crucial role throughout our evolutionary history. To understand the function of food sharing among our early hominin ancestors, we can turn to our nonhuman primate relatives for insight. In this dissertation, I examined the function of food sharing within the Fongoli chimpanzee community, a population of western chimpanzees (*Pan troglodytes verus*) in southeastern Sénégal. I tested four non-mutually exclusive hypotheses that have been used to explain patterns of food sharing: kin selection, generalized reciprocity, sharing-under-pressure, and food-for-sex. I analyzed meat sharing events (n=484) resulting from hunts, along with data on estrous swellings, copulations, prey size, rank, age-sex class, and kinship to determine which variables predict the likelihood of meat sharing during this study period (2006-2019). When I tested the predictions of each hypothesis independently, I found support for kin selection, generalized reciprocity, and food-for-sex. However, when I examined the effects of all variables combined, I found that reciprocity was the strongest predictor of whether or not an individual shared meat. I discuss the significance of these findings among a savanna-dwelling chimpanzee population that systematically hunts vertebrate prey with tools.

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CHAPTER I

INTRODUCTION AND BACKGROUND

1.1 Evolution of Cooperation

1.1.1 Cooperation in Human Societies

Humans form larger, more complex, and more cooperative social groups than any other vertebrate taxa (Silk et al., 2013). To understand the astonishing scale and range of human cooperative activities, we can compare them to those of other animals. Among social mammals, cooperation (defined as “behaviors which provide a benefit to another individual *or* are beneficial to both the actor and the recipient” [Melis & Semmann, 2010]) is generally limited to related individuals. Communication tends to be constrained to a small repertoire of signals, and there is scant to no evidence of a division of labor, trade, or large-scale conflict. Sick or injured animals do not typically receive assistance (at least not considerable assistance) from group members, and strong individuals can steal from weak ones without retribution from the group (Boyd & Richerson, 2009). Certainly, there are exceptions to some of these rules, but in general, these are the patterns that have been observed.

In comparison, humans regularly cooperate with many unrelated individuals. Human societies exhibit a division of labor, trade, and large-scale conflict. Human language offers a way to transmit unlimited messages that can facilitate cooperation *and* language itself is a form of cooperation. Caring for sick, injured, or elderly group members is common, and shared moral systems regulate group interactions through the creation of formal or informal rules that can be enforced by third parties (Boyd & Richerson, 2009).

The question of how this level of complexity emerged has received considerable attention. Current evidence suggests that societies of our Pliocene ancestors were not too

dissimilar from those of other group-living primates, suggesting that the significant changes facilitating the extremely large, cooperative societies we see today likely occurred within the last 2-million years (Foley & Gamble, 2009; Boyd & Richerson, 2009). While some studies focus on the cognitive processes that set humans apart from other primates (e.g., Boyd & Richerson, 2009), research on cooperation among our closest living relatives can inform hypotheses about early hominin behavior. Furthermore, comparing human and nonhuman primate patterns of cooperation can reveal which features are “uniquely human,” and which have a deep evolutionary history.

In this dissertation, I focus on the cooperative behavior that is food sharing. Here, I use models that have been employed to explain human meat-sharing patterns – kin selection, generalized reciprocity, sharing-under-pressure, and food-for-sex – to examine the function of food sharing in a population of savanna-dwelling chimpanzees.

1.1.2 Cooperation in Chimpanzee Societies

Because chimpanzees are our closest living relatives, and because we share a deep phylogenetic history, differences that exist between humans and chimpanzees highlight changes that have occurred during the course of human evolution (Mitani, 2009). In the wild, chimpanzees cooperate by grooming one another, forming short-term coalitions and long-term alliances, hunting and sharing resources with one another, patrolling territory boundaries, and initiating group attacks on members of other communities (Mitani, 2006, 2009).

1.1.2.1 Coalitionary Support

Female chimpanzees have relatively low reproductive rates, giving birth once every 5-6 years on average (Sugiyama, 2003). This results in heavily skewed operational sex ratios, in which the number of reproductively active males is always much higher than the number of

reproductively active females. Having more reproductively active males than females results in high levels of male-male competition for mates and reproductive opportunities. Male-male competition occurs within and between chimpanzee groups, but this competition also creates opportunities for cooperation. For instance, studies show that high social rank is associated with fitness benefits. At some sites, alpha males may sire up to 30%–50% of all infants born during their tenures (Mitani, 2009); however, at others, two or three high ranking males may cooperatively control access to receptive females and share opportunities to mate (Silk, 2005; Watts, 1998). Furthermore, while size and strength help males rise to the top of the dominance hierarchy, research shows that *coalitionary support* (in which a third individual intervenes in an ongoing dispute between two individuals) is a significant predictor of rank, in that males typically obtain the alpha position only if they receive coalitionary support from others. While coalitionary support clearly benefits the recipient of this aid, it is less clear what the benefit is to the third party who puts themselves at risk to offer their services (Mitani, 2009). Classic studies by de Waal (1982, 1989) in captivity and Nishida (1983) in the wild reveal that male chimpanzees *reciprocally* exchange support and engage in more complex “transactions,” such as trading coalitionary support for goods and services (e.g., grooming and meat). Other studies report that alpha males will grant mating opportunities to lower ranking males who help them maintain their dominance rank through coalitionary support (Mitani, 2009)

1.1.2.2 Territory Boundary Patrolling and Intergroup Aggression

Another example of cooperation is that at many chimpanzee field sites, males defend group territories by patrolling boundaries (Wilson et al., 2012). In the 1970s, Jane Goodall discovered that chimpanzees sometimes kill members of neighboring groups (Goodall et al., 1979). Since then, there have been numerous reports of chimpanzees initiating lethal intergroup

attacks (Wilson et al., 2012). This is fascinating because while many primates exhibit territoriality and non-lethal intergroup aggression, intergroup lethal attacks typically only occur among humans and chimpanzees (Goodall et al., 1979; Silk, 2009; Wrangham & Glowacki, 2012).

Observable similarities between chimpanzee intergroup aggression and human warfare inspired the “chimpanzee model of war,” which proposes that intergroup killing is strategic and adaptive. According to the model, chimpanzee groups compete for territory, food, and access to females (Williams et al., 2004). Males help their groups by injuring or killing members of neighboring groups, but only in circumstances that pose little risk of harm to the aggressors (e.g., when there are power imbalances). Indeed, in chimpanzees, lethal attacks have only been observed when there is a strong asymmetry of power between groups – usually when several males from one group encounter a lone male, or a lone female and her offspring, from a neighboring rival group. Successful killings shift the long-term power balances towards the aggressors’ group by exacerbating the disparity in population size and increasing their chances of winning future competitions for resources (Wrangham & Glowacki, 2012).

Most intergroup attacks occur when subgroups of mostly adult males patrol the boundaries of their group’s home range. Patrolling and killing can be costly in terms of time, energy, and the risk of death or injury (even though males tend to attack only when they greatly outnumber the target). However, there are benefits, as well. Large groups of chimpanzees have been reported to kill all or most males in smaller groups over the course of several months or years. As this happens, the winning group tends to acquire portions of territory from the losing group, which could result in increased access to food and increased access to parous females if females from the losing group transfer into the winning group (Langergraber et al., 2017; Mitani

et al., 2010; Nishida et al., 1985). Thus, possible benefits of patrolling and intergroup killing include increased access to food, increased number of females in the group, increased female reproductive rates (associated with increased food), and increased survival of group members (especially infants). However, as researchers have pointed out, not all males share these benefits equally. For instance, males who obtain most of the matings may benefit the most from patrolling/killing, since they are more likely to be the fathers of infants and juveniles in the group, and since they are more likely to mate with any new females who join the group. By that same logic, males who currently have fewer offspring or who have poor future mating prospects have less to gain from patrolling/killing. Male philopatry may increase incentives to participate in patrolling – because males remain in their natal troops their entire lives, and because male chimps can live for over 50 years, those who patrol when they are young may gain future benefits, even if they stand to benefit less immediately (Langergraber et al., 2017; Watts & Mitani, 2001).

1.1.2.3 Vertebrate Hunting and Resource Sharing

Another crucial aspect of chimpanzee ecology that sets them apart from other nonhuman primates is that they hunt and consume the meat of several vertebrate species. Other nonhuman primate species occasionally engage in hunting, but only chimpanzees and humans are described as “regular” and “frequent” hunters (Stanford, 1999). Although most chimpanzee communities hunt vertebrates, there is considerable variation in hunting practices across populations in terms of prey selection, hunting frequency, and hunting techniques (Newton-Fisher, 2014).

Chimpanzee hunts can be solitary or social. For instance, at Gombe, most hunts are carried out by one individual (Busse 1978; Teleki 1973), whereas at Mahale and Tai, group hunts are more frequently observed (Boesch & Boesch-Achermann, 2000; Newton-Fisher, 2014).

Boesch & Boesch (1989) operationally defined four terms used to describe social hunts. According to their definitions, hunting *similarity* means that hunters direct similar actions towards the same prey, but there is no temporal or spatial congruence between the hunters; hunting *synchrony* involves temporal congruence; hunting *coordination* involves temporal and spatial congruence; and hunting *collaboration* means that individuals perform different complementary actions directed at the same prey (Boesch & Boesch, 1989). Boesch & Boesch (1989) state that these four hunting strategies – similarity, synchrony, coordination, and collaboration – all represent cooperative hunts with varying degrees of organizational complexity between hunters. However, others have questioned the conditions under which a hunt should be considered cooperative. According to Newton-Fisher (2014), the fact that chimpanzees sometimes adopt different roles and respond to one another's actions during hunts is evidence of social cooperation, but in order to be *functionally* cooperative, individuals hunting in groups should be more successful than individuals hunting alone. Research comparing success rates of social hunts versus solitary hunts has yielded mixed results. At Gombe, Ngogo, and Tai, the probability of capturing prey increases with the number of hunters involved, but it has been argued that this success is attributable the fact that more individuals are reaching for prey; not necessarily that the hunters are working together (Stanford, 1998; Gilby et al., 2006; Newton-Fisher, 2014). However, at Kanyawara, a synergistic effect has been reported for social hunts (Gilby et al. 2008; Newton-Fisher, 2014).

Another example of chimpanzee cooperation is the sharing of resources. Meat sharing has been observed at virtually all sites where chimpanzees hunt vertebrates, but here, too, we see considerable variation. For instance, at Mahale, the alpha male entirely controls the distribution of meat, whereas at Tai, all individuals who participated in a hunt share the resulting meat

(Boesch et al., 2002; Nishida et al., 1992). At most sites where chimpanzees hunt vertebrates, higher-ranking males will seize prey captured by lower-ranking individuals (Pickering, 2013). However, at the Fongoli site, research indicates that dominant males took prey from lower-ranking individuals less than 5% of the time (Pruetz et al., 2015). This social tolerance creates additional opportunities for meat sharing by individuals other than high-ranking adult males. The Fongoli community is also unique in that individuals habitually transfer wild plant foods and other non-meat resources to unrelated group members; this behavior is extremely uncommon among chimpanzees (Pruetz & Lindshield, 2012). Resource sharing (meat sharing, in particular) will be discussed in greater detail starting with Section 1.2 of this chapter.

1.1.2.4 Key Differences Between Chimpanzee and Human Patterns of Cooperation

Mitani (2009) describes instances of male chimpanzees cooperating in coalitions, hunting parties, meat sharing, and territorial boundary patrols. All of these behaviors indicate a level of cooperation that exceeds most other mammals. However, the current evidence that we have from long-term chimpanzee studies suggests that cooperation is typically limited to pairs or small groups of individuals. Additionally, we do not see cooperation *between* social groups, only within. Unlike chimpanzee cooperation, human cooperation is often characterized by extensive networks of individuals. Cooperation within *and* between social groups can be observed, even between individuals who are unrelated and may never encounter one another again (Mitani, 2009). It is important to note, however, that while the scale and range of human cooperation exceeds that of chimpanzees, both human and chimpanzee cooperation are exceptional compared to other social mammals.

1.1.3 Hypotheses to Explain the Evolution of Cooperation

1.1.3.1 Kin Selection

Cooperation is typically defined as a behavior that provides a benefit to another individual *or* is beneficial to both the actor and the recipient. In other words, the recipient's fitness increases and the actor's fitness either remains unaffected or it also increases. Altruism, on the other hand, refers to a behavior that provides a benefit to the recipient at the *cost* of the actor. In other words, true altruism decreases an actor's fitness while increasing the recipient's fitness. Since we assume that natural selection will favor behaviors that increase an individual's survival and reproduction, observing altruism in nature begs the question of how this tendency could have evolved. In his classic paper, *The Genetical Evolution of Social Behavior*, W.D. Hamilton (1964) developed a mathematical model to address this question.

The rationale behind Hamilton's (1964) model, which is now known as kin selection, draws from Wright's "coefficient of relationship" (also referred to as the "coefficient of relatedness" in recent literature), which describes the proportion of genes shared with one's relative by common descent (Wright, 1922). In other words, biological kin are more likely to share copies of a gene than individuals who are not biologically related. Therefore, if altruists enhance the survival and reproduction of related individuals, some of their genetic material may still get passed on to the next generation even if the actor sacrifices their life in the process. This would explain how genes associated with altruism might proliferate despite altruism itself being maladaptive to the individual. Altruism therefore increases an actor's *inclusive* fitness (i.e., one's own fitness plus that of relatives discounted by relatedness), assuming it benefits related individuals who will survive *and* reproduce (Hamilton, 1964).

Hamilton's rule for when acts of altruism should be favored by selection is typically simplified as: $rB > C$, where r = coefficient of relatedness, B = benefit of the action (e.g., increased kin survivorship), and C = cost of the action (e.g., decreased personal survivorship).

The coefficient of relatedness (r) – which refers to the proportion of DNA two individuals are likely to share due to common descent – is calculated as: $r = 1/2^x$, where x = degrees of separation between the two individuals. For instance, in organisms with a diploid mating system (such as primates), there is one degree of separation between ego and their parents, full siblings, or offspring; there are two degrees of separation between ego and their aunts, uncles, nieces, nephews, and grandparents; three degrees of separation between first cousins, etc. Thus, the coefficient of relatedness between a parent and an offspring or between full siblings is 0.5; the coefficient of relatedness between an aunt/uncle and a niece/nephew or between a grandparent and grandchild is 0.25; the coefficient of relatedness between first cousins is 0.125; and it gets exponentially smaller as two individuals become more distantly related.

Hamilton's rule makes two key predictions about the evolution of altruistic behaviors via kin selection: 1) altruism should be limited to kin because if r is 0, the inequality cannot be satisfied; and 2) altruism that is especially costly should be restricted to *close* kin because when $r = 0.5$, the benefits only need to exceed twice the costs in order to satisfy the inequality; however, when $r = 0.125$, the benefits need to exceed 8 times the cost, and that will continue to increase exponentially (Hamilton, 1964; Silk, 2002).

The concept of inclusive fitness, which is the defining feature of kin selection, is not without critique. Nowak et al. (2010) argue that inclusive fitness theory is not a general evolutionary framework; it is a specific mathematical approach with limitations. They hold that in order to invoke inclusive fitness theory, all observed interactions must be additive and pairwise, selection must be weak overall, and groups must exhibit special population structures. Their main argument is that because these assumptions are easily violated in nature, inclusive fitness theory explains very few scenarios. They add that in the few instances in which kin

selection could explain interactions, “standard” natural selection would make the same predictions; therefore, inclusive fitness theory does not make any unique predictions (Nowak et al., 2010).

Strassman et al. (2011) respond to Nowak et al. (2010) by critiquing the initial assumption that inclusive fitness theory and “standard natural selection theory” are distinct from one another. According to Strassman et al. (2011), inclusive fitness theory uses population genetics to make testable predictions about how natural selection operates. For this reason, it is unsurprising that kin selection generates similar or identical predictions to ones obtained through natural selection. Strassman et al. (2011) also critique Nowak et al.’s understanding of inclusive fitness theory by pointing out that the strict assumptions described by Nowak et al. (e.g., pairwise interactions, additivity, weak selection, special population structures) are not assumptions of Hamilton’s original formulations. Contrary to Nowak et al.’s (2010) position, Strassman et al. (2011) suggest that inclusive fitness theory *is* a general framework in which the main distinction is the partitioning of natural selection into direct and indirect fitness components. They also emphasize Hamilton’s original point, which is that altruism between relatives will be favored if the fitness benefits are great enough to outweigh the costs (Strassman et al., 2011).

Kinship in Chimpanzees

Among many catarrhine monkey species that are female-philopatric and male-dispersing, females behave nepotistically toward sisters and other maternal relatives, whereas the more distantly related males within social groups tend to cooperate less with one another (Silk, 2002). However, chimpanzees are male-philopatric and female-dispersing, and studies have shown that male chimpanzees are much more affiliative and cooperative than female chimpanzees (Mitani et

al., 2002). This has been interpreted as evidence that kin selection plays a role in the evolution of male chimpanzee cooperation (Goodall, 1986; Langergraber et al., 2007; Morin et al., 1994).

Yet, there is little evidence that males bias their social behaviors nepotistically toward maternal brothers (Goldberg & Wrangham, 1997; Langergraber et al., 2007; Mitani et al., 2000, 2002).

Langergraber et al. (2007) examined the role of kinship in cooperation among wild chimpanzees at Ngogo, Kibale National Park, Uganda. They found that male chimpanzees preferentially affiliated and cooperated with their maternal brothers. However, paternal brothers failed to affiliate and cooperate the same way as maternal brothers, despite the fact that paternal brothers are as closely related to one another as are maternal brothers. The authors conclude that male chimpanzees show clear and consistent biases in social behaviors toward maternal brothers, confirming the importance of maternal kinship in cooperation. However, paternal brothers do not preferentially interact with one another, and most males who were part of highly affiliative and cooperative dyads were unrelated or distantly related. The authors interpret this as evidence that male chimpanzees probably obtain indirect fitness benefits by affiliating and cooperating with their maternal brothers, *and* direct fitness benefits by forming mutualistic and reciprocal relationships with others (Langergraber et al., 2007).

Langergraber et al. (2009) examined whether kinship played a role in the strength of social bonds among female chimpanzees of the Ngogo community. Their findings revealed that close kin dyads (i.e., mother–daughter dyads and sibling dyads) are very rare, and that the vast majority of female dyads that formed strong social bonds were *not* closely related. Additionally, “subgroups” of females who frequently associate with one another in similar areas of the territory did not consist of relatives. The authors conclude that kinship plays a limited role in

structuring same-sex social relationships in female chimpanzees at Ngogo (Langergraber et al., 2009).

1.1.3.2 Reciprocal Altruism

Reciprocal altruism (Trivers, 1971) is an alternate hypothesis put forth to explain the evolution of altruism (i.e., behaviors that provide a benefit to the recipient at a cost to the actor). Though reciprocal altruism and kin selection are not necessarily mutually exclusive, reciprocal altruism aimed to explain seemingly altruistic acts between unrelated individuals. Trivers (1971) argued that if recipients are likely to return the favor, an altruistic behavior that appears to decrease an actor's fitness in that moment, might actually *increase* their fitness in the long run. Thus, altruistic behaviors could be favored by natural selection if they occur between other altruists who are likely to reciprocate.

One of the best-known examples of reciprocity in nature is food sharing among common vampire bats (*Desmodus rotundus*). Vampire bats feed on blood and will die after ~70-hours of not eating. However, before a bat starves to death, a roost-mate who obtained enough food will often regurgitate blood to feed the hungry bat. The act of regurgitating blood for a roost-mate is energetically costly; however, if there is a chance that the donor bat will struggle to obtain food in the future, and if sharing food now makes the recipient bat more likely to reciprocate later on when the roles are reversed, the immediate cost of sharing now may enhance long-term survival and reproduction (Trivers, 1971; Wilkinson, 1984). Since it was first reported that vampire bats share blood reciprocally, skeptics have questioned whether there is another explanation for this behavior aside from reciprocal altruism. However, Carter & Wilkinson (2013) tested the predictions of reciprocal altruism, kin selection, and harassment (“sharing-under-pressure”) and found that food received was the best predictor of food given across dyads (8.5 times more

important than relatedness). Additionally, donors (rather than recipients) initiated food sharing in most cases, which is inconsistent with a harassment model (Carter & Wilkinson, 2013; Wilkinson, 1984).

Reciprocity in Chimpanzees

As previously mentioned, within chimpanzee communities, individuals cooperate by grooming one another, forming short-term coalitions and long-term alliances, hunting and sharing resources with one another, patrolling territory boundaries, and initiating group attacks on members of other communities (Mitani, 2006). Researchers have tested if (and to what extent) reciprocity plays a role in facilitating these cooperative behaviors. In captivity, there is evidence that chimpanzees groom one another reciprocally (de Waal, 1989). There is also evidence of reciprocal trade networks in which the currencies differ, such as grooming-for-food exchanges (de Waal, 1997; Hemelrijk & Ek, 1991). Regarding tests of reciprocity in the wild, Mitani (2006) reports that male chimpanzees at Ngogo engaged in reciprocal grooming, coalitionary support, and meat-sharing. Correlations were significant even after controlling for factors like male age and rank, genetic relatedness, association frequency, and the number of times individuals were together at hunts (Mitani, 2006). Despite observations that reciprocity affects chimpanzee cooperation in certain instances, other studies report no evidence of reciprocity during experimental tasks (e.g., Brosnan et al., 2009; Yamamoto & Tanaka, 2010). Additionally, some studies report that initial observations of what appeared to be reciprocal networks were not statistically significant after controlling for confounding factors, such as kinship, rank differences, or relationship quality (e.g., Jaeggi et al., 2013). Thus, the importance of reciprocity in chimpanzee societies remains unclear, playing a role in some contexts more than others.

1.1.3.3 Group Selection and Multilevel Selection (AKA “Revised Group Selection”)

In addition to kin selection and reciprocal altruism, early group selection (also known as “naïve group selection”) also sought to explain the evolution of seemingly altruistic behaviors (e.g., Wynne-Edwards, 1962). It is important to note, however, that the concept of group selection has changed considerably since its initial description. In fact, the revised form of group selection (also known as “multilevel selection”) is now congruous with individual selection, kin selection, and reciprocal altruism, rather than these being competing hypotheses (as reviewed by Borrello, 2005). Furthermore, many of the scientists who vehemently criticized early group selection have come to accept the new and improved multilevel selection (e.g., Wilson & Wilson, 2007). The following section reviews the history and key developments in multilevel selection.

Early Group Selection (AKA “Naïve Group Selection”)

An assumption of natural selection is that population size is directly limited by access to resources. When the number of individuals exceeds the available resources, individuals must compete with one another. This results in differential survival and reproduction, since not all individuals will obtain sufficient resources (Darwin, 1859). The relationship between population size and resource availability is therefore crucial, because over-population could result in over-exploitation of resources, which could result in permanent damage to a habitat and/or mass starvation of the population (Wiens, 1966). In his book, *Animal Dispersion in Relation to Social Behaviour*, Wynne-Edwards (1962) proposed that some animals exhibit population-regulatory mechanisms, and that these mechanisms likely evolved to benefit the entire social group.

Some key arguments of Wynne-Edwards’ version of group selection are as follows: 1) Groups have characteristics of their own, which are lacking in individuals (e.g., territorialism, hierarchies, altruism). He argues that these could only have evolved through group selection; 2)

Group selection is functionally and conceptually distinct from natural selection at the individual level; 3) Often the interests of the group conflict with those of individuals. When this is the case, group selection overrides selection at the individual level; 4) Group selection operates through the success or failure of entire groups; and 5) These groups are localized and persistent through time, reducing intergroup gene flow, and leading to local adaptation (Wynne-Edwards, 1962).

One of the main criticisms of early group selection was that Wynne-Edwards insisted the group was the only level at which selection for a social behavior could occur. With his group selection, natural selection operates at group level and all individuals in the group either succeed or fail (Wynne-Edwards, 1962, pg. 275). A major school of thought opposing group selection was the “gene-centric” view of evolution, introduced by George C. Williams in 1966 and expanded upon by Richard Dawkins a decade later (Dawkins, 1976; Williams, 1966). According to Dawkins (1976), organisms are vehicles for genes, and alleles whose phenotypic effects promote their own propagation will be favorably selected compared to competitor alleles within the population.

In 1971, Williams edited a book called *Group Selection* that contained essays from evolutionary biologists critiquing group selection as an evolutionary force (Williams, 1971). This volume included W.D. Hamilton’s (1964) classic paper on inclusive fitness and kin selection. As previously mentioned, Wynne-Edwards (1962) believed that group selection could explain apparently altruistic acts, but Williams (1971), Hamilton (1964), Maynard Smith (1964), Dawkins (1989), and others argued that group selection was a weak evolutionary mechanism and unnecessary to explain observations of altruism (Birch & Okasha, 2014).

Relation to Other Hypotheses

In nature, there are many examples of cooperation between group members and what appears to be altruistic acts by individuals (i.e., actions that benefit the recipient at a cost to the actor). For evolutionary biologists who vehemently reject the idea of naïve group selection, these observations require an alternate evolutionary explanation. *Reciprocal altruism* (Trivers, 1971) and *kin selection* (Hamilton, 1964) were proposed as ways to explain altruism in the context of individual fitness. *However*, according to D.S. Wilson (1977), reciprocal altruism and kin selection are not actually alternatives to group selection. They themselves are special cases of multilevel selection because when using game theory to model kin selection or altruism, altruistic acts are always disadvantageous for that individual's fitness. Thus, Wilson argues that even behaviors that could be explained by kin selection or reciprocal altruism require group selection to evolve. Additionally, as previously mentioned, kin selection cannot explain cooperation among large groups of unrelated individuals, which is why group selection ("multilevel selection") is sometimes invoked.

Multilevel Selection

Multilevel selection, as pioneered by D.S. Wilson (1977), argues that depending on the context, selection can operate at the level of the gene, the individual, or the group. For instance, we can imagine a scenario in which very aggressive hens produce a large number of eggs, while non-aggressive hens produce fewer eggs. If we have a group comprised of both aggressive and non-aggressive hens, at the individual level, the aggressive hens will have higher fitness than the non-aggressive hens. However, if we have one group of all aggressive hens and one group of all non-aggressive hens, the group of non-aggressive hens would likely fare better overall, because they would be less stressed, whereas the group of all aggressive hens would be constantly fighting and harming one another, which would decrease egg production (Muir, 1996).

Multilevel selection differs from early group selection in that Wynne-Edwards saw the group as the unit, meaning the whole population or deme. In contrast, D.S. Wilson's unit is the trait group. According to D.S. Wilson, classic natural selection at the individual level acts within the trait group, but there is then differential selection on trait groups within a deme. Thus, D.S. Wilson's model is *intrademic* group selection, whereas naïve group selection was *interdemic*. As reviews of multilevel selection explain, "Kin selection methods aim at identifying character states that maximize fitness, whereas multilevel selection methods aim at examining the effects of selection on trait changes. Far from being alternative approaches to the same problem these two approaches are complementary methods that can be used together to obtain a complete understanding of the evolution of a social behavior system" (Goodnight, 2013, pg. 1546).

A major contribution to multilevel selection theory was the "Price Equation" (Price, 1970), which uses covariance between a trait and its fitness outcomes to understand the effects that gene transmission and natural selection have on the proportion of genes within each new generation of a population. Its relevance to multilevel selection is that it was crucial for modeling what happens when there is conflict between levels of the biological hierarchy (e.g., gene, individual, and group). Importantly, in 1971, after being shown Price's Equation, W.D. Hamilton (famous for introducing kin selection) acknowledged that multilevel analysis was an important part of evolutionary theory (Hamilton, 1971). Even some of the strongest critics of naïve group selection (e.g., E.O. Wilson and George Williams) started to accept multilevel selection. In fact, E.O. Wilson, who used to be an adamant individual selectionist, published a paper with D.S. Wilson about multilevel selection (Wilson & Wilson, 2007).

Multilevel Selection in Chimpanzees

Among chimpanzees, one example of a behavior that can be examined through the lens of multilevel selection is alarm calling. Schel et al. (2013) report that upon encountering snake models, wild chimpanzees produced alarm calls in an intentional manner. Additionally, they found that chimpanzees who had seen the snake were more likely to increase their production of calls upon the arrival of a “friend” (compared to a “non-friend”), and upon the arrival of a higher-ranking individual (Schel et al., 2013). Among the same community, Crockford et al. (2012) found that chimpanzees were more likely to alarm call in the presence of unaware group members (i.e., individuals who could not see the snake model) than in the presence of aware group members.

Reciprocal altruism is often invoked to explain the evolution of alarm calling (e.g., Seyfarth & Cheney, 1984). However, if this were the best model, we would expect all members of a group to alarm call at approximately the same frequency, which does not seem to be the case. Kin selection could explain this behavior if alarm calling only occurs in the presence of relatives, which does not seem to be the case. Instead, we can use multilevel selection theory to consider how alarm calling might be maintained in a population. On an individual level, the cost of alarm calling could be high or low to callers depending on the scenario; however, the benefit to the group is typically large even if there are only a few callers in the group. Assuming that alarm calling decreases death from predation, groups that contain callers are likely to have lower mortality rates than groups that do not. Within the group, primates that alarm call may have relatively lower fitness compared to those that do not alarm call (for instance, if they are eaten by predators before producing as many offspring as other individuals); however, they may still have relatively higher fitness compared to individuals in groups in which alarm calling does not occur as frequently, since the group will have a higher survival rate overall.

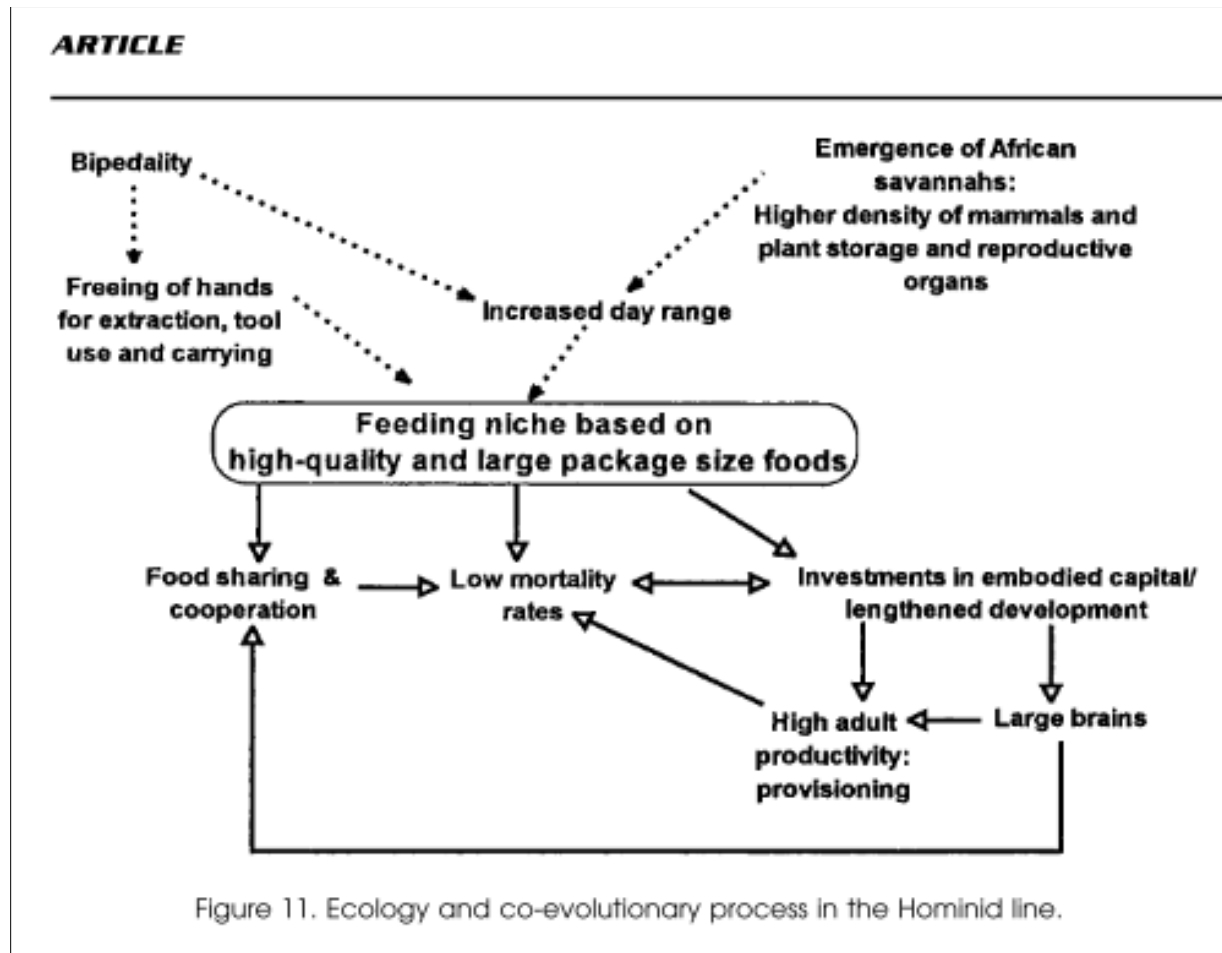
1.2 Food Sharing

The cooperative behavior on which this dissertation focuses is **food sharing**. Food sharing is often considered to be a component of large, complex, cooperative human societies since it is a universal behavior associated with notions of fairness, generosity, reciprocity, and egalitarianism. In their classic paper, Kaplan et al. (2000) describe the importance of food sharing for supporting the unique life history patterns of humans. As they explain, human life histories have four distinctive characteristics: an exceptionally long lifespan, an extended period of juvenile dependence, support of reproduction by older post-reproductive individuals, and male support of reproduction by providing food to females and their offspring. They propose that these four life history characteristics plus our extreme intelligence are co-evolved responses to a dietary shift toward higher-quality, nutrient-dense, difficult-to-acquire food resources. Their rationale is that in order to exploit the high-quality, difficult-to-acquire resources that humans consume, past humans would have required high levels of knowledge, skill, coordination, and strength. These abilities require time to develop and learn, which creates an extended period of childhood. When we examine individual productivity rates (i.e., how many calories an individual is finding or producing themselves through hunting, gathering, etc.), we see that childhoods are typically characterized as “low productivity” periods (i.e., individuals consume more calories than they can produce). However, this low productivity during childhood is later compensated by high productivity during adulthood. According to the authors, this leads to selection for longer juvenile periods (*if* productivity increases with body size and if growth stops at maturity), for lower mortality, and for longer lifespans. Importantly, **food sharing enabled this system by allowing humans to focus on high-mean-return, but high-variance foraging strategies by pooling the risk involved**. In other words, humans are able to try for higher-quality, nutrient-

dense, difficult-to-acquire food resources if other group members are willing to share food with them in the event that they return empty-handed (Kaplan et al., 2000).

To demonstrate their crucial point that food sharing facilitated human life history patterns, Kaplan et al. (2000) examine data from chimpanzees and hunter-gatherers (Hadza, Ache, and Hiwi). Their data reveal that hunter-gatherers have a juvenile period that is 1.4x longer than that of chimpanzees and a mean adult lifespan that is 2.5x longer than that of chimpanzees. However, despite having longer childhoods, slower growth rates, and longer lives than chimpanzees, the hunter-gatherer women achieved *higher* fertility rates than the chimpanzee females. According to the authors, food sharing is what makes this possible – hunter-gatherer children are energetically dependent on older individuals until they reach sexual maturity, meaning they require food to be shared with them. Additionally, the nutritional demands of gestation, lactation, and child-rearing require far more calories than a pregnant woman (or a woman with young children) can realistically obtain herself. Luckily, adult hunter-gatherer men from this study acquired significantly more food than members of any other age-sex category; food that can be shared with group members including women and children (Kaplan et al., 2000). While sharing food with mates and children could be interpreted as a direct investment in one's total fitness, sharing food with unrelated (and non-mate) group members does not have as obvious a fitness benefit. This is why we must invoke various hypotheses that have been developed to explain food sharing.

Figure 1. Ecology and coevolutionary process in the Hominid line (Reprinted with permission from Kaplan et al. 2000, pg. 179, Figure 11) *1



1.3 Current Food Sharing Models

Four major hypotheses are typically used to explain food sharing with conspecifics: kin selection (e.g., Hamilton, 1964), reciprocity (e.g., Trivers, 1971), sharing-under-pressure (Blurton Jones, 1987; Wrangham, 1975), and food-for-sex (Teleki, 1973). 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 transfers serve different purposes in different contexts (Feistner & McGrew, 1989; Jaeggi & Van Schaik, 2011; Silk et al., 2013).

*Reprinted with permission from "A theory of human life history evolution: Diet, intelligence, and longevity" by Kaplan et al., 2000. *Evolutionary Anthropology*, 9, 156-185. Copyright [2000] by John Wiley and Sons.

1.3.1 Kin Selection

As described more fully above, kin selection proposes that individuals act in ways that increase their inclusive fitness by enhancing the survival and reproduction of closely related individuals (Hamilton, 1964). Kin selection is beneficial when the benefits to the recipient(s), discounted by the coefficient of relatedness, outweigh the costs to the actor ($r \times B > C$).

Regarding food sharing, kin selection predicts that individuals share with related group members more frequently than with unrelated group members. It also predicts that individuals share with close kin (e.g., siblings) more frequently than with distant kin (e.g., cousins).

1.3.2 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 the recipients return the favor (Trivers, 1971). A strict form of reciprocal altruism (AKA “tit-for-tat reciprocity”) assumes that exchanges are balanced, and that reciprocation occurs in the same “currency” as the initial act (e.g., food-for-food) (Stevens & Gilby, 2004). Due to differences in marginal values, food transfers between individuals do not need to be perfectly balanced, as long as both individuals do slightly better than they would have if they had not shared (Gurven, 2004; Hill & Kaplan, 1993; Nolin, 2010). In this case, food sharing reflects a pattern of generalized reciprocity. Regardless of whether transfers are precisely balanced, any form of reciprocity (tit-for-tat or generalized) should be contingent on past and future shares from partners. Thus, we can evaluate reciprocity-based hypotheses by testing for contingent exchange (defined as “a statistical correlation between frequency or amounts given and received within dyads” [Nolin, 2010]).

1.3.3 Sharing-Under-Pressure

The Sharing-Under-Pressure hypothesis (Wrangham, 1975) and a version of this hypothesis that appears in the human literature, the "Tolerated Theft" hypothesis (Blurton Jones, 1987), both predict that possessors of food may share with non-possessors as a way to avoid the costs of defending the food item from persistent beggars (Gilby, 2006). These "costs" could include an increase in the amount of energy expended, a decrease in foraging efficiency, and injuries sustained while fighting off beggars. In order for this model to function as an explanation, the cost of harassment to the owner must outweigh the benefit they are losing by sharing food. Additionally, increased harassment should increase the probability of possessors sharing (Stevens & Gilby, 2004; Stevens & Stephens, 2002).

1.3.4 Food-for-Sex

The food-for-sex hypothesis proposes that males exchange food for mating opportunities (Teleki, 1973). It predicts that: 1) Males share with adult females more than with any other age-sex class, 2) Males are more likely to share food with estrous females than with anestrus females, and 3) Males that share food more frequently will obtain more mating opportunities than they would otherwise (Mitani & Watts, 2001). In the human literature, a similar hypothesis, the "showoff hypothesis," proposes that men hunt and distribute meat in order to enhance their social status or to obtain mating opportunities (Hawkes, 1991). With the showoff hypothesis, another key prediction is that decisions to hunt should be influenced by the presence of females, since males want to show off their hunting abilities.

1.4 Review of Food Sharing Studies

To comprehend the function and significance of food sharing among the Fongoli chimpanzee community, it is useful to contextualize this research within the existing food sharing literature. Food sharing is not unique to humans and chimpanzees, nor is it unique to

primates more broadly. Indeed, it has also been observed among populations of insects (e.g., Boggs, 1995), birds (e.g., Massen et al., 2020), social carnivores, cetaceans, and bats. However, as we will see, the nature of sharing may differ between taxa. The following table and subsequent discussion highlight key research on food sharing among these diverse groups. This table is not exhaustive, nor does it include food transfers from mothers to their infants, since that behavior is seen in many animals. Instead, it notes key studies in which adult animals transferred food to other adult group members, or to infants and juveniles who were not their own (e.g., callitrichids).

Table 1. Populations among which food sharing with adult group members has been reported

Study group	Habitat	Reference (not exhaustive)
Birds		
Azure-winged magpies (<i>Cyanopica cyanus</i>)	Captive	(Massen et al., 2020)
Cliff swallows (<i>Hirundo pyrrhonota</i>)	Wild (Nebraska, USA)	Brown et al. 1991
Eurasian jays (<i>Garrulus glandarius</i>)	Captive	(Ostojić et al., 2013)
Pinyon jays (<i>Gymnorhinus cyanocephalus</i>)	Captive (captured from Arizona and California)	(Duque & Stevens, 2016)
Ravens (<i>Corvus corax</i>)	Wild (Maine, USA)	(Heinrich & Marzluff, 1995)
Red-crested pochards (<i>Netta rufina</i>)	Wild (Spain)	(Amat, 2000)
Non-Primate Mammals		
Killer whales (<i>Orcinus orca</i>)	Wild (off the Canadian west coast from Vancouver Island, BC, to SE Alaska, USA)	(Wright et al., 2016)
Meerkats (<i>Suricata suricatta</i>)	Wild (South African Kalahari)	(Brotherton et al., 2001)
Vampire bats (<i>Desmodus rotundus</i>)	Captive (Organization for Bat Conservation, Bloomfield Hills, MI, USA)	(Carter & Wilkinson, 2013)
Platyrrhine Monkeys		
Black lion tamarins (<i>Leontopithecus chrysopygus</i>)	Captive	(Feistner & Price, 2000)

Brown capuchins (<i>Cebus apella</i>)	Captive (Yerkes Regional Primate Research Center, Lawrenceville, GA, USA)	(De Waal, 1997, 2000)
Buffy-headed marmoset (<i>Callithrix flaviceps</i>)	Wild (Brazil)	(Ferrari, 1987)
Coimbra-Filho's Titi monkeys (<i>Callicebus coimbrai</i>)	Wild (Northeast Brazil)	(Souza-Alves et al., 2019)
Cotton-top tamarins (<i>Saguinus oedipus</i>)	Captive	(Hauser et al., 2003)
Golden lion tamarins (<i>Leontopithecus rosalia</i>)	Wild (Brazil)	(Troisi, 2021; Troisi et al., 2021)
Owl monkeys (<i>Aotus azarai azarai</i>)	Wild (Argentina)	(Wolovich et al., 2008)
White-faced capuchins (<i>Cebus capucinus</i>)	Wild (Costa Rica)	(Perry & Rose, 1994)
Catarrhine Monkeys		
Douc langurs (<i>Pygathrix nemaeus nemaeus</i>)	Captive (San Diego Zoo, San Diego, CA, USA)	(Kavanagh, 1972)
Nicobar long-tailed macaques (<i>Macaca fascicularis</i>)	Wild (India)	(Mazumder & Kaburu, 2021)
Guinea baboons (<i>Papio papio</i>)	Wild (Senegal)	(Goffe & Fischer, 2016)
Asian and African Apes (excluding <i>Pan</i> and <i>Homo</i>)		
Lar gibbons (<i>Hylobates lar</i>)	Wild (Thailand)	(Nettelbeck, 1998)
Lar gibbons (<i>Hylobates lar</i>)	Captive (Phoenix Zoo, Phoenix, AZ, USA)	(Schessler & Nash, 1977)
Orangutans (<i>Pongo pygmaeus wurmbii</i>)	Wild (Borneo, Indonesia)	(Van Noordwijk & Van Schaik, 2009)
Orangutans (<i>Pongo abelii</i>)	Wild (Sumatra, Indonesia)	(Van Noordwijk & Van Schaik, 2009)
Orangutans (<i>Pongo abelii</i>)	Captive (Berlin & Dortmund zoological gardens, Germany)	(Kopp & Liebal, 2016)
Genus <i>Pan</i>: Bonobos and Chimpanzees		
Bonobos (<i>Pan paniscus</i>)	Wild (Democratic Republic of Congo)	(Fruth & Hohmann, 2018; Goldstone et al., 2016; Hare & Kwtuenda, 2010)
Bossou chimpanzees (<i>Pan troglodytes verus</i>)	Wild (Republic of Guinea)	(Hockings et al., 2007)
Fongoli chimpanzees (<i>P. t. verus</i>)	Wild (Senegal)	(Jill D. Pruett & Lindshield, 2012)
Gombe National Park chimpanzees (<i>P. t. schweinfurthii</i>)	Wild (Tanzania)	(Gilby, 2006; McGrew, 1975; Stanford, 1999; Wrangham, 1975)

Mahale mountain chimpanzees (<i>P. t. schweinfurthii</i>)	Wild (Tanzania)	(Nakamura & Itoh, 2001; Toshisada Nishida et al., 1992)
Ngogo chimpanzees, Kibale National Park (<i>P. t. schweinfurthii</i>)	Wild (Uganda)	(Mitani & Watts, 2001)
Sonso chimpanzees, Budongo Forest (<i>P. t. schweinfurthii</i>)	Wild (Uganda)	(Slocombe & Newton-Fisher, 2005; Wittig et al., 2014)
Tai National Park chimpanzees (<i>P. t. verus</i>)	Wild (Côte d'Ivoire)	(Boesch & Boesch, 1989; Samuni et al., 2018)
Michale E. Keeling Center chimpanzees (<i>P. troglodytes</i>)	Captive (Michale E. Keeling Center for Comparative Medicine and Research, Bastrop, TX, USA)	(Silk et al., 2013)
Yerkes Primate Center chimpanzees (<i>P. troglodytes</i>)	Captive (Yerkes Regional Primate Research Center, Lawrenceville, GA, USA)	(de Waal, 1989, 1997; Eppley et al., 2013)
Genus <i>Homo</i>: Extant Human Foraging Societies		
Ache	Paraguay	(Gurven et al., 2001, 2002; Gurven et al., 2000a; Kaplan et al., 1984a; Kaplan & Hill, 1985)
Achuar, Quichua, and Zapara speakers in Conambo	Ecuadorian Amazon	(Patton, 2005)
Agta	Philippines	(Dyble et al., 2016)
Aka (Mbindjele BaYaka)	Dominican Republic of Congo	(Dyble et al., 2016; Kitanishi, 1998)
Hiwi	Venezuela	(Gurven et al., 2000b)
Hadza	Tanzania	(Hawkes et al., 2001) (Marlowe, 2004)
Inuit of Akulivik	Canada (northern Quebec)	(Kishigami, 2006)
!Kung (Ju/'hoansi); San	Namibia; Kalahari	(Kent, 1993; Wiessner, 1977, 2002)
Lamalera	Indonesia	(Nolin, 2008, 2012)
Ye'kwana (Makiritare)	Venezuelan Amazon	(Hames & McCabe, 2007)

While food sharing has been observed across a diverse range of taxa, the patterning and complexity of food sharing among primates is markedly different than in other taxa. These differences will be explored in the following sections, in which I discuss key findings of human and nonhuman primate food sharing studies.

1.4.1 Food Sharing Among Humans

1.4.1.1 Hunter-Gatherer Societies

Extant foraging societies are often used to make inferences about early humans based on the knowledge that foraging is the ancestral subsistence mode of humans, and that we were hunter-gatherers for 90% of our history as a species (Ember, 2020). However, we know that no extant populations are direct mirrors into the lives of early humans since cultures evolve substantially over time. Additionally, there is archaeological and ethnographic evidence that foraging populations have traded with food producing populations throughout prehistory, history, and today. That said, anthropologists from the last 50-100 years have accrued rich archaeological, paleoanthropological, and ethnographic records that can be used to develop and test hypotheses about early humans. Cross-cultural analyses reveal similarities and differences among foraging societies. Examining the conditions that predict variation can provide valuable insight that can inform our inferences about early humans. Furthermore, by revealing gaps in our current knowledge, these cross-cultural analyses can highlight future areas of research (Ember, 2020). This is all to say that while we should be careful not to suggest that hunter-gatherer culture has remained frozen in time, impervious to change, there are ways to responsibly use ethnographic data to inform inferences about the behaviors of early humans.

The majority of food sharing research among extant foraging societies comes from the Ache of Eastern Paraguay, the Hadza of Tanzania, the Hiwi of Venezuela, and the Lamalera of Indonesia. However, sharing has also been described among the Aka of Northeastern Congo, the Agta of the Philippines, the San of the Kalahari desert (and the Ju'hoansi of Namibia, specifically), and among Achuar, Quichua, and Zapara speakers in Conambo (an indigenous community of horticultural foragers in the Ecuadorian Amazon).

Ache of Eastern Paraguay

Early research on the Ache reveals that they share food extensively *and* that they exhibit significant variation in the extent to which different foods are shared (Kaplan et al., 1984b).

Kaplan and Hill (1985) used this variation to test predictions of alternative hypotheses for the evolution of food sharing among adult conspecifics. They report that close kin are no more likely to receive food from acquirers than non-kin individuals, which does not support the predictions of kin selection (Kaplan & Hill, 1985). According to the authors, synchrony of acquisition (i.e., the mean standard deviation in the amount of each resource acquired on each day) and package size (i.e., the mean number of calories acquired of a resource at one time) significantly predicted variation in the extent to which resources were shared. This finding is consistent with the predictions of both the tit-for-tat reciprocity hypothesis and the tolerated theft hypothesis.

However, several other observations were inconsistent with tolerated theft. First, the tolerated theft model assumes that patterns of sharing are determined by contests over food, and it predicts that individuals weigh the costs of defending a portion of what they acquire versus the benefits of keeping all of it. However, among the Ache, food acquirers were significantly *less* likely to eat their own kills than they were to share with others (Kaplan et al., 1984b). Additionally, if food acquirers were worried about meat being stolen from them (as predicted by tolerated theft), we would expect them to eat as much of the kill as possible before other group members arrived. However, instead of consuming it themselves when given the chance, they waited until the end of the day when it could be consumed by the entire band (Kaplan et al., 1984b; Kaplan & Hill, 1985).

Regarding reciprocity, inter-individual variation in foraging ability does *not* seem to result in differential food consumption. Thus, Ache food sharing patterns seem to reflect a band-

level pooling of resources, rather than a strict tit-for-tat reciprocity. This finding could suggest that food sharing among the Ache evolved through group selection, rather than individual selection, since food sharing benefits the entire band.

Almost two decades later, Gurven et al. (2002) reanalyzed data reported by Kaplan & Hill (1985) and Gurven et al. (2001) in order to evaluate variation in food sharing patterns based on three aspects of sharing: 1) Differences in resource type and production, 2) Differences in group size, and 3) Differences in proximate determinants of food transfers. They test the predictions of four food sharing hypotheses in particular: nepotism (kin selection), tolerated-theft, generalized reciprocity, and costly signaling.

Based on forest food sharing data (collected from 1981 to 1982) and reservation food sharing data (collected in 1998), nepotism seems to explain patterns of food sharing *within* nuclear families in both forest and settlement contexts. However, *between* nuclear families at the settlement, food sharing seems highly dependent on food receiving, which highlights the importance of reciprocity. The authors conclude that reciprocity, tolerated theft, costly signaling, *and* nepotism are all useful for understanding different aspects of Ache food sharing. In other words, food sharing serves different purposes in different contexts (Gurven et al., 2002).

Hadza of Tanzania

Marlowe (2004) evaluates motivations of food sharing using data from games he played with Hadza hunter-gatherers in Tanzania. Specifically, he uses the ultimatum and dictator games to measure sharing propensity. These “games” are social and economic experiments in which one player is told to divide a sum of money with another player. In the ultimatum game, the second player has an active role – they can choose to accept or reject the offer, but if they reject the offer, both players receive nothing. In the dictator game (a derivative of the ultimatum game),

the second player's role is passive in that they cannot reject the offer; the entire outcome is therefore determined by the first player (Marlowe, 2004). In this study, Marlowe (2004) evaluates five hypotheses for sharing: 1) Mutualism (which predicts food for foraging partners), 2) Nepotism (i.e., kin selection), 3) Reciprocity, 4) Costly signaling, and 5) Tolerated scrounging (AKA "tolerated theft" or "sharing-under-pressure"). The game results indicate that: 1) Higher offers were made in larger camps, and 2) When players could reject offers, there was a high rejection rate of low offers. According to Marlowe, the first result supports the predictions of costly signaling, and the second result supports the predictions of reciprocity; however, both of these results together support the predictions of tolerated scrounging (Marlowe, 2004).

Marlowe's (2004) game results are interesting to compare to actual Hadza food sharing observations. As Hawkes et al. (2001) report, in real life, it is not necessary to beg or threaten possessors in order to obtain a portion of food; just knowing that individuals saw the food is usually enough to motivate possessors to share. This likely has to do with notions of stinginess versus generosity – for instance, it is acceptable for a food possessor to only share small game with his offspring, but it would be unacceptable to keep large game within the household without sharing. According to Marlowe, there are no formal rules for how to distribute meat (in most instances); however, large game appears to be fairly evenly shared among all individuals, with the food acquirer possibly getting a slightly larger portion than others (Hawkes et al., 2001; Marlowe, 2004). Another interesting observation is that in real life, the Hadza believe that people who refuse to share are bad people and should therefore be avoided. Thus, Marlowe (2004) suggests that during the games, people might have felt pressured to make higher offers in larger groups, since the consequences of being accused of stinginess in a large group could be worse than in a small group.

One fascinating inconsistency between the game results and real-life observations is that central place foraging tends to increase chances for scrounging, since people who return to camp with food (possessors) are likely to encounter people who do not have food (potential recipients). Thus, if tolerated scrounging is the best model for predicting and explaining Hadza food sharing patterns, it does not seem advantageous to bring food back to the main camp. To explain this phenomenon, Marlowe suggests that the primary motivator for bringing food back could be household provisioning, since it would be too dangerous for women with young offspring to go foraging. Based on his observations, when someone is able to sneak food in undetected, they tend to preferentially share with close kin and mates. Thus, he argues that men might acquire the foods that are most susceptible to scrounging since those foods would signal their “quality” to other group members. However, when the men have wives and children, they may want to share that food with their households, but they lose much of it to scrounging. Thus, while the game results are most indicative of tolerated scrounging, Marlowe suggests that costly signaling, reciprocity, *and* tolerated scrounging all play a role in explaining food sharing among the Hadza (Marlowe, 2004).

Hiwi of Venezuela

To understand the ecology of food sharing among the Hiwi of Venezuela, Gurven et al. (2000) examine how the amount of food transferred from family A to family B is influenced by genetic kinship, distance between households, family size, and the amount of food transferred from family B to family A. Regarding the effects of kinship, the authors found that the strongest predictor of food consumption by an individual after a food acquisition event is whether the individual is a member of the acquirer’s nuclear family. Thus, the authors argue that kin selection may be important, but only for explaining *within*-family transactions. *Between* nuclear

families, there is an observable kin bias in food transfers; however, the overall effect of kinship on the proportion of food obtained from other families is small compared to other factors such as contingency, family size, and residential distance. That said, the authors have trouble divorcing kinship and residential distance because individuals did share food with close kin more frequently, but close kin also tended to live in closer proximity to one another. Thus, the authors suggest that a variable they call “proximity to acquirer” may be the important mechanism in this case, rather than genetic relatedness (Gurven et al., 2000).

Regarding tolerated theft, the authors found that residential distance and package size are important determinants of how much food a family receives, which would support some predictions of the tolerated theft hypothesis. However, they also observed a contingency effect that violates a key assumption of tolerated theft, which is that food is sacrificed when there is a difference in marginal value and resource holding potential between the possessor and potential recipients. Furthermore, only a small number of families received food after an acquisition event, out of the large number of potential recipient families. With tolerated theft, we would expect all or most potential recipients to receive some food. Lastly, the tolerated theft model predicts that share amounts should be equal; however, the authors found that portions of food shared between nuclear families were generally smaller than those kept within the nuclear family, suggesting unequal distribution (Gurven et al., 2000).

The authors argue that reciprocal altruism is the best model for understanding overall food sharing among the Hiwi. This is based on the evidence that amount of food received by a nuclear family is the strongest predictor of the amount of food that nuclear family will give to another nuclear family. Because food acquirers only share with a few partners per acquisition

event, the authors conclude that the Hiwi appear to be engaging in small reciprocal food sharing networks with other families (Gurven et al., 2000).

Lamalera of Indonesia

Among the Lamalera, primary and secondary share networks have been described (e.g., Alvard & Nolin, 2002). The primary share occurs shortly after hunts when meat is divided among “share-right holders.” Share-right holders include members of the boat-owning corporation, the craftsmen who built the boat and maintain the gear, and the crewmen who participated in the hunt (Alvard & Nolin, 2002; Nolin, 2010). During the primary share, meat distribution is determined by a complex system of norms, which factors in the anatomy of the prey species and the specific roles of the share-right holders (Alvard & Nolin, 2002). After a household receives its portion of meat from the primary share, the secondary shares occur. In contrast to the primary distribution (during which there is no “giver” and distribution is based on norms and defined property rights), the secondary distribution is unrestricted, and givers decide who receives food. Thus, to understand factors that motivate food sharing, it is useful to focus on these secondary shares (Nolin, 2010). While there are no official norms or formal reciprocal partnerships that determine secondary distribution, prior research shows that husbands, wives, and all other adults living in the household are consulted on sharing decisions (Nolin, 2008, 2010).

Nolin (2010) conducted interviews about food sharing patterns and used participants’ responses to create a social network of sharing between households. Although relying on self-reports of past sharing behavior could bias the data, this form of data collection provided a full census of village-wide sharing (so in this case, completion was prioritized over accuracy). According to the results, kinship, proximity, and reciprocity *all* had a positive effect on the

likelihood of between-household sharing during the secondary distribution of food. However, reciprocity had the *greatest* effect, and it explained more of the variation in sharing than either proximity or kinship. Therefore, it appears that reciprocal altruism is the best model for explaining Lamalera food sharing patterns (for secondary shares), but that proximity and kinship can influence reciprocity, resulting in a tendency to reciprocally share with closer kin (Nolin, 2010).

Ye'kwana of Toki

Hames & McCabe (2007) examined patterns of food sharing among residents of the Ye'kwana village of Toki to test the predictions of reciprocal altruism, kin selection, tolerated scrounging, and “egalitarian exchange” (which makes similar predictions to tolerated scrounging). The authors found a correlation between proportion shared and proportion received between household dyads, which supports the hypothesis of reciprocal altruism. Propinquity (i.e., proximity) was initially significantly correlated with sharing, but it became an insignificant factor for proportion received when controlling for proportion given. The authors found no support for kin selection or tolerated scrounging. Importantly, however, the authors did not examine *all* food sharing; they examined *meals* shared, which refers specifically to “food consumption acts according to whether one is a host or a guest in the household, as well as the movement of people between households in the context of food consumption.” It is unclear how this distinction might have affected their results.

1.4.1.2 Social Function of Food Sharing in Societies in Which Resources Can Be Accumulated

Aside from its primary function of keeping us alive, food can be associated with comfort, pleasure, identity, family, and community. Throughout history and still to this day, food has been

used to assert one's social status and to impress others. Additionally, most rites of passage (i.e., ceremonies marking major life-events) in virtually all societies include a ritualized or ceremonial distribution and consumption of food. It is therefore apparent that the sociocultural, political, and economic aspects of food sharing are just as important as biological ones (Fieldhouse, 1995).

Food sharing is certainly not limited to foraging societies. In fact, in societies in which wealth can be accumulated, food sharing often becomes more elaborate and more performative. In some societies, the use of food as a way to establish social status has resulted in "competitive food giving" (Fieldhouse, 1995). For instance, among the Massim of New Guinea, giving food is a form of social control. Individuals who have been accused of a transgression are given more food than they can return. This draws attention to the transgression, makes the wrongdoer feel shamed, and restores honor to the victim (Fieldhouse, 1995; Young, 1971).

One of the best-known examples of "competitive food giving" is that of the *potlatch* – a ceremonial feast in which Indigenous peoples of the Pacific Northwest U.S. and Canada gave away material wealth (Boas, 1888; Fieldhouse, 1995; Mauss, 1960). Potlatches often marked major life-events such as birth, puberty, marriage, and death. They could serve a "face-saving" function, in which an individual who had violated a social rule and/or had suffered embarrassment or misfortune could redeem themselves and maintain their social status. Potlatches were always public ceremonies comprised of dancing, feasting, speech-making, and gift-giving. Gifts of food, money, property, and eventually, manufactured goods obtained through trading with White settlers were distributed to guests according to rank. Those in attendance typically felt obligated to return the wealth – plus interest – by holding their own potlatches when feasible (Fieldhouse, 1995).

Even though it could take years to accumulate enough wealth to host a potlatch, gifts were often destroyed to add to the performance and to gain status. For this reason, outsiders (e.g., White settlers) who did not understand the ceremonial functions of potlatches viewed them as wasteful and impoverishing. Consequently, the Canadian government created a law in 1884 (“*An Act further to amend “The Indian Act, 1880”, SC 1884, c 27, s 3*”) that threatened to imprison anyone directly or indirectly involved with potlatches. The law was abolished in 1951, but by that point Indigenous cultures had changed so much that potlatches never regained their original prominence (Fieldhouse, 1995).

Gifts and counter-gifts of food remain socially significant in contemporary western societies – for instance, the tradition of dinner parties among upper and middle-class families. According to Gudeman (2001), host families seek to impress others with their hospitality and elaborate meals. In these instances, prestige can be associated with the food items themselves, the methods of preparation, or the manner in which they are served. It is often a *faux pas* to show up without some sort of counter-gift (e.g., a dessert or a bottle of wine), and guests typically feel obligated to reciprocate by hosting their own dinner party in return (Fieldhouse, 1995; Gudeman, 2001).

In sum, food sharing can be a valuable tool or a powerful weapon depending on the social context. It can be used to demonstrate wealth and prestige, to reinforce political relationships or family bonds, or to convey friendship or mutual respect. However, it can also be used to shame those who have committed offenses or to create debts that must be settled through future favors. While these findings come from observations of food sharing in human societies, we will see that food sharing among chimpanzees is also driven by important social and political factors.

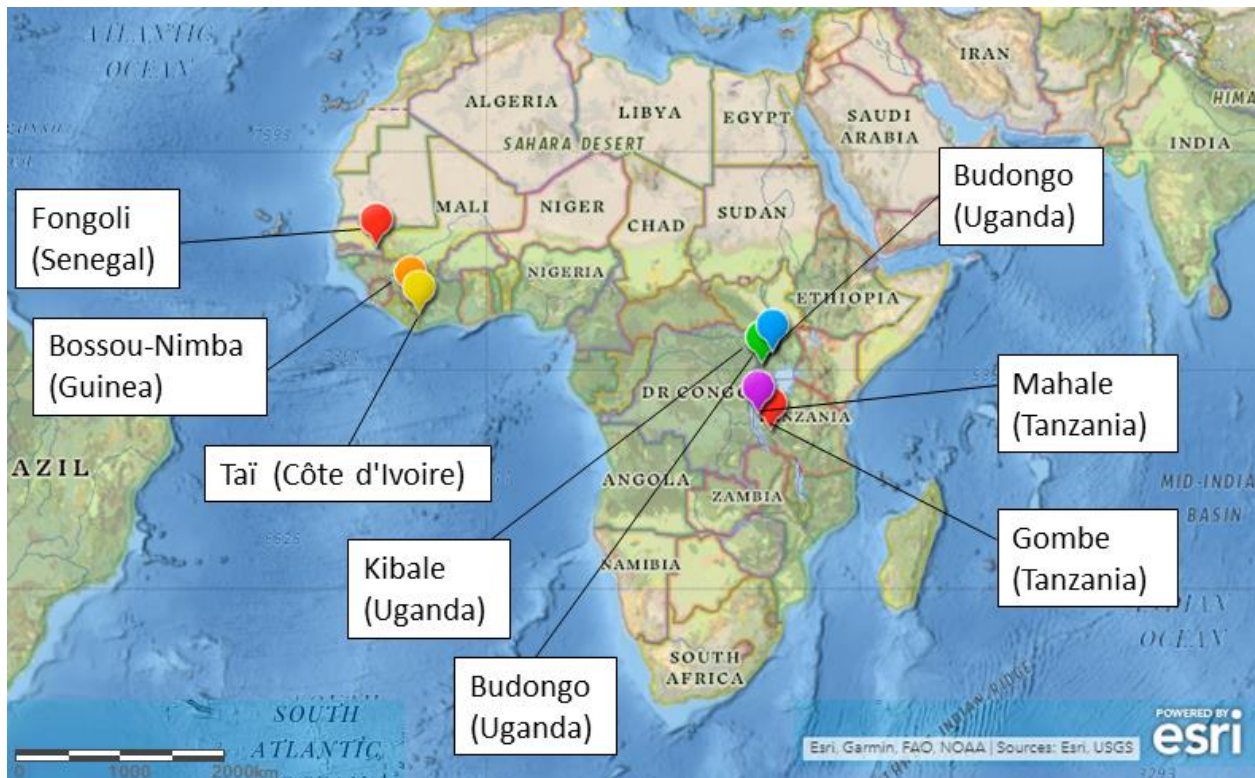
1.4.2 Food Sharing Among Chimpanzees

Decades of research on chimpanzee feeding ecology indicate that meat only constitutes a small fraction of the chimpanzee diet (e.g., Pruett, 2006). However, it plays a crucial role among many populations. First, hunting at many sites involves varying degrees of cooperation. Then, after the prey is captured, meat is often distributed among group members. This distribution may appear to be chaotic to a human observer. However, it is typically a strategic process in which dominance displays, tolerated theft, and even the bartering of meat for sexual access can all reflect complex social interactions (Stanford, 1999). Thus, while chimpanzee meat consumption is interesting from a nutritional aspect, the underlying social factors of hunting and sharing are even more intriguing from an anthropological viewpoint regarding the evolution of cooperation and sharing in an evolutionary context.

Approximately 150,000 to 300,000 chimpanzees exist in the wild, mostly in unprotected forested or partially forested habitats across equatorial Africa, from the western-most chimpanzees in Senegal to the eastern-most chimpanzees in Uganda and Tanzania. Though once continuously distributed throughout this range, today's chimpanzee distribution is more fragmented due to recent population declines and local extinctions (Clark Arcadi, 2018). In *Wild Chimpanzees: Social Behavior of an Endangered Species*, Clark Arcadi (2018) describes the seven oldest chimpanzee study sites that operate year-round to continuously collect behavioral, ecological, and demographic data (Clark Arcadi, 2018). After decades of research from these sites, primatologists have enough data to produce chimpanzee ethnologies. This is extremely valuable since ethnological research allows us to test hypotheses regarding tool manufacture and use, feeding ecology, social structure, learning, and other aspects of chimpanzee behavioral ecology, across their geographic range.

In the following subsections, I will summarize key findings on food sharing from these seven sites (Clark Arcadi, 2018) to provide an overview of what we know so far. This background will help contextualize this dissertation, since I examine patterns of food sharing in a different chimpanzee community: the savanna-dwelling chimpanzees of the Fongoli site in southeastern Senegal.

Figure 2. Map of seven long-term chimpanzee field sites described by Clark Arcadi (2018), plus the Fongoli site



1.4.2.1 Gombe Stream Research Center (Gombe National Park, Tanzania)

Gilby (2006) tested whether patterns of food sharing among Gombe chimpanzees (*P.t. schweinfurthii*) could be explained by sharing-under-pressure or reciprocal exchange. However, unlike other models of reciprocal exchange, Gilby’s is not limited to “meat-for-meat” exchanges; it also includes “meat-for-sex” and “meat-for-allies” exchanges. His “meat-for-sex” hypothesis (referred to elsewhere as the “food-for-sex” hypothesis) predicts that food possessors will be

more likely to share with sexually receptive females and that there will be a correlation between food sharing and mating opportunities. The “meat-for-allies” hypothesis predicts that males use food sharing as a social tool to establish and maintain bonds with other males (Gilby, 2006).

According to his results, the sharing-under-pressure hypothesis was consistently supported – the probability of sharing increased with the occurrence and duration of harassment, and harassment decreased once food had been shared. On the other hand, the reciprocal exchange hypothesis received mixed support – among males, grooming rate did not influence food sharing. Between males and females, female sexual receptivity did not affect the probability of sharing, nor did food sharing increase the probability of mating. Meat possessors were more likely to share with frequent female grooming partners, and those shares tended to be larger amounts of food. However, this pattern might have been prompted by increased harassment from those individuals. Thus, Gilby (2006) concludes that meat sharing among the Gombe chimpanzees is largely explained by the sharing-under-pressure hypothesis, while the role of reciprocal exchange remains unclear.

1.4.2.2 Mahale Mountains Chimpanzee Research Project (Mahale Mountains National Park, Tanzania)

Nishida et al. (1992) analyzed patterns of food sharing by the alpha male chimpanzee (*P.t. schweinfurthii*) at Mahale over the course of a decade. The alpha in this study tended to share with his presumed mother, with old, infertile females, with “non-threatening, middle-ranking” males, and with “old but influential” males. However, he avoided sharing with young adult males who were rising in the hierarchies, and he also avoided sharing with beta males. Additionally, there was a significant positive correlation between grooming exchanged between the alpha male and other males, and the frequency with which he shared food with them. The

authors conclude that the alpha male's sharing patterns reflect a food-for-grooming reciprocal exchange system, and that the alpha male likely shared meat as a way to develop and maintain alliances with other males. Interestingly, they write that at Mahale, reciprocal exchange through the same "currency" rarely occurs because the alpha male controls access to all carcasses (Nishida et al., 1992).

1.4.2.3 Bossou-Nimba Chimpanzee Research Project (Republic of Guinea)

According to Hockings et al. (2007), meat sharing is rarely observed among chimpanzee (*P.t. verus*) at Bossou given the scarcity of mammalian prey. However, they analyzed data from 59 observations of plant-food sharing and reported that males shared with one maximally swollen female in 16% of those events. Interestingly, male sharers were never observed to mate with the female immediately after sharing, but by incorporating long-term reproductive data from the site, the authors found that the adult male who shared with this female the most also engaged in more consortships with her, and he received more grooming from her than the other males did (including the alpha male). Though this paper focused on the sharing of plant food items among Bossou chimpanzees, the authors briefly mention that an adult female chimpanzee caught and shared a tree pangolin during the study period (Hockings et al., 2007).

1.4.2.4 Tai Chimpanzee Project (Tai National Park, Ivory Coast)

The meat-for-sex (AKA "food-for-sex") model assumes that food sharing reflects an exchange benefitting both parties – males increase their mating success and females increase their caloric intake. In theory, this mutually advantageous trade sounds like a good explanation for why individuals share food. However, in wild chimpanzees, most studies that have directly tested this hypothesis report null results (e.g., Ngogo chimpanzees [Mitani & Watts, 2001], Gombe chimpanzees [Gilby, 2006]). According to Gomes & Boesch (2009), previous tests of the

food-for-sex hypothesis have been limited in that they focused on *short-term* exchanges of meat for sex. By extending their study period to 22 months, Gomes & Boesch (2009) found that female chimpanzees (*P.t. verus*) at Tai copulated more frequently with males who shared food with them. Importantly, they ruled out alternative explanations by controlling for male age and rank, female age and rank, female begging frequency, and other factors. They therefore concluded that food sharing in Tai chimpanzees may confer future benefits (i.e., increased copulations over the course of months/years) rather than short-term benefits (i.e., increased copulations immediately).

Samuni et al. (2018) tested the predictions of sharing-under-pressure, reciprocal altruism, and costly signaling in two wild chimpanzee groups at Tai National Park. However, it is worth noting that their version of reciprocal altruism treats previous grooming episodes as the currency (rather than previous food shares), and their version of the costly signaling hypothesis predicts that males are more likely to share with females in estrus (a prediction also made by the food-for-sex hypothesis). The authors found that begging pressure had a significant *negative* effect on sharing likelihood, which contradicts the sharing-under-pressure predictions. They also report that neither rank nor estrus status appeared to affect sharing. Instead, the data reveal that food possessors were more likely to share with group members who have been mutual long-term grooming partners, even when controlling for relatedness and the absence or presence of harassment. However, the metric “grooming received” did not affect sharing likelihood, suggesting that food was not traded for grooming on a *short-term* basis. Lastly, the authors found that urinary oxytocin levels were higher after food sharing and they conclude that the emotional connection of social bonds (which they associate with oxytocin levels) possibly facilitates the long-term cooperative exchanges they observed (Samuni et al., 2018).

1.4.2.5 Kibale Chimpanzee Project – Kanyawara Community (Kibale National Park, Uganda)

In order to test the food-for-sex hypothesis among the Kanyawara chimpanzee (*P.t. schweinfurthii*) community, Gilby et al. (2010) analyzed data from 126 successful hunts that occurred over the course of 17 years. According to the authors, the presence of sexually receptive females did not increase hunting probability, males did not preferentially share with sexually receptive females, and sharing with females did not increase a male's *short-term* mating success. They note that males may share meat with females as part of a *long-term* mating strategy, as observed at Tai (Gomes & Boesch, 2009). However, they raise some concerns with the food-for-sex hypothesis in general, including the assumption that females should be reluctant to mate unless males share meat. They argue that females in multi-male, multi-female social groups stand to benefit from mating promiscuously because it may confuse paternity, thereby discouraging infanticide (Hrdy, 1979), it may facilitate sperm competition (Clutton-Brock & Harvey, 1976), and it may increase chances of fertilization. Rather than exchanging meat for sex, the authors suggest that males may share with females for the same reason they share with males – to avoid the costs associated with defending meat from beggars (i.e., sharing-under-pressure hypothesis), as has been reported at other sites (Gilby, 2006). While I agree with their statement that mating with multiple males could be an adaptive reproductive strategy for females, I do not think it precludes the possibility that males sharing meat with females could also influence mating decisions.

1.4.2.6 Ngogo Chimpanzee Project – Ngogo Community (Kibale National Park, Uganda)

Mitani & Watts (2001) test various hypotheses that use ecological and social factors to explain hunting and meat sharing among chimpanzees (*P.t. schweinfurthii*) at Ngogo, Uganda.

Regarding the exchange of meat for sex, male chimpanzees shared meat with estrous females more often than with non-estrous females, which would initially appear to support the food-for-sex hypothesis. However, despite the tendency to share with estrous females more than with non-estrous females, the sharing of meat with estrous females was still infrequent. Perhaps more importantly, males did not appear to gain any form of mating advantage by sharing meat. Thus, the food-to-sex hypothesis does not seem to explain patterns of food sharing at Ngogo. Instead, the authors discuss another way meat sharing may be used to develop and maintain social ties among group members. Rather than sharing with females to increase mating opportunities, the authors suggest that adult males may share with other adult males to increase their chances of receiving food or coalitionary support from those males in return. This is based on a significant association between the number of times males shared meat with one another and the number of times those males received/offered coalitionary support. Additionally, males were more likely to share meat with males who have previously shared with them, suggesting that reciprocity is important. Based on their observations, they conclude that the best explanation for food sharing at Ngogo (during this study period) is that meat sharing facilitates social exchanges (i.e., meat and coalitionary aid) between males (Mitani & Watts, 2001).

1.4.2.7 Budongo Conservation Field Station (Budongo Forest, Uganda)

One study involving the Budongo chimpanzees (*P.t. schweinfurthii*) reports that food-sharing events are associated with significantly higher urinary oxytocin levels than non-sharing social feeding events. According to the authors, this is evidence that food sharing is a key behavior for social bonding in chimpanzees (Wittig et al., 2014).

1.4.2.8 Highlights from Captive Studies

Jaeggi et al. (2013) tested for short-term contingencies of grooming on food sharing and vice versa among one group of captive chimpanzees and two groups of bonobos. They found significant effects of grooming on food sharing and vice versa in the chimpanzee group, but the effects disappeared when controlling for factors like kinship and rank differences. Instead, they recall a previous study (Jaeggi et al., 2010) which seemed to indicate *long-term* contingency of food, grooming, and coalitional support. They (Jaeggi et al., 2013) suggest that the findings are consistent with a “partner choice model” in which the likelihood of providing a service (food sharing, grooming, support, etc.) depends on the history of past interactions throughout the course of a relationship, rather than one or a few recent events (Jaeggi et al., 2010, 2013). According to Jaeggi et al. (2013) this could be why studies examining short-term contingencies in primates yield mixed results, while exchanges tend to become more balanced over time.

Silk et al. (2013) examined the effects of kinship, relationship quality, reciprocity, and begging intensity on patterns of food shares in six captive groups of chimpanzees (Michael E. Keeling Center for Comparative Medicine and Research, Bastrop, TX, USA). The chimpanzees in this study shared frozen fruit disks that were provisioned to them. According to the authors, the disks are like prey carcasses in that they are a valued, limited resource, they take a long time to consume, and individuals have the option to monopolize the food item or break off bits to share with others. Interestingly, all of the hypotheses in this study received some support, leading the authors to suggest that kinship, relationship quality, reciprocity, and the avoidance of conflict all motivate chimpanzees to share food. They conclude that food sharing likely serves multiple functions in chimpanzees: enhancing the welfare of closely related group members, strengthening social relationships with favored partners, and reducing the costs of persistent begging (Silk et al., 2013).

1.5 Research Objectives

In summary, food sharing is hypothesized to have played a crucial role in the evolution of human cooperation (Kaplan et al., 2009; Samuni et al., 2018). Throughout our evolutionary history, and among extant foraging societies, food sharing helps to support periods of infant, child, and adolescent development, and to supplement daily food shortages throughout adulthood, such as those resulting from day-to-day variance in hunting success (Jaeggi & Gurven, 2018; Kaplan & Hill, 1985). Because it impacts life history patterns, economic life, and social life, food sharing is an important topic to explore anthropologically (Jaeggi & Gurven, 2018; Kaplan & Gurven, 2001).

To understand the evolution of food sharing, anthropologists have turned to extant foraging populations, based on the knowledge that foraging is the ancestral subsistence mode of humans, and that we were hunter-gatherers for 90% of our history as a species (Ember, 2020). However, a number of these studies highlight methodological difficulties including the institution of marriage and other cultural factors convoluting the study of food sharing (e.g., discrepancy over whether to treat between-household shares or within-household shares as the unit of analysis). Furthermore, due to globalization and capitalism, we see an increased reliance on store-bought foods among populations that once subsisted entirely on hunted or gathered foods items. Thus, if the goal is to understand patterns of food sharing among our early hominin ancestors/relatives – which is valuable since food sharing has played a crucial role throughout our evolutionary history – nonhuman primates may be a useful referential model (Kaplan et al., 2009).

Through referential models based on homology and analogy (Moore, 1996), chimpanzees are often used to form hypotheses about human social organization since they are our closest

living relatives, they participate in a wide range of collective activities, and they are the only nonhuman primates that regularly share hunted meat with other adult group members in the wild (Jaeggi & Van Schaik, 2011; Silk et al., 2013). **I will approach the topic of food sharing by examining the function of meat transfers within a population of savanna-dwelling chimpanzees (*Pan troglodytes verus*) at Fongoli, Sénégal.** This community is an intriguing study group for a number of reasons, which will be discussed in the following chapter (Chapter 2: Methods).

CHAPTER II

METHODS

2.1 Study Site and Study Subjects

The Fongoli chimpanzee community is a population of western chimpanzees (*Pan troglodytes verus*) that resides in the Kedougou region in southeastern Sénégal (12°40 N, 12°13 W). The Sudano-Guinean vegetation at Fongoli is described as a woodland-savanna mosaic habitat. Grassland and woodland (including bamboo woodland) habitats account for more than 90% of the chimpanzees' ~90 km² home range. Because grasses can grow to be over 2 meters in height, visibility is often poor during the late rainy season and early dry season. Closed habitats (gallery forest and ecotone forest) account for less than 5% of the home range. Anthropogenic features, such as villages, artisanal gold mines, dirt roads, and crop fields constitute approximately 5% of the home range (Pruetz & Herzog 2017). The dry season lasts more than seven 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 the chimpanzees do not typically consume these crops (Pruetz & Lindshield, 2012). Since 2005, there has only been one report of a Fongoli chimpanzee being hunted by humans (Fongoli Savanna Chim Project, unpublished data).

At the Fongoli site, relatedness among individuals is currently based on matrilineal data only. As with chimpanzee females elsewhere, those at Fongoli typically disperse at sexual maturity; however, approximately 30% of females here have stayed in their natal troop 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.

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). Between 2005 and 2019, the Fongoli community varied with 29 to 36 individuals per year. The number of adult males in the group varied from 10 to 12 per year (n=19 in total), and the number of adult females varied from 7 to 8 per year (n=13 total) (FSCP, unpublished data).

The chimpanzees at Fongoli are an intriguing study community for a number of reasons, three of which are particularly relevant to this study. First, while most studies of chimpanzees have focused on forest-dwelling groups, the Fongoli chimpanzees inhabit a savanna mosaic landscape, which makes them a particularly useful analogous model for human evolution given that many of the earliest hominins dealt with similar environmental pressures (Moore, 1996; Potts, 1998; Pruettz & Bertolani, 2009; Pruettz et al., 2015). Second, Fongoli chimpanzees are the only known nonhuman population that regularly hunts vertebrate prey with tools. Observations of tool-assisted hunting among Fongoli chimpanzees can be placed in a referential model to inform hypotheses about the evolution of hunting behaviors in hominins (Pruettz et al., 2015) (see Figure 2 below). Third, females at Fongoli hunt more frequently than females at other sites. Out of 308 hunts by Fongoli chimpanzees between 2005 and 2014, females were responsible for 30% of all hunts, and 59.5% of hunts involving tools (Pruettz et al., 2015). This is fascinating given that there are more males than females in the group – at Fongoli, the adult male:female ratio ranged from 1.4 to 1.7 during this study period, which is the opposite of what we see at most

chimpanzee sites (Pruetz et al., 2017). The observation that females hunt more frequently at Fongoli could be influenced by the fact that at most sites where chimpanzees hunt vertebrates, dominant males tend to monopolize prey carcasses. Reports suggest that more dominant individuals take ~25% of prey captured by lower-ranking individuals (Pickering, 2013). 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. However, at Fongoli, dominant males took prey from lower-ranking individuals less than 5% of the time (Pruetz et al., 2015). Increased hunting by females creates additional opportunities for meat sharing by females, which has not been explored in depth in chimpanzees.

Figure 3. Tool-assisted hunting by a Fongoli chimpanzee. Male chimpanzee uses a tree branch with a modified end to stab into a hollow tree branch that houses a galago (images courtesy of BBC). Figure reprinted with permission from Pruetz et al. 2015, Figure 1, Royal Society Open Science. *²



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2.2 Hypotheses and Predictions

The goal of this dissertation is to **examine the function of meat sharing within the Fongoli chimpanzee community**. Specifically, I test four major hypotheses that have been put forth to explain resource sharing among chimpanzees: kin selection, generalized reciprocity, sharing-under-pressure, and food-for-sex. These hypotheses differ in what they consider to be the benefits of sharing; however, they are not mutually exclusive, and it is possible that transfers serve different purposes in different contexts (Silk et al., 2013). For this reason, I test the predictions of each hypothesis independently (Chapters 3-6), and then also test the predictions of multiple hypotheses simultaneously (Chapter 7), to see which variable(s) are the strongest predictors of food sharing. For more background information on each of the four hypotheses, see Chapter 1.

Table 2 (below) presents an overview of my research methods including the key predictions of each major food sharing hypothesis, the testable predictions of those hypotheses, the variables used to test those predictions, and the appropriate statistical analyses.

Table 2. Study Hypotheses & Predictions

<i>Hypothesis</i>	<i>Predictions</i>	<i>Variables</i>	<i>Statistical Analyses</i>
Kin selection	1. Possessors share with kin > non-kin 2. Possessors share with close kin > distant kin	<ul style="list-style-type: none"> • Matrilineal kinship (i.e., biological relatedness of all individuals through the maternal line) • Number of successful begs/shares and unsuccessful begs 	<ul style="list-style-type: none"> • Generalized linear mixed model (binary logistic)
Reciprocity	3. Possessors share with individuals who have previously shared with them > individuals who have not	<ul style="list-style-type: none"> • Number of successful begs/shares and unsuccessful begs 	<ul style="list-style-type: none"> • Generalized linear mixed model (binary logistic) • Pearson correlation

“Sharing-under-pressure” hypothesis	4. Shares preceded by begs > shares not preceded by begs 5. Low-to-high ranking shares > high-to-low ranking shares 6. Shares from larger prey > shares from smaller prey 7. “Passive” shares (share types T2-T3) > “active” shares (T4-T6) or pure theft (T1)	<ul style="list-style-type: none"> • Age-sex classes and social ranks of all individuals • Number of successful begs/shares and unsuccessful begs • Type of prey item shared (to estimate weight in kg) • Sharing type (T1-T6) 	<ul style="list-style-type: none"> • Chi-square
Food-for-sex	7. Male possessors share with females > males 8. Male possessors share with estrous females > anestrus females 9. Males who share with females more frequently also copulate with those females more frequently	<ul style="list-style-type: none"> • Age-sex classes and social ranks of all individuals • Number of successful begs/shares and unsuccessful begs • Number of copulations between two individuals • Female estrous score at time of share 	<ul style="list-style-type: none"> • Chi-square • Generalized linear mixed model (binary logistic) • Spearman & Pearson correlation

To test these hypotheses and predictions, I analyzed data collected by Fongoli Savanna Chimpanzee Project (FSCP) personnel (Pruetz and colleagues) between 2006 and 2019. These data included records of meat sharing, estrous swellings, copulations, prey size, social rank, age-sex class, and matrilineal kinship in order to determine which variables predict likelihood of food sharing.

2.3 Data Collection

The data for this study were collected by FSCP personnel (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 (Pruetz et al., 2015). Adult males (n=10-12 per year, 19 total) were the object of focal samples twice per month during all-day

(night nest to night nest, or approximately 10-13 hours per day) follows, 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. Data collected at Fongoli follow the ethogram of Nishida et al. (1999) regarding basic activity and detailed social behaviors.

2.3.1 Estrous Classifications and Copulations

Female reproductive state may elicit or affect food sharing behavior in Fongoli chimpanzees (Pruetz & Lindshield, 2012). For this reason, adult and adolescent females were scored daily using a standard four-point scale (0-3) to describe the degree of tumescence in the anogenital region (with 0 indicating a fully detumescent female and 3 indicating a fully tumescent female). Copulations included in this study were recorded *ad libitum* from January 2006 through June 2017 while focal sampling the adult males at five-minute intervals.

2.3.2 Meat Sharing

Data on hunting, meat eating, and meat sharing (and lack of sharing in meat-eating events) for this study were collected opportunistically between January 2006 and June 2017. For all observed sharing events, the following were recorded: 1) identity of sharer, 2) identity of recipient, 3) sharing order (e.g., primary, secondary, 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, pg. 551), and modified by Pruetz and Lindshield (2012) (Table 3).

Table 3. Sharing Type (as per Boesch & Boesch 1989:551, modified by Pruetz & Lindshield 2012)

<i>Sharing Type (Transfer Score)</i>	<i>Description of Transfer</i>
<i>Theft (T1)</i>	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.

<i>Recovery (T2)</i>	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 & 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.
<i>Passive transfer (T3)</i>	The receiver takes an item held by the owner, and the owner passively tolerates the receiver's behavior.
<i>Active-passive transfer (T4)</i>	Similar to T3 except the owner moves to facilitate the exchange.
<i>Active Transfer (T5)</i>	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.
<i>Giving (T6)</i>	The owner allotted the majority of an item to the recipient.

2.4 Data Analysis

Between 2005-2017, there were 484 observations of either “successful” begs (i.e., events in which meat was actually transferred) *or* of “unsuccessful” begs (i.e., those that did not result in meat being transferred). Of these 484 observations, 18 transfers were scored as type T1 (theft), meaning the recipient forcefully took meat from the possessor. These 18 instances of theft were omitted from kinship, reciprocity, and food-for-sex analyses, since the goal was to examine which variables affect the likelihood of meat being shared (not stolen). With these data, I tested the predictions of each food sharing hypothesis independently (presented in Chapters 3-6). Then, I tested the predictions of multiple hypotheses simultaneously (presented in Chapter 7), since the four major hypotheses are not mutually exclusive.

Because the approach (i.e., the sample included in the analyses and the statistical analysis used) varies depending on which hypothesis is being evaluated, the methods for each model will be discussed in more detail in the respective chapters (i.e., Chapter 3: Kin Selection, Chapter 4:

Generalized Reciprocity, Chapter 5: Sharing-Under-Pressure, Chapter 6: Food-for-Sex, and Chapter 7: Multiple Hypotheses Simultaneously). The explanatory and outcome variables (i.e., independent and dependent variables) used in this study are described in the following tables (Tables 4 and 5).

Table 4. Explanatory variables in this study

Variable	Type	Description	Possible values
Age-sex class of share	Categorical	The relationship between the food possessor's age/sex and the beggar/recipient's age/sex Because there were very few shares involving infants, juveniles, and adolescents, these three age categories were combined into one category of "subadult"	1=adult male to adult female 2=adult male to adult male 3=adult male to subadult female 4=adult male to subadult male 5=adult female to adult female 6=adult female to adult male 7=adult female to subadult female 8=adult female to subadult male
Estrous score	Categorical	Describes the degree of tumescence in the anogenital region of adolescent and adult females	0=fully detumescent female (min. swelling) 1=some swelling 2=partial swelling 3=fully tumescent female (max swelling)
Kin01	Categorical (dichotomous)	The relatedness of two individuals, based on matrilineal kinship	0=not related 1=related
Kin category	Categorical	The relatedness of two individuals, based on matrilineal kinship	0=not related 1=more distantly related 2=more closely related
Previous shares B-A 01	Categorical (dichotomous)	Describes whether an individual B has shared with individual A at least once prior to the current event from A to B	0=B has not previously shared with A 1=B has previously shared with A at least once

Previous shares B-A (total)	Discrete	The total number of times an individual B has shared with individual A prior to the current event from A to B	Integers ≥ 0
Prey size category	Categorical	The estimated weight of prey items captured, prior to any sharing	1= prey < 2 kg 2= prey 2-4.5 kg 3= prey > 4.5 kg
Rank direction	Categorical	The relationship between the food possessor's rank and the beggar/recipient's rank	0=lower ranking possessor, higher ranking beggar/recipient 1= higher ranking possessor, lower ranking beggar/recipient
Share order	Categorical	Order in which share occurred. A primary share means the captor themselves shared, and so on	1= primary 2=secondary 3=tertiary 4=quaternary 5=quinary
Transfer score ("share type")	Categorical	The nature in which food was transferred from possessor to recipient, with increasing levels of intentionality; originally described by Boesch & Boesch (1989), and modified by Pruett & Lindshield (2012)	1=theft 2=recovery 3=passive sharing 4=active-passive sharing 5=active sharing 6=gift

Table 5. Outcome variables in this study

Variable	Type	Description	Possible values
Share success 01	Categorical (dichotomous)	Whether or not meat was shared during the event	0=meat was not shared 1=meat was shared
Successful shares (total)	Discrete	The total number of times that food was actually shared	Integers ≥ 0

CHAPTER III

KIN SELECTION

3.1 Background

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 food sharing, it is predicted that:

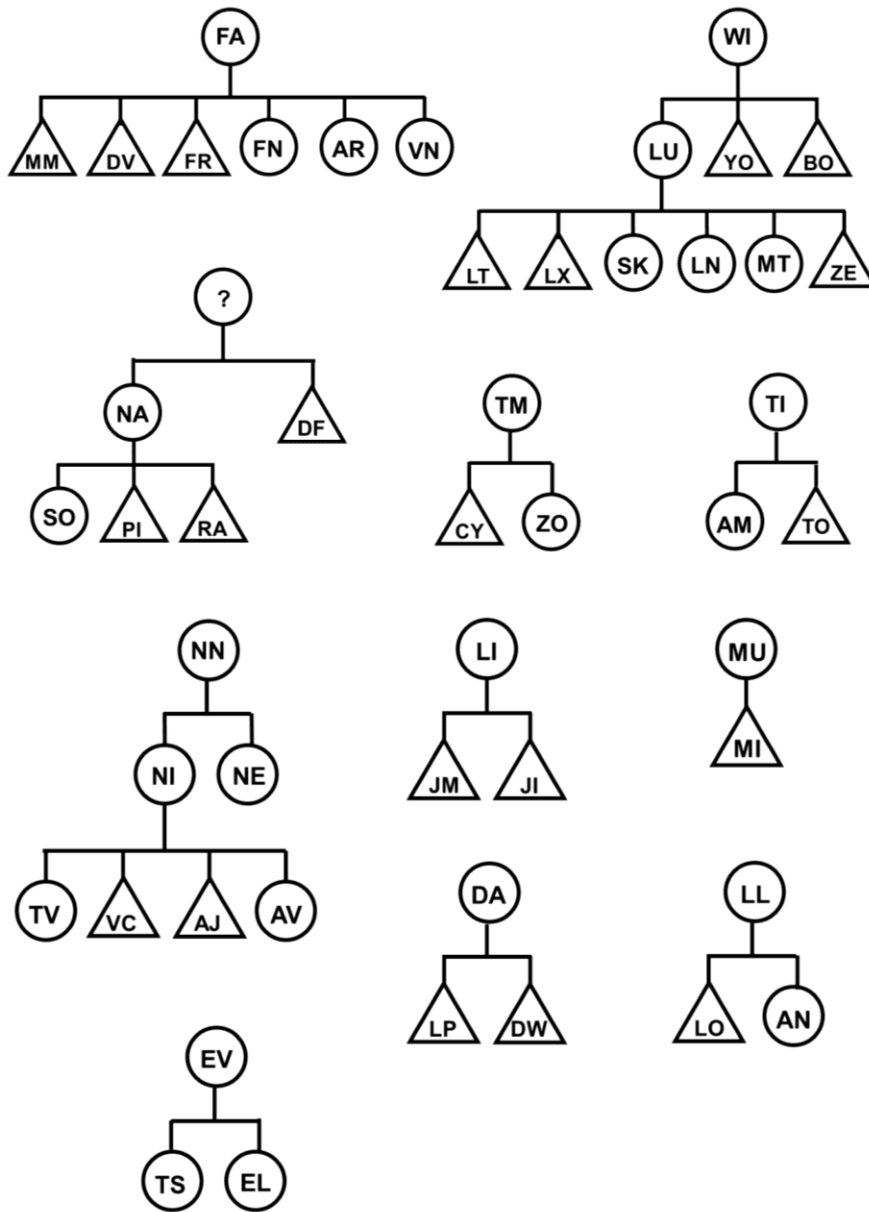
P₁: Food possessors are more likely to share with related individuals than with unrelated individuals.

P₂: Food possessors are more likely to share with closer kin (with whom they share a greater proportion of their genes) than with more distant kin.

For more information on kin selection and its key predictions, see Chapter 1: Introduction and Background.

At the Fongoli site, relatedness is currently based on matrilineal data only (Figure 3). As with chimpanzee females elsewhere, those at Fongoli typically disperse at sexual maturity; however, approximately 30% of females here have stayed in their natal troop into adulthood (FSCP, unpublished data). 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.

Figure 4. Fongoli Chimpanzee Matrilineal Kinship Diagram



3.2 Methods

3.2.1 Categorizing Kin

Because we do not have data on paternity at this time, kinship was assigned based on matrilineal ties. In Excel, I created a column containing all possible dyad combinations. I also created a table of all known mothers and their offspring. Mother-offspring dyads were assigned to the category of “close kin,” because they have a coefficient of relatedness of 0.5, meaning

they share 50% of their genetic material with one another. For the remaining dyads, I indexed the mothers of both individuals. If the individuals had the same mother, they were marked as siblings. If the two individuals had different mothers, they were marked as not 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. Full siblings (i.e., ones that share a mother *and* a father) and half-siblings (i.e., ones that share either a mother *or* a father) have different coefficients of relatedness – the coefficient of relatedness for full siblings is 0.5, whereas the coefficient of relatedness for half siblings is only 0.25, since they are only inheriting shared genetic material from one parent instead of both. Despite this distinction, I did not differentiate between full and half siblings in this study because without knowing fathers, we do not know whether individuals share both parents or just mothers. Sibling dyads (i.e., individuals who share a mother) were also placed in the category of “close kin,” along with mother-offspring dyads. This is not a perfect method since two individuals who have different mothers but the same father would have the same coefficient of relatedness as two individuals who have the same mother but different fathers, but this is the best way to categorize kinship when we only have matrilineal data available.

Grandparent-grandchild dyads and aunt/uncle-niece/nephew dyads were categorized as “distant kin,” since they are two degrees removed from one another. It is worth noting that grandparent-grandchild dyads, aunt/uncle-niece/nephew dyads, and half sibling dyads all have a coefficient of relatedness of 0.25. However, as previously noted, it is not possible to reliably differentiate between full and half siblings. Thus, in this study, all “siblings” are considered “close kin,” while the grandparent-grandchild dyads and aunt/uncle-niece/nephew dyads are considered “distant kin”.

The approach used in this study is similar to that of Silk et al. (2013), in which the authors note, “Paternal relatedness was not known for all dyads and is not included in the analyses. For the purposes of these analyses, we assumed that siblings were related by 0.25 and that the single uncle-niece dyad was related by 0.125” (Silk et al., 2013, p. 942). The main difference between that study and the present one is that I decided not to assign coefficients of relatedness, since they might not be entirely accurate.

Table 6. How to categorize kin relationships if matrilineal and patrilineal data were available

Type of relationship	Coefficient of relatedness (<i>r</i>)
Mother-Offspring	$1/2^1 = 0.5$
Full siblings (share mom and dad)	$1/2^1 = 0.5$
Half siblings (share either mom <i>or</i> dad)	$1/2^2 = 0.25$
Aunt/Uncle-Niece/Nephew	$1/2^2 = 0.25$
Grandparent-Grandchild	$1/2^2 = 0.25$
Cousins	$1/2^3 = 0.125$
Unrelated	0

Table 7. How I have categorized kin relationships for this study based on matrilineal kinship only

Type of relationship	Kinship category
Mother-Offspring	2 (closer relatives)
Siblings (could be full sibs could be half sibs; unsure without paternity data)	2 (closer relatives)
Aunt/Uncle-Niece/Nephew	1 (more distant relatives)
Grandparent-Grandchild	1 (more distant relatives)
Unrelated	0=unrelated
Unknown	-1=unknown relatedness (excluded from kinship analyses)

3.2.2 Statistical Analyses

Between 2005-2017, there were 484 observations of either “successful” begs (i.e., events in which food was actually transferred) *or* of “unsuccessful” begs (i.e., those that did not result in sharing). The 18 instances of theft were excluded from analyses, leaving 466 observations. Of these 466 observations, **158** occurred between dyads of known relatedness, meaning we knew with certainty whether or not the two individuals were related. The predictions of kin selection were tested using these observations.

3.2.2.1 P1: Food possessors are more likely to share with related individuals

To test the first prediction of kin selection, that individuals are more likely to share with related individuals, I performed two statistical tests in SPSS. The first analysis was a generalized linear mixed model (GLMM) with a binary logistic output. For this model, share success (i.e., was food shared? 1=yes, 0=no) was the response variable, kinship (1=related, 0=unrelated) was a fixed effect, and Dyad ID was a random effect to control for the fact that some dyads are represented in the sample more than others. This analysis examines how relatedness affects the likelihood of a food possessor sharing with a recipient.

The second analysis was a Mann-Whitney U test in which the independent variable was still relatedness (1=related, 0=unrelated), but the dependent variable was shares as an ordinal variable (i.e., total number of shares between those individuals). While the GLMM examined whether relatedness affects the likelihood of meat being shared, the Mann-Whitney U test examines whether related dyads share at higher rates than unrelated dyads. For both of these tests, the sample included 158 observations between dyads of known relatedness.

3.2.2.2 P2: Food possessors are more likely to share with close kin than with distant kin or non-kin

To test the second prediction of kin selection, that individuals are more likely to share with close kin, I planned to perform statistical analyses using three kin categories (2=close kin, 1=distant kin, 0=non-kin) rather than just the two categories (1=related or 0=unrelated). However, the sample size for begs/shares between distant kin is too small to draw meaningful conclusions about sharing patterns between these three categories. Out of the 466 observations of successful and unsuccessful begs, there were only two observations of begging between individuals known to be distantly related. Neither of these begs were successful (i.e., neither resulted in food being transferred), which confounds the analyses. The second prediction therefore remains untested in this study.

3.3 Results

3.3.1 P₁: Food possessors are more likely to share with related individuals

The GLMM indicates that kinship is a significant predictor of sharing success, in which food possessors are more likely to share with a related group member than an unrelated group member ($F=5.434$, $S.E.=0.354$, $Wald=5.327$, $df=1$, $p=0.021$, $Exp(B)=2.264$, $n=158$). The Mann-Whitney U test shows that among dyads that shared food, related individuals shared at a higher rate than unrelated individuals ($U=3508$, $z=2.18$, $p=0.029$, $effect\ size=0.17$, $n=158$).

3.3.2 P₂: Food possessors are more likely to share with close kin

Not addressed (see section 3.2.2.2).

3.4 Summary

The results from this study support the main prediction of kin selection. There is a statistically significant association between kinship and sharing in which related individuals are more likely to share than unrelated individuals. There are two caveats with these results: First, all analyses from this study are based on matrilineal kinship only, since we do not know paternity.

The implications of this are discussed earlier in this chapter (3.2.1 Categorizing Kin). Second, in this study, there were very few observations of begging/sharing between “distant kin.” The vast majority of begs/shares occurred between “close kin” (i.e., mother-offspring dyads, sibling dyads), between unrelated individuals, or between individuals of unknown relatedness (who were excluded from kinship analyses). Thus, we could not test the prediction that close kin share at higher rates than distant kin. Despite the limitations noted here, the results clearly indicate that kinship influences patterns of sharing. These results are discussed more extensively in Chapter 8: Discussion and Conclusion.

CHAPTER IV
GENERALIZED RECIPROCITY

4.1 Background

Reciprocal altruism refers to the idea that individuals “trade” altruistic acts, so that ultimately, both individuals will have higher fitness than if they had not acted altruistically (Trivers, 1971). A strict form of reciprocal altruism assumes that reciprocation occurs in the same “currency” (e.g., food-for-food) as the initial act, and that exchanges are balanced (i.e., the same amount/frequency that was initially given is later received) (Stevens & Gilby, 2004). In the context of food sharing, specifically, it has been suggested that transfers between individuals do not need to be perfectly balanced, as long as both individuals do slightly better than they would have if they had not shared (e.g., Gurven, 2004; Hill & Kaplan, 1993; Nolin, 2010). In this latter case, food sharing reflects a pattern of generalized reciprocity. Regardless of whether or not transfers are precisely balanced, any form of reciprocity (i.e., strict tit-for-tat reciprocity or generalized reciprocity) should be contingent on past and future shares from partners. Thus, we can evaluate reciprocity-based hypotheses by testing for a correlation between frequencies or amounts of food given and received within dyads (Nolin, 2010)

Generalized reciprocity predicts the following:

P₁: Food possessors are more likely to share with group members who have previously shared with them.

P₂: There will be a correlation between the total number of times food has been shared and received within dyads.

4.2 Methods

4.2.1 Shares Among All Group Members

In Excel, I created a formula to calculate the number of times an individual B has *previously* shared with individual A prior to that current begging/sharing event from A to B. For instance, if we want to test whether reciprocal sharing influences the success of a share from SI to BN that occurred on 01-FEB-13, the formula would report the number of times that BN shared with SI before 01-FEB-13.

I used two analyses to test the predictions of generalized reciprocity. First, I used a generalized linear mixed model (class: binary logistic) to assess whether previous shares from individual B to individual A would affect the likelihood of individual A sharing with individual B during the current event. In one GLMM, I examined previous reciprocal shares as a dichotomous variable (i.e., “Has individual B shared with individual A at least once prior to this sharing event from A to B?” 1=yes, 0=no), and in another, I examined the total number of previous shares from B to A before the current sharing event. For both of these GLMMs, the fixed effect was previous reciprocal shares (either 0/1 or the total number of previous shares), the random effect was Dyad ID (to control for the fact that this is not an independent sample, and some dyads are represented in the dataset more than others), and the outcome variable was share success (either 1=food was shared, or 0=food was not shared). For these models, the sample included **463** successful shares or unsuccessful begs (out of n=484), since I excluded the 18 observations of theft, and excluded three events for which we knew the beggar/recipient’s age-sex class (e.g., adult female), but not their identity. These GLMMs test the first prediction of reciprocity, which is that food possessors will be more likely to share with individuals who have previously shared with them.

To test the second prediction, that there will be a significant correlation between the number of times food was shared and received within dyads, I used a Pearson correlation test.

This test examined whether there is a linear relationship between the total number of shares from A-B and the total number of shares from B-A during the study period. For this analysis, the sample included n=258 unique dyads between which sharing occurred.

4.2.2 Shares Among Adult Males Only

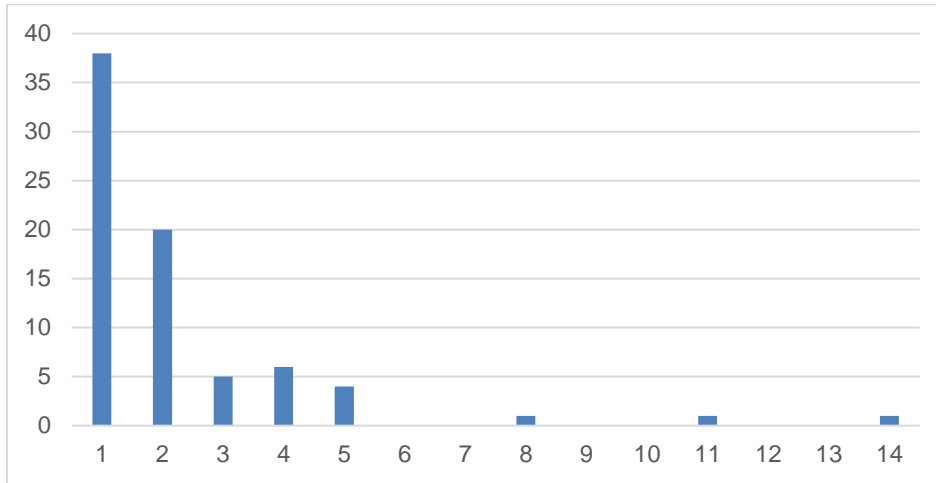
Out of the 305 successful shares (actual food transfers) observed during this study, the most common age-sex transfer was adult males to adult males (n=171), accounting for 56.1% of all shares. For this reason, I also ran reciprocity-based analyses in which I focused on shares between adult males only. Similar to the first set of analyses for all group members, the adult male analyses included two GLMMs (binary logistic) and a Pearson correlation test. The first GLMM examined previous reciprocal shares as a binary variable – i.e., has Male B shared with Male A before this current event, in which Male A is the food possessor? The second GLMM examined the total number of previous shares from Male B to Male A before this current event. For both GLMMs, the sample included n=263 observations involving male possessors and male beggars/recipients. For the correlation test, the sample included n=39 unique male-male dyads between which sharing occurred.

4.3 Results

4.3.1 Shares Among All Group Members

Out of 463 total begging/sharing events between identified individuals, the number of times that the beggar/recipient of the current share *previously* shared with the current food possessor ranged from 0 (n=400 events) to 14 (n=1) (see Figure 4 for full distribution of previous reciprocal shares > 0).

Figure 5. Frequency distribution of previous shares from B to A before current share from A to B



The first GLMM indicates that food possessors were 2.083 times more likely to share with group members who had previously shared with them at least once, and this effect was statistically significant ($B=0.734$, $S.E.=0.284$, $Wald=6.661$, $df=1$, $p=0.10$, $Exp(B)=2.083$, $n=463$). The second GLMM indicates that food possessors were more likely to share with those who had previously shared with them more frequently ($B=0.137$, $S.E.=0.067$, $Wald=4.180$, $df=1$, $p=0.041$, $Exp(B)=1.147$, $n=463$).

The Pearson correlation test indicates a significant correlation between the total number of times food was shared and received within dyads ($r=0.260$, $p < 0.001$, $n=258$).

4.3.2 Shares Among Adult Males Only

The first GLMM indicates that male food possessors were 2.453 times more likely to share with males who had previously shared with them at least once, and this effect was statistically significant ($B=0.897$, $S.E.=0.354$, $Wald=6.414$, $df=1$, $p=0.11$, $Exp(B)=2.453$, $n=263$). The second GLMM indicates that male food possessors were more likely to share with males who had previously shared with them more frequently ($B=0.448$, $S.E.=0.173$, $Wald=6.740$, $df=1$, $p=0.009$, $Exp(B)=1.566$, $n=263$).

The Pearson correlation test does not indicate a statistically significant association between the total number of times food was shared and received within male-male dyads ($r=0.259$, $p=0.116$, $n=39$).

4.4 Summary

4.4.1 Shares Among All Group Members

Tests of reciprocity in this study offer clear evidence that current meat sharing events are influenced by previous interactions. Meat possessors were more than twice as likely to share with group members who had shared with them at least once before. Furthermore, during this study period, there was a statistically significant correlation between the number of times an individual A shared food with individual B, and the number of times individual B shared food with individual A. While it may not be the *only* predictor of meat sharing among Fongoli chimpanzees, reciprocity is undoubtedly important.

4.4.2 Shares Among Adult Males Only

In a study from nearly twenty years ago, Mitani & Watts (2001) report that shares between adult males occurred more frequently than shares between any other age-sex classes. They also found that male carcass possessors were more likely to share meat with males who had previously shared with them, and/or with males who had previously offered coalitionary support, suggesting that reciprocity is important in chimpanzees in Kibale, Uganda.

In the present study, I also found that adult males shared with other adult males more frequently than with other age-sex classes. Meat transfers from adult male possessors to adult male recipients constituted more than half of the reported shares (171 out of 305 transfers) (for further discussion, see Chapter 6: Food-for-Sex). For this reason, I decided to run an additional set of analyses testing for reciprocal exchanges between adult males. These analyses yielded

mixed results. According to the binary logistic regression, male food possessors were more than twice as likely to share with males who had previously shared with them at least once. However, according to the Person's correlation test, there does not appear to be a statistically significant association between the number of times male A shared with male B, and the number of times male B shared with male A during this study period. While reciprocity is a strong predictor of food sharing among the Fongoli chimpanzee community as a whole, the role of reciprocity in explaining male-to-male food shares, specifically, remains uncertain.

CHAPTER V
SHARING-UNDER-PRESSURE

5.1 Background

The sharing-under-pressure hypothesis (Wrangham, 1975) and a version of this hypothesis, known as the "tolerated theft" hypothesis (Blurton Jones, 1987), both predict that possessors of food may share with non-possessors as a way to avoid the costs of defending the food item from persistent beggars. Examples of costs include increased energy expended, decreased foraging efficiency, and any injuries sustained while fighting off beggars (Gilby, 2006).

The sharing-under-pressure hypothesis (and similar models) predicts:

P₁: Sharing will occur more frequently after individuals begged.

P₂: Shares from lower ranking individuals to higher ranking individuals will occur more frequently than shares from higher ranking individuals to lower ranking individuals.

P₃: Sharing will occur more frequently when the prey is larger.

P₄: "Passive shares" will be more frequent than "active shares" or pure theft.

5.2 Methods

5.2.1 P₁: Shares preceded by begs

The first prediction of this hypothesis cannot be evaluated at this time, but will be revisited in the future.

5.2.2 P₂: Shares by social rank direction

To test the second prediction (about rank and direction of transfer), I created a label called "ID-Year" for both sharers and recipients. I used that ID to index each individual's rank at the time of the food sharing event. I examined shares between adults only (since subadult ranks

can be ambiguous), and I assumed that all adult males outranked all adult females, as other chimpanzee food sharing studies have done (e.g., Silk et al. 2013). For this reason, sex and dominance rank category are confounded, which is important to note. When the possessor outranked the beggar (higher ranking to lower ranking), I assigned the dyad a score of 1. When beggar outranked the possessor (lower ranking to higher ranking), I assigned the dyad a score of 0. Out of the 484 total observations, **391** observations involved possessors and beggars who were both adults of known rank. I used a chi-square test to see if there was a statistically significant difference in share success based on the rank relationship (i.e., higher ranking to lower ranking vs. lower ranking to higher ranking).

5.2.3 P_3 : Shares by prey size

To test the third prediction (about prey size), I sorted prey items into three categories based on estimated weight. Aside from one banded mongoose, Fongoli chimpanzees primarily hunted galagos (*Galago senegalensis*) (AKA “bushbabies”), juvenile patas monkeys (*Erythrocebus patas*), juvenile vervet monkeys (*Chlorocebus aethiops*), juvenile baboons (*Papio papio*), and bushbuck fawns (*Tragelaphus scriptus*). Adult and juvenile galagos are all quite small, with estimated weights under 0.5 kg. The estimated weights of juvenile patas, vervet monkeys, and baboons overlap with one another, ranging from approximately 2-4.5 kg. Lastly, bushbuck fawns weigh approximately 4.5 kg at birth, so any bushbucks captured by chimpanzees would weigh approximately 4.5 kg or more. I therefore sorted prey items into three categories: Category 1 contains prey items weighing less than 2 kg (i.e., galagos), category 2 contains prey items weighing 2-4.5 kg (i.e., juvenile patas monkey, vervet monkeys, baboons, and the one banded mongoose), and category 3 contains prey items weighing more than 4.5 kg (i.e., bushbucks).

I only included primary shares (i.e., meat shared from the original food possessor; not secondary, tertiary, etc. shares), since it would be difficult to estimate the starting weight of smaller portions of meat (e.g., a piece of an arm). Out of the 484 total observations, there were **238** primary shares for which the prey size category is known. I used a chi-square test to assess the prediction that larger prey items are more likely to be shared than smaller prey items.

Table 8. Determining prey size categories

Prey Size Category	Prey Included	Citation
Category 1 (< 2 kg)	Galagos (<i>Galago senegalensis</i>) (AKA “bushbabies”)	(Fleagle, 2013)
Category 2 (2-4.5 kg)	Juvenile patas monkeys (<i>Erythrocebus patas</i>)	(Isbell, 2013)
	Juvenile vervet monkeys (<i>Chlorocebus aethiops</i>)	(Isbell & Jaffe, 2013)
	Juvenile guinea baboons (<i>Papio papio</i>)	(Altmann, 1980)
Category 3 (> 4.5 kg)	Bushbuck fawns (<i>Tragelaphus scriptus</i>)	(Ciszek, 1999)

5.2.4 P4: Shares by share type

To test the fourth prediction, that “passive shares” will be more frequently observed than “active shares” or pure theft, I examined the observed frequencies of each share type. For this analysis, the sample included n=231 successful shares for which a share type has been recorded, since begs that were unsuccessful (meaning ones that did not result in shares) would not receive a transfer score (Boesch & Boesch 1989; Pruett & Lindshield 2012) (Table 3 on pg. 48). I calculated the total and relative frequencies of each sharing type to see if “passive shares” (i.e., T2 and T3) were more frequently observed than “active shares” (i.e., T4, T5, and T6) or theft (T1).

5.3 Results

5.3.1 P₁: Shares preceded by begs

Not addressed (see section 5.2.1).

5.3.2 P₂: Shares by social rank direction

According to the chi-square test, there is not a significant difference in share success for different rank relationships. Shares from higher ranking possessors to lower ranking beggars occurred slightly *more* frequently than we would predict by chance, and shares from lower ranking possessors to higher ranking beggars occurred slightly *less* frequently than we would predict (Table 8), but this pattern was not statistically significant ($\chi^2=1.88$, $df=1$, $p=0.170$, $n=391$).

Table 9. Shares by rank direction

Rank direction	Meat shared observed [expected]	Meat not shared observed [expected]	Row totals
High to low	87 [80.8]	42 [48.2]	129
Low to high	158 [164.2]	104 [97.8]	262
Column totals	245	146	391

5.3.3 P₃: Shares by prey size

According to the chi-square test, there is not a statistically significant difference in share success of primary shares based on prey size category ($\chi^2=0.532$, $df=2$, $p=0.766$, $n=239$). The observed values were all very close to what we would predict by chance (Table 9).

Table 10. Shares by prey size category

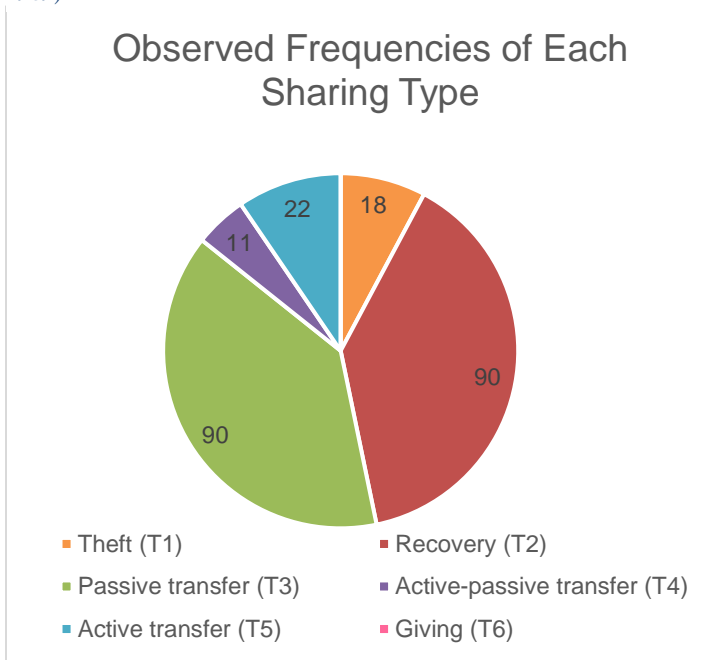
Prey size category	Meat shared observed [expected]	Meat not shared observed [expected]	Row totals
Category 1 (< 2 kg)	48 [48.8]	30 [29.2]	78

Category 2 (2-4.5 kg)	85 [85.8]	52 [51.2]	137
Category 3 (> 4.5 kg)	16 [14.4]	7 [8.6]	23
Column totals	149	89	239

5.3.4 P₄: Shares by share type

Out of the 484 observations of successful meat shares or unsuccessful begging attempts, **231** were successful shares for which a transfer type is recorded. Transfer type 2 (“recovery”) and transfer type 3 (“passive active share”) were by far the most frequently observed at ~39.0% each (Figure 5).

Figure 6. Observed frequencies of each share type (Boesch & Boesch 1989)



Share type	Frequency	Percentage of total
Theft (T1)	18	7.792208
Recovery (T2)	90	38.96104
Passive Transfer (T3)	90	38.96104
Active-Passive Transfer (T4)	11	4.761905
Active Transfer (T5)	22	9.52381
Giving (T6)	0	0

5.4 Summary

This study found mixed support for the sharing-under-pressure hypothesis. There was not a statistically significant difference in share success for different rank relationships – i.e., shares

from lower ranking food possessors to higher ranking beggars/recipients were not more likely to occur than shares from higher ranking possessors to lower ranking beggars/recipients, as the hypothesis predicts. Sharing-under-pressure also predicts that prey size will have a significant effect on sharing, with larger prey being shared at higher rates than smaller prey. The data do not support this prediction either. For all three prey size categories, the observed numbers of shares were all very close to the expected values, and the difference in share success between categories was not statistically significant. One result that does yield support for the sharing-under-pressure hypothesis is the observation that “passive” shares occurred more frequently than “active” shares. Out of the six sharing types described by Boesch & Boesch (1989) and modified by Pruetz & Lindshield (2012), sharing types T2 (“recovery”) and T3 (“passive transfer”) were observed far more frequently than either theft or more “active” sharing types. Importantly, “passive” shares are still selective in that possessors are (de Waal 1997). If ten chimpanzees beg for meat, and a food possessor denies eight of the beggars’ attempts to take meat, but allows two individuals to take a portion, that is still exercising choice. The results of these analyses are discussed more extensively in Chapter 8: Discussion and Conclusion.

CHAPTER VI
FOOD-FOR-SEX

6.1 Background

The food-for-sex hypothesis proposes that males share food with females in exchange for mating opportunities. These transactions would be mutually beneficial, as they would allow females to increase their caloric intake and males to increase their mating success. The food-for-sex hypothesis predicts the following:

P₁: Adult male to adult female shares will occur more frequently than shares between other age-sex classes.

P₂: Shares with females in estrus will occur more frequently than shares with females not in estrus (estrus measured on a 0-3 scale, where 0=no swelling and 3=max swelling).

P₃: Males who share food with females more frequently will also copulate with those females more frequently.

6.2 Methods

6.2.1 P₁: Adult male to adult female shares occur more frequently than shares between other age-sex classes

I used three chi-square tests to examine whether adult male to adult female shares were more likely to occur than shares between other age-sex classes. The first chi-square test included observations between all age-sex classes (n=466). Because there were so few begging/sharing events involving infants, juveniles, and adolescents, these three age categories were grouped together as “subadults.” The second chi-square only included observations between adults (n=455). The third chi-square only included observations involving male food possessors (n=363).

6.2.2 P₂: Shares with estrous females will occur more frequently than shares with anestrus females

In order to test the second prediction of the food-for-sex hypothesis, it is necessary to know a female's estrous status at the time of the beg/share. To match food sharing events to estrous scores, I created a label "date_ID" in both the estrus and the food sharing databases (e.g., 04-March-2017-FA in the food sharing database would indicate that FA received meat on March 4th, 2017, whereas 04-March-2017-FA in the estrus database would refer to FA's estrous score on March 4th, 2017 (0-3 or no data)). Out of the 466 sharing/begging observations, only **45** shares met the following conditions: 1) the share was from an adult male to an adult female, and 2) the share could be matched to an estrous score for the day the food share occurred.

I used a GLMM (binary logistic) to examine whether male food possessors were more likely to share with females with higher estrous scores. For this analysis, the response variable was share success (1=food shared, 0=food not shared), the fixed effect was estrous score (0-3), and the random effect was Dyad ID. I also used a Spearman correlation test to examine the association between estrous scores (0-3) and total number of successful food shares.

6.2.3 P₃: Males who share with females more frequently will also copulate with females more frequently

I used Pearson correlation tests to assess relationships between the total number of food shares and the total number of copulations within male-female dyads. In order to control for the fact that some individuals have been in the group longer than others, I analyzed data from the entire study period (2005-2017), as well as data divided into shorter durations of time (i.e., 2005-2009, 2010-2013, and 2014-2017). For the entire study period of 2005-2017, the sample included

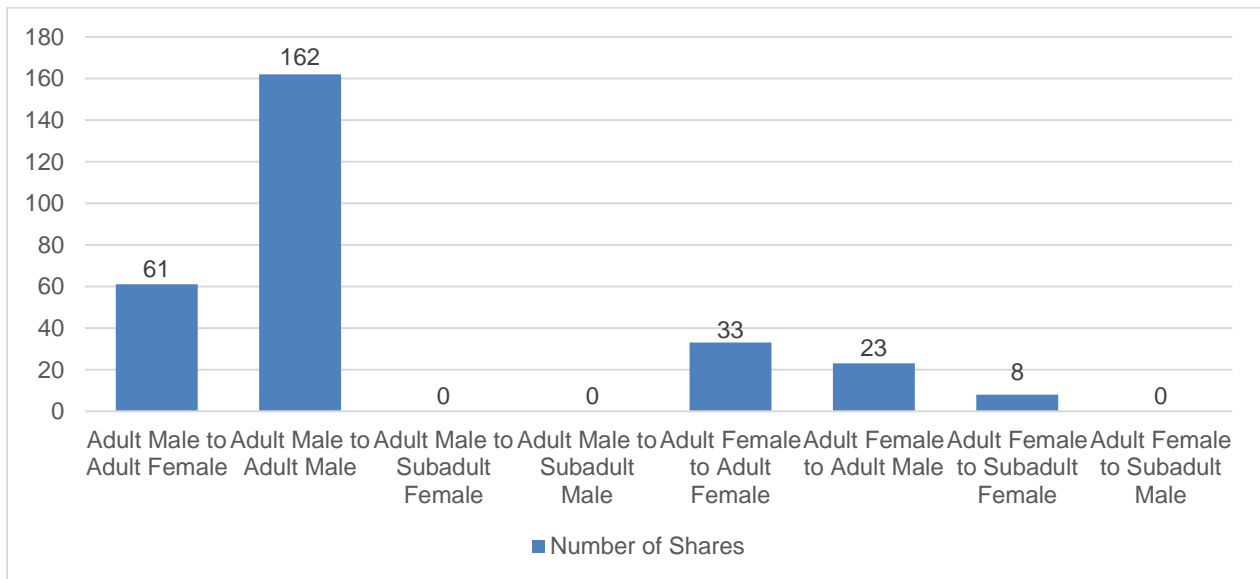
n=438 unique male-female dyads that existed in the group at the same time (n=387 dyads from 2005-2009, n=273 dyads from 2010-2014, and n=418 dyads from 2015-2017).

6.3 Results

6.3.1 P₁: Adult male to adult female shares occur more frequently than shares between other age-sex classes

A frequency distribution of successful shares reveals that adult male to adult female sharing was not the most frequently observed type of share (Figure 6). In fact, most successful shares were from adult males to other adult males, constituting 56.45% (n=162) of the total number of observed shares (n=287).

Figure 7. Frequency of successful shares by age-sex class



According to the chi-square tests, the difference in share success between sexes is not statistically significant when we include all age-sex classes ($\chi^2 = 5.74$, $df=7$, Yates' $\chi^2 = 2.89$, Yates' $p=0.90$, $n=466$), when we include observations between adults only ($\chi^2 = 2.68$, $df=3$, $p=0.44$, Yates' $\chi^2 = 2.05$, Yates' $p=0.56$, $n=455$), or when we include observations involving male food possessors only ($\chi^2 = 2.24$, $p=0.13$, $n=363$). Nevertheless, while the chi-square tests do not

indicate a statistically significant difference, the pattern revealed here is that males share with other males more likely than we would expect, and they share with females less likely than we would expect. Thus, we can reject the first prediction that males are significantly more likely to share with females.

6.3.2 P₂: Shares with estrous females will occur more frequently than shares with anestrus females

According to the GLMM examining the effects of estrous score on the likelihood of males sharing food, females with higher estrous scores were actually *less* likely to receive food than females with an estrous score of 0. However, this result is not statistically significant ($B = -0.041$, $\text{Exp}(B) = 0.960$, $\chi^2 = 0.004$, $p = 0.952$, $n = 45$). Additionally, the Spearman correlation test did not indicate a statistically significant association between estrous scores and food shares ($\rho = 0.087$, $p = 0.573$, $n = 34$, $\text{power} = 0.077$). Both of these findings suggest that estrous score has little to no effect on sharing success.

6.3.3 P₃: Males who share with females more frequently will also copulate with females more frequently

6.3.3.1 Entire study period (2005-2017)

For the entire study period (2005-2017), the sample included $n = 438$ unique male-female dyads that existed in the group at the same time, 67 successful food shares within male-female dyads (range=0-5), and 1067 copulations within male-female dyads (range=0-37). A Pearson correlation test indicates a statistically significant association between the total number of times a male shared food with a female and the total number of times those two copulated during the entire study period of 2005-2017 ($r = 0.219$, $p < 0.001$, $n = 438$, $\text{power} = 0.996$).

6.3.3.2 2005-2009 only

For the 2005-2009 period, the sample included $n=387$ unique male-female dyads that existed in the group during those years, 12 successful food shares within male-female dyads (range=0-2), and 426 copulations within male-female dyads (range=0-18). A Pearson correlation test indicates a statistically significant association between the total number of times a male shared food with a female and the total number of times those two copulated during this time period ($r=0.124$, $p=0.015$, $n=387$, power=0.686).

6.3.3.3 2010-2014 only

For the 2010-2014 period, the sample included $n=273$ unique male-female dyads that existed in the group during those years, 33 successful food shares within male-female dyads (range=0-5), and 597 copulations within male-female dyads (range=0-33). A Pearson correlation test indicates a statistically significant association between the total number of times a male shared food with a female and the total number of times those two copulated during these years ($r=0.202$, $p<0.001$, $n=273$, power=0.921).

6.3.3.4 2015-2017 only

Lastly, for the 2015-2017 period, the sample included $n=418$ unique male-female dyads that existed in the group during those years, 14 successful food shares within male-female dyads (range=0-2), and 232 copulations within male-female dyads (range=0-14). Interestingly, this time period was the only duration for which there was not a significant correlation between total number of times a male shared food with a female and the total number of times those two copulated ($r=0.062$, $p=0.204$, $n=418$, power=0.245).

6.4 Summary

Tests of the food-for-sex hypothesis in this study yield mixed results. The first prediction, that adult male to adult female shares will be observed more frequently than shares between other age-sex categories, is rejected. Adult male to adult male shares constituted $n=162$ of the 287 successful shares, whereas adult male to adult female shares were only observed 61 times. Furthermore, the differences in share success between age-sex categories were not statistically significant, meaning males were not statistically more likely to share with females than we would predict by chance.

The second prediction, that males are more likely to share with estrous females, is also rejected. Estrous females were not statistically more likely to receive food than anestrus females. However, it is important to note that the sample size was extremely small for this analysis. Out of the 466 observations of begging/sharing in the dataset, only 45 observations involved female beggars/recipients with recorded estrous scores.

Tests of the third prediction, that males who share with females more frequently will also copulate with females more frequently, do provide support for the food-for-sex hypothesis. For the entire study period of 2005-2017, there was a statistically significant association between the total number of times a male shared food with a female and the total number of times those two individuals copulated. Among studies that evaluate the food-for-sex hypothesis, 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). Others 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). In order to see whether the mating benefits associated with food sharing

in this study (i.e., increased mating opportunities) could be characterized as short-term or long-term benefits, and in order to control for the fact that some individuals have been in the group longer than others, I also tested for correlations between food shares and copulations during shorter periods of time. The results indicate a statistically significant association between shares and copulations during the 2005-2009 period and the 2010-2014 period, but not the 2015-2017 period. That said, the last analysis (2015-2017) had an unusually small power size (0.245). It is possible that the reason there does not appear to be a significant association between shares and copulations during that time period is because there were fewer food shares and fewer copulations observed. The important takeaway is that for the entire dataset, there is a significant association between increased food shares and increased copulations, which means that overall, food sharing could be enhancing mating prospects, even if the time frame of these benefits remains equivocal. These results are discussed more extensively in Chapter 8: Discussion and Conclusion.

CHAPTER VII
TESTS OF MULTIPLE HYPOTHESES SIMULTANEOUSLY

7.1 Background

The four main hypotheses used to explain food sharing among humans and nonhuman primates include: kin selection, generalized reciprocity, sharing-under-pressure, and 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 *or* multiple functions simultaneously (Silk et al., 2013). I tested the predictions of each of the four hypotheses independently, and present those results in Chapters 3-6. However, because the hypotheses are not mutually exclusive, I also tested the predictions of multiple hypotheses simultaneously. The methods and results of those analyses are presented in this chapter.

7.2 Methods

I used a GLMM (binary logistic) to examine the effects of different variables on the likelihood that an individual will share food. This model tested predictions of all four food sharing hypotheses by including kinship, previous reciprocal shares, rank, prey size, sharer sex, and recipient sex as the fixed effects. Dyad ID was the random effect, and share success was the response variable.

7.3 Results

According to the model, reciprocity (total number of previous reciprocal shares) was the only statistically significant predictor of sharing. Food possessors were 1.44 times more likely to share with individuals who had previously shared with them ($F=3.896$, $S.E.=0.185$, $df=1$, $\text{Exp}(B)=1.441$, $p=0.49$). The full results are presented below (Table 11).

Table 11. GLMM: Results of all variables in the model

	F	B	Std. Error	t	df	Exp(B)	p-value
Kin (close)	0.44	0.137	0.581	0.235	2	1.147	0.814
Kin (distant)	--	-10.594	196.970	-0.054	--	2.505E ⁻⁵	0.957
Number of previous shares from B to A	3.896	0.365	0.185	1.974	1	1.441	0.049
Rank direction (low to high)	0.020	-0.048	0.334	-0.143	1	0.953	0.887
Prey size (larger)	1.870	0.390	0.285	1.368	1	1.477	0.172
Sharer sex (male)	0.148	0.176	0.457	0.385	1	0.839	0.701
Recipient sex (male)	0.734	0.277	0.323	0.857	1	1.319	0.392
Intercept (constant)	0.880	0.076	0.501	0.152	7	1.079	0.879

7.4 Summary

When we examine the effects of several variables simultaneously, we start to see a more complete picture of how different factors influence patterns of food sharing among the Fongoli chimpanzees. As discussed in previous chapters, all four hypotheses included in this study received at least partial support when evaluated independently, with some receiving more support than others. However, the results of the model examining several variables (Table 11) indicate that when kinship, previous reciprocal shares, rank, prey size, sharer sex, and recipient sex are all considered, previous reciprocal shares was the only variable that had a statistically significant effect on sharing.

CHAPTER VIII

DISCUSSION AND CONCLUSION

8.1 Summary of Key Results

In this dissertation, I used models that have been employed to explain human meat sharing patterns (i.e., kin selection, generalized reciprocity, sharing-under-pressure, and food-for-sex) to examine the function of meat sharing in savanna chimpanzees at the Fongoli site. I evaluated the predictions of each hypothesis independently, and then also in combination with others.

In Chapter 3, I discussed the analyses pertaining to kin selection. Most notably, the first prediction of kin selection received support from both analyses. There was a statistically significant association between kinship and sharing in which related individuals were more likely to share than unrelated individuals, and it also appeared that close kin shared at a higher percentage than other kin categories (see Table 12 for recap).

Table 12. Summary of kin selection results

Prediction	Results	Support for kin selection?
P ₁ : Food possessors are more likely to share with related individuals than with unrelated individuals (two kin categories)	<ul style="list-style-type: none">• GLMM: Kinship is a statistically significant predictor of sharing likelihood; food possessors are 2.26 times more likely to share with a related group member than with an unrelated group member (F=5.434, S.E.=0.354, Wald=5.327, df=1, p=0.021, Exp(B)=2.264, n=158)• Mann-Whitney U: Related dyads share more than unrelated dyads (U=3508, z=2.18, p=0.029, effect size=0.17, n=158)	✓

P ₂ : Food possessors are more likely to share with close kin (three kin categories)	<ul style="list-style-type: none"> • Unable to test at this time due to the small sample size of begs/shares between distant kin (2 begs, 0 shares). 	?
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As discussed in Chapter 4, reciprocity appears to play an important role in food sharing at Fongoli. Among all group members, food possessors were more than twice as likely to share with individuals who had previously shared with them at least once, and within dyads, there was a statistically significant correlation between the number of times individual A shared food with individual B, and the number of times individual B shared food with individual A. These findings support the predictions of generalized reciprocity (see Table 13 for recap).

Among adult males only, food possessors were more than twice as likely to share with males who had previously shared with them at least once; however, there did not appear to be a statistically significant association between the number of times male A shared with male B, and the number of times male B shared with male A during this study period. The role of reciprocity in explaining male-to-male food shares at Fongoli therefore requires further investigation.

Table 13. Summary of generalized reciprocity results (all group members)

Prediction	Results	Support for reciprocity?
P ₁ : Food possessors are more likely to share with individuals who have previously shared with them	<ul style="list-style-type: none"> • GLMM (previous shares 0/1): Food possessors were 2.19 times more likely to share with individuals who had previously shared with them at least once ($B=0.734$, $S.E.=0.284$, $Wald=6.661$, $df=1$, $p=0.10$, $Exp(B)=2.083$, $n=463$) • GLMM (total # of previous reciprocal shares): Food possessors were more likely to share with individuals who have shared with them more frequently in the past ($B=0.1.37$, $S.E.=0.067$, $Wald=4.180$, $df=1$, $p=0.041$, $Exp(B)=1.147$, $n=463$) 	✓

P ₂ : Correlation between amount of food given and amount of food received within dyads	<ul style="list-style-type: none"> • Pearson’s correlation: Significant correlation between the total number of times food was shared and received within dyads ($r=0.260$, $p < 0.001$, $n=258$) 	✓
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As discussed in Chapter 5, one prediction of the sharing-under-pressure hypothesis received support. Based on the data available, I was unable to test the first prediction of the hypothesis, which is that meat possessors are more likely to share with individuals after begging occurs (see section 5.2.1 for more information). The second and third predictions were not supported, as neither prey size nor rank appeared to play a significant role in the observed patterns of meat sharing. The fourth prediction *was* supported, as “passive” shares were observed more frequently than “active” shares. We cannot entirely reject the sharing-under-pressure hypothesis as an explanation for food sharing at Fongoli, since one of the four predictions received support. However, the results suggest that it is not the most appropriate model overall (see Table 14 for recap).

Table 14. Summary of sharing-under-pressure results


Prediction	Results	Support for sharing-under-pressure?
P ₁ : Sharing is more likely to occur after individuals beg for food	<ul style="list-style-type: none"> • N/A (see 5.2.1) 	?
P ₂ : Ranks of sharer & beggar/recipient affect likelihood of sharing	<ul style="list-style-type: none"> • Chi-square: No significant difference in share success for different rank relationships; high-to-low shares occurred slightly <i>more</i> frequently than we would predict by chance, and low-to-high shares occurred slightly <i>less</i> frequently than we would predict, but pattern was not statistically significant ($\chi^2=1.88$, $df=1$, $p=0.170$, $n=391$) 	✗

P ₃ : Sharing will occur more frequently when the prey item is larger	<ul style="list-style-type: none"> • Chi-square: No significant difference in share success of primary shares based on prey size category ($\chi^2=0.532$, $df=2$, $p=0.766$, $n=239$) 	✗
P ₄ : “Passive shares” (T2-T3) will be more frequent than “active shares” (T4-T6) or pure theft (T1)	<ul style="list-style-type: none"> • Relative frequencies: T2 (“recovery”) and T3 (“passive active share”) were the most frequently observed share types at 39.0% each ($n=231$) 	✓

In Chapter 6, I discussed the food-for-sex analyses. The results indicate that estrous females were not significantly more likely to receive food than anoestrous females, nor was there a significant association between estrous scores and food shares. However, within male-female dyads, there appeared to be a significant association between the number of times the male shared food with the female, and the number of times those two copulated. This could suggest that although a female’s estrous status might not influence a male food possessor’s immediate decision of whether or not to share meat, there might be fitness benefits associated with meat sharing. In other words, if females are more likely to mate with generous food sharers, there may be incentive for males to share meat, and/or males who share food more frequently *may* increase their total fitness by siring more offspring than males who do not share food as frequently. It is important to note that in this study, male-to-male food shares were far more common than male-to-female food shares, which technically violates one of the predictions of the food-for-sex hypothesis. However, it is still possible that the desire to mate influences a male’s decision to share meat even if it is not the *only* motivating factor. This is presumably why previous studies (e.g., Silk et al., 2013) emphasize that different food sharing hypotheses are not mutually exclusive. However, we would need to also consider alternate hypotheses since food-for-sex cannot explain sharing between other age-sex classes.

Table 15. Summary of food-for-sex results

Prediction	Results	Support for food-for-sex?
<p>P₁: Adult male to adult female shares occur more frequently than shares between other age-sex classes</p>	<ul style="list-style-type: none"> • Relative frequencies: Adult male to adult female shares (n=61) are not the most frequently observed; male to male shares are (n=162, out of 287 successful shares) • Chi-square test: Difference in share success between categories is not statistically significant when we include all age-sex categories (Yates' $\chi^2 = 2.89$, Yates' p=0.90, df=7, n=466), when we include observations between adults only (Yates' $\chi^2 = 2.68$, Yates' p=0.44, df=3, n=455), or when we include observations with male food possessors only ($\chi^2 = 2.24$, p=0.13, df=1 n=363) 	<p>✗</p>
<p>P₂: Shares with estrous females will occur more frequently than shares with anestrus females</p>	<ul style="list-style-type: none"> • GLMM: Estrous females are not significantly more likely to receive food than anoestrous females; in fact, females with higher estrous scores were less likely to receive food than females with an estrous score of 0, but this result was not statistically significant ($B = -0.041$, $\text{Exp}(B) = 0.960$, $\text{Wald} = 0.004$, p=0.952, n=45). • Spearman correlation: No significant association between estrous scores and food shares (correlation coefficient=0.087 p=0.573, n=45, power=0.077) 	<p>✗</p>

<p>P₃: Males who share with females more frequently will also copulate with females more frequently</p>	<ul style="list-style-type: none"> • Pearson correlation 2005-2017: Significant correlation between food shares and copulations for entire study period of 2005-2017 ($r=0.219$, $p<0.001$, $n=438$, power=0.996) • Pearson correlation 2005-2009: Significant correlation between shares and copulations ($r=0.124$, $p=0.015$, $n=387$, power=0.686) • Pearson correlation 2010-2014: Significant correlation between shares and copulations ($r=0.202$, $p<0.001$, $n=273$, power=0.921) • Pearson correlation 2015-2017: No significant correlation between shares and copulations ($r=0.062$, $p=0.204$, $n=418$, power=0.245) 	
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Lastly, in the previous chapter, I discuss a GLMM used to test the predictions of multiple hypotheses combined. This model indicates that reciprocity (i.e., previous reciprocal shares) was the only statistically significant variable. Reciprocity therefore appears to be the strongest and most consistent predictor of food sharing among Fongoli chimpanzees, even if it not the only variable motivating the decision to share (see Table 16 for recap).

Table 16. Summary of models testing the predictions of multiple hypotheses simultaneously

Hypotheses being tested	Model results	Significant predictor(s) of sharing
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<p>H₁: Kin selection H₂: Generalized reciprocity H₃: Sharing-under-pressure H₄: Food-for-sex</p>	<ul style="list-style-type: none"> • GLMM: Reciprocity is the only statistically significant predictor of food sharing. Summary of results: <ul style="list-style-type: none"> ▪ Kinship (F=0.44, S.E.=0.581, df=2, Exp(B)=1.441, p=0.814). ▪ Previous reciprocal shares (F=3.896, S.E.=0.185, df=1, Exp(B)=1.441, p=0.49) ▪ Rank direction (F=0.020, S.E.=0.334, df=1, Exp(B)=0.953, p=0.887) ▪ Prey size (F=1.870, S.E.=0.285, df=1, Exp(B)=1.477, p=0.172) ▪ Sharer sex (F=0.148, S.E.=0.457, df=1, Exp(B)=0.839, p=0.701) ▪ Recipient sex (F=0.734, S.E.=0.323, df=1, Exp(B)=1.319, p=0.879) 	<p>Reciprocity (F=3.896, S.E.=0.185, df=1, Exp(B)=1.441, p=0.49)</p>
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8.2 Discussion

8.2.1 How these results compare to previous findings

Before discussing the results of this study and how they compare to previous findings (see **Error! Reference source not found.** for summary), it is crucial to situate this research in a broader social-ecological context. **Fongoli chimpanzees exhibit an exceptionally high level of social tolerance, which allows individuals other than adult males to capture and retain control of prey** (Pruetz et al., 2015). 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). However, at Fongoli, dominant males took prey from lower-ranking individuals less than 5% of the time (Pruetz et al., 2015). This tolerance creates additional opportunities for meat sharing by a greater number of individuals.

Table 17. Comparing these 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) Sharing-under-pressure Food-for-sex	Reciprocity appears to be the strongest predictor of food sharing overall, with kinship also playing an important role. Mixed support for sharing-under-pressure and food-for-sex.
Yerkes Primate Center chimpanzees	Captive (Lawrenceville, GA, USA)	Plant foods	Reciprocity (food-for-grooming) (de Waal, 1989; de Waal, 1997)	Food-for-grooming (de Waal, 1989; de Waal, 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-coalitionary support among males (Mitani & Watts, 2001)	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)	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)
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)

In the present study, I found that reciprocity was the strongest and most consistent predictor of meat sharing. Food possessors were more than twice as likely to share with individuals who had previously shared with them, and there was a significant association between the number of times food was shared and received within dyads. In other chimpanzee populations, reciprocal exchanges have been reported numerous times (Table 17 on pg. 91). However, a key difference is that in most of these studies, the reciprocated “currency” was not necessarily food. 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). This variation is perhaps related to the degree of social tolerance at a site. For instance, at some sites, it has explicitly 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). In contrast, a higher level of social tolerance at Fongoli may facilitate food-for-food reciprocity.

It is worth noting that some studies also consider food-for-sex exchanges to be a form of reciprocity (e.g., Gilby, 2006, 2010). This is especially interesting, because the prediction that meat sharing will correlate with mating opportunities was the only prediction of the food-for-sex hypothesis that received support in this study. I found that while males did not preferentially share with females in estrus (or even females in general), 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. 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.

Finally, the social tolerance observed at Fongoli could explain why sharing-under-pressure received less support than it has at other sites, *and* why kinship appeared to play an important role in explaining patterns of food sharing. First, at sites where higher-ranking individuals frequently seize prey from lower-ranking individuals, the transfers would likely reflect a pattern consistent with sharing-under-pressure (which predicts that transfers from lower-ranking possessors to higher-ranking recipients will occur most frequently). Additionally, if higher-ranking individuals are unrelated to lower-ranking individuals from whom they take prey, it may skew the results of kinship analyses. At Fongoli, dominant males took prey from lower-ranking individuals far less frequently than at other sites (Pruetz et al., 2015), which could explain why the sharing-under-pressure hypothesis received minimal support in this study. The increased social tolerance at Fongoli could also explain the support for kin selection, since a greater number of individuals would have the option to preferentially share with kin.

8.2.2 Multilevel Selection?

As discussed in section 1.1.1, the question of how cooperative and altruistic behaviors evolve and are maintained in populations has received considerable attention. Several major hypotheses have stemmed from this dialogue including (but not limited to) kin selection (Hamilton, 1964), reciprocal altruism (Trivers, 1971), and naïve/revisted group selection (i.e., multilevel selection) (e.g., Wynne-Edwards, 1986; Wilson, 1977). Since these hypotheses were first developed, it has been demonstrated that kin selection and multilevel selection are different ways of conceptualizing the same evolutionary process. As West et al. (2006) argue, these models are mathematically identical, and are therefore both valid (Hamilton, 1975; Grafen, 1984; Wade, 1985; Frank, 1986, Taylor, 1990; Queller, 1992; Gardner et al., 2007; reviewed by West et al., 2006). West et al. (2006) explain that kin selection and multilevel selection make many of

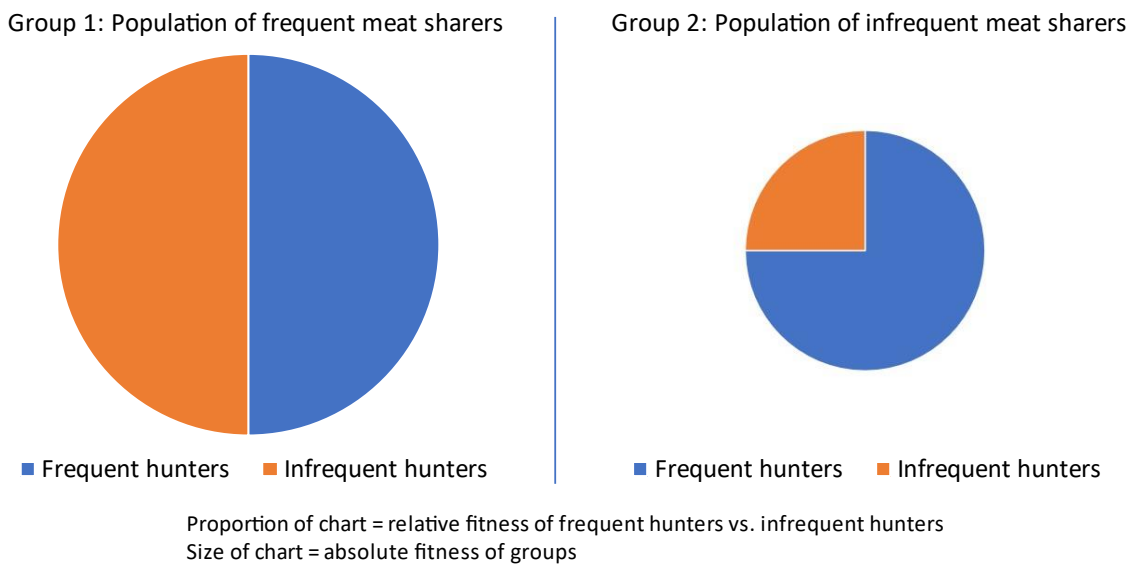
the same predictions (e.g., cooperation is favored when group benefits are increased and individual costs are decreased; cooperation is favored when there is greater between-group genetic variance compared to within-group variance), and that in all instances in which both kin selection and multilevel selection have been evoked to address the same question, both models give identical results (Frank, 1986a; Bourke & Franks, 1995; Wenseleers et al., 2004; Gardner et al., 2007; reviewed by West et al., 2006).

The results of this dissertation indicate that kinship plays a role in meat sharing patterns, but kin selection alone would not be able to explain all observations of meat sharing, particularly those between unrelated group members. Furthermore, this study reveals that while kin are more likely to share meat with one another than non-kin, reciprocity is the strongest predictor of sharing among all group members, even when controlling for kinship and other variables. Lastly, meat-for-sex exchanges seem to characterize a subset of the shares.

We can imagine a hypothetical scenario in which we have two populations of chimpanzees: one group that routinely shares meat and one group that rarely shares meat. In a group that rarely shares meat, successful hunters may have higher individual fitness (assuming there is a link between meat consumption, survival, and reproduction) relative to other members of the group, but the overall fitness of the group might be lower if the majority of group members are not acquiring or receiving meat. In contrast, in a group that routinely shares meat, individual hunters might not necessarily have higher fitness relative to other group members (assuming that all or most group members receive some meat), but the overall fitness of the group might be higher compared to a group in which meat sharing is uncommon. To envision the fitness outcomes of these scenarios, we can picture two pie charts in which the absolute fitness of the group is depicted by the size of the pie chart (Figure 8). In both populations (the population

that frequently shares and the population that does not), we have two possible phenotypes for individuals: frequent hunters or infrequent hunters. The resulting combinations are: 1) frequent hunter in a population that frequently shares meat, 2) infrequent hunter in a population that frequently shares meat, 3) frequent hunter in a population that infrequently shares meat, and 4) infrequent hunter in a population that infrequently shares meat. For both of these pie charts, the size of the pie slice represents the absolute fitness of frequent hunters vs. infrequent hunters, whereas the proportion of the pie represents their relative fitness. We can see that in the population of frequent meat sharers, frequent hunters do not have higher fitness relative to infrequent hunters, but the population that frequently shares has a higher group fitness compared to the population that does not (Figure 8).

Figure 8. Fitness outcomes of hypothetical populations that differ in their frequencies of meat sharing



Based on the results from this dissertation, it is not yet possible to determine if, or to what extent, multilevel selection explains the evolution of meat sharing in this population of

chimpanzees. However, given theoretical advancements to multilevel selection theory during the 21st century, it may be valuable for future research to consider this possibility.

8.2.3 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). 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 (Lindshield et al., 2021).

Though recognizing that chimpanzees inhabit a range of environments that cannot be classified as solely “forest” or “savanna”, Lindshield et al. (2021) heuristically use the terms “forest chimpanzees” to refer to *Pan troglodytes* living in environments with higher forest cover and higher annual rainfall, and “savanna chimpanzees” to refer to *P. troglodytes* living in environments with lower annual rainfall, higher rainfall seasonality, and higher temperatures. Typically, savanna habitats are characterized as one of the following: 1) open and deciduous habitats (e.g., woodlands, wooded grasslands, and grasslands), 2) closed and evergreen habitats (e.g., gallery or thicket forests), and 3) transitional “ecotone” habitats that cannot be classified as mostly open or mostly closed (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. First, home ranges of savanna chimpanzees can exceed 100 km², whereas those of forest chimpanzees range from 3 to 30 km² on average (Humble et al., 2016). Second, population

densities are lower among savanna chimpanzees (~0.09 individuals/km²) compared to forest chimpanzees (~1.9 individuals/km²) (Lindshield et al. 2021). Third, savanna chimpanzee parties tend to be highly cohesive. For instance, at Fongoli, all or most community members can be seen together within a single day (Pruetz & Bertolani, 2009). Fourth, savanna chimpanzee diets tend to be lower in plant species richness (e.g., McGrew et al., 1988; Pruetz, 2006; Keeley et al., 2011; Yoshikawa & Ogawa, 2015) compared to diets of chimpanzees in forested habitats (e.g., Piel et al., 2017; Matthews et al., 2019, 2020). Fifth, savanna chimpanzees appear to consume meat less frequently than forest chimpanzees (Wessling et al., 2018, 2019; Moore et al., 2017). Sixth, at Fongoli specifically, chimpanzees adjust their behavior to prevent hyperthermia (i.e., minimizing exertion during especially hot conditions and using cooler microclimates within their home range [Pruetz & Bertolani, 2009]).

Paleoecological reconstructions indicate that some early hominins also inhabited savanna mosaic landscapes (reviewed by Domínguez-Rodrigo, 2014), and that environmental pressures associated with open and dry landscapes may have contributed to the evolutionary split of the Homo and Pan lineages (Domínguez-Rodrigo, 2014; Cerling et al., 2011; Foley, 1987; 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 (Domínguez-Rodrigo, 2014; Sayers & Lovejoy, 2008). However, studying savanna chimpanzees can reveal how great apes adapt to highly seasonal, dry, hot, and open landscapes. 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 (Suziki, 1969; Moore, 1996; McGrew et al., 1981; Pruetz & Bertolani, 2009). Through this framework, the results of this dissertation can be used to form and test hypotheses about food sharing among early hominins.

8.3 Future Research

8.3.1 Kin Selection

As previously discussed, the kinship analyses conducted in this study were based on matrilineal data only, as paternity data is not presently available. Future research could benefit from including both matrilineal and patrilineal kinship when possible. Doing so would shed light on whether paternal kin and maternal 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. For instance, if we know mothers *and* fathers of most group members, we can determine coefficients of relatedness (e.g., 0.5, 0.25, 0.125), rather than the kin categories used in this study (i.e., “closer kin”, “more distant kin”, “non-kin”). This information would allow us to differentiate full-siblings from half-siblings, and to identify distant relatives through the father’s side, as well (e.g., “aunts/uncles”, “cousins”, and “grandparents”). 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.

8.3.2 Reciprocity

The results of this study highlight the importance of reciprocity in explaining patterns of meat sharing. However, this study focuses on reciprocal exchanges that occur in the same “currency” – that is, food-for-food exchanges. In the future, it might be worth also examining

transactions that occur in different currencies, such as food-for-grooming exchanges or food-for-coalitionary support exchanges. This is something that has been explored in other chimpanzee populations, but has yet to be examined in savanna chimpanzees. Analyzing these exchanges, however, may prove to be challenging in terms of standardization. Testing for food-for-food contingency is relatively straightforward, but testing for significant associations between multiple different “currencies” might yield equivocal results.

8.3.3 Sharing-Under-Pressure

A limitation of this study, as it pertains to the sharing-under-pressure model, is that one of the key predictions of the hypothesis could not be evaluated since the absence/presence of begging was only recorded if food was **not** transferred. In the future, it would be valuable to describe all instances of begging – ones that did not result in food transfers *and* ones that did – to evaluate whether increased begging results in increased meat sharing.

8.3.4 Food-for-Sex

The food-for-sex analyses included in this study indicate that estrous status did not have a significant effect on meat sharing by male food possessors. However, this nonsignificant result could be due to the very small sample size of this analysis. Out of the 484 sharing/begging observations in this study, only 45 observations met the following conditions: 1) It involved a male food possessor and a female beggar/recipient, and 2) There was an estrous score recorded for the female beggar/recipient the same day of the hunt (and subsequent begs/shares). In the future, if a greater number of food shares to females can be associated with estrous scores, a larger sample size might reveal meaningful patterns.

8.4 Conclusions

Food sharing is hypothesized to have played a crucial role in the evolution of human cooperation (Kaplan et al., 2009; Samuni et al., 2018). Throughout our evolutionary history, and among extant foraging societies, food sharing helps to support periods of infant, child, and adolescent development, and to supplement daily food shortages throughout adulthood, such as those resulting from day-to-day variance in hunting success (Jaeggi & Gurven, 2018; Kaplan & Hill, 1985). Because it impacts life history patterns, economic life, and social life, food sharing is an important topic to explore anthropologically (Jaeggi & Gurven, 2018; Kaplan & Gurven, 2001).

Through referential models based on homology and analogy (Moore, 1996), chimpanzees are often used to form hypotheses about human social organization since they are our closest living relatives, they participate in a wide range of collective activities, and they are the only nonhuman primates that regularly share hunted meat with other adult group members in the wild (Jaeggi & Van Schaik, 2011; Silk et al., 2013). I approached the topic of food sharing by examining the function of meat transfers within a population of western chimpanzees at Fongoli, 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 (Moore, 1996; Potts, 1998; Pruetz & Bertolani, 2009; Pruetz et al., 2015).

The findings from this study highlight that several factors influence food sharing among this community. When the predictions different hypotheses were tested independently, there were significant associations between kinship and sharing, and between sharing and copulations, yielding support for both kin selection and food-for-sex. However, when the predictions of

several hypotheses were tested concurrently, the only statistically significant predictor of food sharing was reciprocity – food possessors were more than twice as likely to share with individuals who had previously shared with them, and within dyads, there was a significant correlation between the number of times food was shared and received. These results suggest that, overall, reciprocity was the strongest predictor of food sharing, but that kinship and mating benefits likely play a role too. It is 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. However, until further research is conducted, this interpretation remains speculative. The results of this study emphasize the complexity of chimpanzee food sharing behaviors, especially at a site where social tolerance offers increased opportunities for food sharing by individuals other than dominant males. These findings can be placed in a referential model to inform hypotheses about food sharing in early hominins.

REFERENCES

- Altmann, J. (1980). *Baboon Mothers and Infants*. Harvard University Press, Cambridge, Mass.
- Alvard, M. S., & Nolin, D. A. (2002). Rousseau's Whale Hunt? Coordination among Big-Game Hunters. *Current Anthropology*, 43(4), 533–559.
- Amat, J. A. (2000). Courtship feeding, food sharing, or tolerated food theft among paired Red-crested Pochards (*Netta rufina*)? *Journal Für Ornithologie*, 141(3), 327–334. <https://doi.org/10.1007/bf02462242>
- Birch, J., & Okasha, S. (2015). Kin selection and its critics. *BioScience*, 65(1), 22–32. <https://doi.org/10.1093/biosci/biu196>
- Blaffer Hrdy, S. (1979). Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, 1, 13–40.
- Blurton Jones, N. G. (1987). Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. *Social Science Information*, 26(1), 31–54. <https://doi.org/10.1177/053901887026001002>
- Boas, F. (1888). The Indians of British Columbia. *Popular Science Monthly*, 32.
- Boesch, C., Uehara, S., & Ihobe, H. (2002). Variation in chimpanzee-red colobus interactions. In C. Boesch, G. Hohmann, & L. Marchant (Eds.), *Behavioural Diversity in Chimpanzees and Bonobos* (pp. 221–229). 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.
- Boesch C., Boesch-Achermann, H. (2000). *The chimpanzees of the Tai forest*. Oxford University Press
- Boggs, C. (1995). Male nuptial gifts: Phenotypic consequences and evolutionary implications. In S. Leather & J. Hardie (Eds.), *Insect Reproduction*. CRC Press.
- Borrello, M. E. (2005). The rise, fall, and resurrection of group selection. *Endeavour*, 29, 43e47.
- Boyd, R., & Richerson, P. J. (2009). Culture and the evolution of human cooperation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1533), 3281–3288. <https://doi.org/10.1098/rstb.2009.0134>
- Brosnan, S. F., Silk, J. B., Henrich, J., Mareno, M. C., Lambeth, S. P., & Schapiro, S. J. (2009). Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task. *Animal Cognition*, 12(4), 587–597. <https://doi.org/10.1007/s10071-009-0218-z>
- Brotherton, P. N. M., Clutton-Brock, T. H., O'Riain, M. J., Gaynor, D., Sharpe, L., Kansky, R., & McIlrath, G. M. (2001). Offspring food allocation by parents and helpers in a cooperative mammal. *Behavioral Ecology*, 12(5), 590–599. <https://doi.org/10.1093/beheco/12.5.590>
- Busse, C. D. (1978). Do Chimpanzees Hunt Cooperatively? *The American Naturalist*, 112(986), 767–770. <https://doi.org/doi.org/10.1086/283318>

- Carter, G. G., & Wilkinson, G. S. (2013). Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proceedings of the Royal Society B*, 280, 20122573. <https://doi.org/10.1098/rspb.2012.2573>
- Cerling, T. E., Wynn, J. G., Andanje, S. A., et al. (2011). Woody cover and hominin environments in the past 6 million years. *Nature*, 476, 51-56.
- Ciszek, D. 1999. "*Tragelaphus scriptus*" (Online), Animal Diversity Web. Accessed March 20, 2022 at https://animaldiversity.org/accounts/Tragelaphus_scriptus/
- Clark Arcadi, A. (2018). *Wild Chimpanzees: Social Behavior of an Endangered Species* (First). Cambridge University Press.
- Clutton-Brock, T. H., & Harvey, P. H. (1976). Evolutionary rules and primate societies. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing Points in Ethology* (pp. 195–238). Cambridge University Press.
- Crockford, C., Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology*, 22, 142–146. <https://doi.org/10.1016/j.cub.2011.11.053>
- Darwin, C. (1859). *The Origin of Species by Means of Natural Selection, or, The Preservation of Favoured Races in the Struggle for Life*. London: John Murray.
- Dawkins, R. (1976). *The Selfish Gene*. Oxford University Press.
- de Waal, F. B. M. (1982). *Chimpanzee Politics: Power and Sex Among Apes*. Harper & Row.
- de Waal, F. B. M. (1989). Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution*, 18(5), 433–459. [https://doi.org/10.1016/0047-2484\(89\)90074-2](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(6), 375–386. [https://doi.org/10.1016/S1090-5138\(97\)00085-8](https://doi.org/10.1016/S1090-5138(97)00085-8)
- De Waal, F. B. M. (1997). Food Transfers Through Mesh in Brown Capuchins. *Journal of Comparative Psychology*, 111(4), 370–378. <https://doi.org/10.1037/0735-7036.111.4.370>
- De Waal, F. B. M. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour*, 60(2), 253–261. <https://doi.org/10.1006/anbe.2000.1471>
- Domínguez-Rodrigo, M. (2014). Is the “savanna hypothesis” a dead concept for explaining the emergence of the earliest hominins? *Current Anthropology*, 55, 59-81.
- Duque, J. F., & Stevens, J. R. (2016). Voluntary food sharing in pinyon jays: the role of reciprocity and dominance. *Animal Behaviour*, 122, 135–144. <https://doi.org/10.1016/j.anbehav.2016.09.020>
- Dyble, M., Thompson, J., Smith, D., Vinicuis, L., Mace, R., Migliano, A. B., Dyble, M., Thompson, J., Smith, D., Salali, G. D., Chaudhary, N., Page, A. E., Vinicuis, L., Mace, R., & Migliano, A. B. (2016). Networks of Food Sharing Reveal the Functional Significance of Multilevel Sociality in Two Hunter-Gatherer Groups. *Current Biology*, 26(15), 2017–2021. <https://doi.org/10.1016/j.cub.2016.05.064>

- Ember, C. R. (2020). *Hunter-Gatherers (Foragers)*. 1–19.
- Eppley, T. M., Suchak, M., Crick, J., & de Waal, F. B. M. (2013). Perseverance and food sharing among closely affiliated female chimpanzees. *Primates*, *54*(4), 319–324. <https://doi.org/10.1007/s10329-013-0374-2>
- Feistner, A. T. C., & McGrew, W. C. (1989). Food-sharing in primates: A critical review. In P. Seth & S. S (Eds.), *Perspectives in Primate Biology* (Vol. 3, pp. 21–36). Today & Tomorrow Printers and Publishers.
- Feistner, A. T. C., & Price, E. C. (2000). Food sharing in black lion tamarins (*Leontopithecus chrysopygus*). *American Journal of Primatology*, *52*(1), 47–54. [https://doi.org/10.1002/1098-2345\(200009\)52:1<47::AID-AJP4>3.0.CO;2-D](https://doi.org/10.1002/1098-2345(200009)52:1<47::AID-AJP4>3.0.CO;2-D)
- Ferrari, S. (1987). Food transfer in a wild marmoset group. *Folia Primatologica*, *48*, 203–206.
- Fieldhouse, P. (1995). Social functions of food. In *Food and Nutrition: Customs and Culture* (Second, pp. 78–105). Springer. https://doi.org/https://doi.org/10.1007/978-1-4899-3256-3_4
- Foley, R. (1987). *Another Unique Species: Patterns in Human Evolutionary Ecology*. Longman Scientific and Technical.
- Foley, R., & Gamble, C. (2009). The ecology of social transitions in human evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1533), 3267–3279. <https://doi.org/10.1098/rstb.2009.0136>
- Frank, S.A. (1986). Hierarchical selection theory and sex ratios. I. General solutions for structured populations. *Theoretical Population Biology*, *29*, 312–342.
- Fruth, B., & Hohmann, G. (2018). Food Sharing across Borders. *Human Nature*, *29*(2), 91–103. <https://doi.org/10.1007/s12110-018-9311-9>
- Gardner, A., West, S. A., & Barton, N. H. (2007). The relation between multilocus population genetics and social evolution theory. *The American Naturalist*, *169*(2), 207–226.
- Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour*, *71*(4), 953–963. <https://doi.org/10.1016/j.anbehav.2005.09.009>
- Gilby, I. C., Eberly, L. E. & Wrangham, R. W. (2008). Economic profitability of social predation among wild chimpanzees: individual variation promotes cooperation. *Animal Behaviour*, *75*, 351e360. <https://doi.org/10.1016/j.anbehav.2007.06.008>
- Gilby, I. C., Emery Thompson, M., Ruane, J. D., & Wrangham, R. (2010). No evidence of short-term exchange of meat for sex among chimpanzees. *Journal of Human Evolution*, *59*(1), 44–53. <https://doi.org/10.1016/j.jhevol.2010.02.006>
- Goffe, A. S., & Fischer, J. (2016). Meat sharing between male and female Guinea baboons (*Papio papio*). *Primate Biology*, *3*, 1–8. <https://doi.org/10.5194/pb-3-1-2016>
- Goldberg, T. L., & Wrangham, R. W. (1997). Genetic correlates of social behaviour in wild chimpanzees: Evidence from mitochondrial DNA. *Animal Behaviour*, *54*(3), 559–570.

<https://doi.org/10.1006/anbe.1996.0450>

- Goldstone, L. G., Sommer, V., Nurmi, N., Stephens, C., & Fruth, B. (2016). Food begging and sharing in wild bonobos (*Pan paniscus*): assessing relationship quality? *Primates*, *57*(3), 367–376. <https://doi.org/10.1007/s10329-016-0522-6>
- Gomes, C. M., & Boesch, C. (2009). Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS ONE*, *4*(4), 16–18. <https://doi.org/10.1371/journal.pone.0005116>
- Goodall, J., Bandura, A., Bergmann, E., Busse, C., Matam, H., Mpongo, E., Pierce, A., & Riss, D. (1979). Inter-community interactions in the chimpanzee populations of the Gombe National Park. In D. Hamburg & E. McCown (Eds.), *The Great Apes* (pp. 13–53). Benjamin-Cummings.
- Goodall, Jane. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. Belknap Press of Harvard University.
- Goodnight, C. (2013). On multilevel selection and kin selection: Contextual analysis meets direct fitness. *Evolution*, *67*(6), 1539–1548. <https://doi.org/10.1111/j.1558-5646.2012.01821.x>
- Grafen, A. (1984). Natural selection, kin selection and group selection. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural Ecology: An Evolutionary Approach*, pp. 62–84. Blackwell Scientific Publications, Oxford, UK.
- Gudeman, S. (2001). Reciprocity and the Gift: Extending the Base. In *The Anthropology of Economy: Community, Market, and Culture* (1st ed.). Blackwell Publishers Inc.
- Gurven, M. (2004). To give and to give not: The behavioral ecology of human food transfers. *Behavioral and Brain Sciences*, *27*(04), 543–583. <https://doi.org/10.1017/S0140525X04000123>
- Gurven, M., Allen-arave, W., & Hill, K. (2001). Reservation food sharing among the Ache. *Human Nature*, *12*(4), 273–297.
- Gurven, M., Allen-arave, W., Hill, K., & Hurtado, M. (2000). "It's a Wonderful Life": Signaling generosity among the Ache of Paraguay. *21*, 263–282.
- Gurven, M., Hill, K., & Kaplan, H. (2002). From forest to reservation: Transitions in food-sharing behavior among the Ache of Paraguay. *Journal of Anthropological Research*, *58*(1), 93–120. <https://doi.org/10.1086/jar.58.1.3631070>
- Gurven, M., Hill, K., Kaplan, H., Hurtado, A., & Lyles, R. (2000). *Food Transfers Among Hiwi Foragers of Venezuela: Tests of Reciprocity*. *28*(2), 171–218.
- Hames, R., & McCabe, C. (2007). Meal sharing among the Ye'kwana. *Human Nature*, *18*(1), 1–21. <https://doi.org/10.1007/BF02820843>
- Hamilton, W. D. (1964). The genetical evolution of social behavior. I. *Journal of Theoretical Biology*, *7*, 1–16. <https://doi.org/10.4324/9780203790427-4>
- Hamilton, W. D. (1971). Selection of selfish and altruistic behavior in some extreme models. In J. Eisenberg & W. Dillon (Eds.), *Man and Beast: Comparative Social Behavior* (pp. 57–91). Smithsonian Institution Press.

- Hamilton, W.D. (1975). Innate social aptitudes of man: An approach from evolutionary genetics. In R. Fox (ed.), *Biosocial Anthropology*, pp. 133–155. Wiley, New York.
- Hare, B., & Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. *Current Biology*, 20(5), 230–231. <https://doi.org/10.1016/j.cub.2009.12.038>
- Hauser, M. D., Chen, M. K., Chen, F., & Chuang, E. (2003). Give unto others: Genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proceedings of the Royal Society B: Biological Sciences*, 270(1531), 2363–2370. <https://doi.org/10.1098/rspb.2003.2509>
- Hawkes, K., O’Connell, J., & Nlurton Jones, N. (2001). Hadza meat sharing. *Evolution and Human Behavior*, 22, 113–142.
- Hawkes, Kristen. (1991). Showing off: Tests of a hypothesis about men’s foraging goals. In *Ethology & Sociobiology* (Vol. 12, Issue 1, pp. 29–54). Elsevier Science. [https://doi.org/10.1016/0162-3095\(91\)90011-E](https://doi.org/10.1016/0162-3095(91)90011-E)
- Heinrich, B., & Marzluff, J. (1995). Why ravens share. *American Scientist*, 83(4), 342–349.
- Hemelrijk, C. K., & Ek, A. (1991). Reciprocity and interchange of grooming and “support” in captive chimpanzees. *Animal Behaviour*, 41(6), 923–935. [https://doi.org/10.1016/S0003-3472\(05\)80630-X](https://doi.org/10.1016/S0003-3472(05)80630-X)
- Hill, K., & Kaplan, H. (1993). On Why Male Foragers Hunt and Share Food. *Current Anthropology*, 34(5), 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., Oats, J. F., et al. (2016). *Pan Troglodytes*. IUCN red list of threatened species. <https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T15933A17964454.en>
- Isbell, L. A. (2013). *Erythrocebus patas*: Patas monkey. In T.M. Butynski, J. Kingdon and J. Kalina (eds), *The Mammals of Africa. Volume II: Primates*, pp. 257-264. Bloomsbury Publishing, London.
- Isbell, L. A., & Jaffe, K. L. E. (2013). *Chlorocebus pygerythrus*: Vervet monkey. In T.M. Butynski, J. Kingdon and J. Kalina (eds), *The Mammals of Africa. Volume II: Primates*, pp. 277-283. Bloomsbury Publishing, London.
- Jaeggi, A. V., Stevens, J. M. G., & Van Schaik, C. P. (2010). Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees. *American Journal of Physical Anthropology*, 143(1), 41–51. <https://doi.org/10.1002/ajpa.21288>
- Jaeggi, A. V., & Van Schaik, C. P. (2011). The evolution of food sharing in primates. *Behavioral Ecology and Sociobiology*, 65(11), 2125–2140. <https://doi.org/10.1007/s00265-011-1221-3>
- Jaeggi, A. V., de Groot, E., Stevens, J. M., & van Schaik, C. P. (2013). Mechanisms of reciprocity in primates: testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evolution and Human Behavior*, 34(2), 69–77.

<https://doi.org/10.1016/j.evolhumbehav.2012.09.005>

- Jaeggi, A. V., & Gurven, M. (2018). Food-Sharing Models. *The International Encyclopedia of Anthropology*.
- Kaplan, H., & Gurven, M. (2001). The Natural History of Human Food Sharing and Cooperation: A Review and a New Multi-Individual Approach to the Negotiation of Norms. *Conference on the Structure and Evolution of Strong Reciprocity*, 75–113.
- Kaplan, H., & Hill, K. (1985). Food Sharing among Ache Foragers: Tests of Explanatory Hypotheses. *Current Anthropology*, 26(2), 223–246.
- Kaplan, H., Hill, K., Hawkes, K., & Hurtado, A. (1984a). Food Sharing among Ache Hunter-Gatherers of Eastern Paraguay. *Current Anthropology*, 25(1), 113–115.
- Kaplan, H., Hill, K., Hawkes, K., & Hurtado, A. (1984b). Food Sharing Among Ache Hunter-Gatherers of Eastern Paraguay. *Current Anthropology*, 25(1), 113–115.
<https://doi.org/10.1086/203089>
- Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology*, 9(4), 156–185.
[https://doi.org/10.1002/1520-6505\(2000\)9:4<156::aid-evan5>3.3.co;2-z](https://doi.org/10.1002/1520-6505(2000)9:4<156::aid-evan5>3.3.co;2-z)
- Kaplan, H. S., Hooper, P. L., & Gurven, M. (2009). The evolutionary and ecological roots of human social organization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1533), 3289–3299. <https://doi.org/10.1098/rstb.2009.0115>
- Kavanagh, M. (1972). Food-sharing Behaviour within a Group of Douc Monkeys (*Pygathrix nemaeus nemaeus*). *Nature*, 239, 406–407.
- Keeley, J. E., Pausas, J. G., Rundel, P. W., et al. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, 16, 1360–1385.
<https://doi.org/10.1016/j.tplants.2011.04.002>
- Kent, S. (1993). Sharing in an Egalitarian Kalahari Community. *Man*, 28(3), 479–514.
- Kishigami, N. (2006). Contemporary Inuit Food Sharing: A Case Study from Akulivik, PQ, Canada. *Jinbun-Ronkyu (Journal of the Society of Liberal Arts)*, 75, 15–21.
<http://onlinelibrary.wiley.com/doi/10.1002/cbdv.200490137/abstract>
- Kitanishi, K. (1998). Food sharing among the Aka hunter-gatherers in northeastern Congo. *African Study Monographs, Suppl.* 25(March), 3–32.
- Kopp, K. S., & Liebal, K. (2016). Here you are! – Selective and active food sharing within and between groups in captive Sumatran orangutans (*Pongo abelii*). *Behavioral Ecology and Sociobiology*, 70(8), 1219–1233. <https://doi.org/10.1007/s00265-016-2130-2>
- Langergraber, K. E., Siedel, H., Mitani, J. C., Wrangham, R. W., Reynolds, V., Hunt, K., & Vigilant, L. (2007). The genetic signature of sex-biased migration in patrilocal chimpanzees and humans. *PLoS ONE*, 2(10), 1–7. <https://doi.org/10.1371/journal.pone.0000973>
- Langergraber, K. E., Watts, D. P., Vigilant, L., Mitani, J. C., & Cheney, D. L. (2017). Group augmentation, collective action, and territorial boundary patrols by male chimpanzees.

- Proceedings of the National Academy of Sciences of the United States of America*, 114(28), 7337–7342. <https://doi.org/10.1073/pnas.1701582114>
- Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, 71(10), 840–851. <https://doi.org/10.1002/ajp.20711>
- Lindshield, S., Hernandez-Aguilar, R. A., Korstjens, A. H., Marchant, L. F., Narat, V., Ndiaye, P. I., et al. (2021). Chimpanzees (*Pan troglodytes*) in savanna landscapes. *Evolutionary Anthropology*, 30, 399–420. <https://doi.org/10.1002/evan.21924>
- Manson, J. H., & Wrangham, R. W. (1991). Intergroup aggression in chimpanzees and humans. In *Current Anthropology* (Vol. 32, Issue 4, pp. 369–390). Univ of Chicago Press. <https://doi.org/10.1086/203974>
- Marlowe, F. W. (2004). What Explains Hadza Food Sharing? *Socioeconomic Aspects of Human Behavioral Ecology*, 23, 69–88. [https://doi.org/10.1016/S0190-1281\(04\)23003-7](https://doi.org/10.1016/S0190-1281(04)23003-7)
- Marlowe, F. W., Wittig, R. M., Crockford, C., Deschner, T., Langergraber, K. E., Ziegler, T. E., Zuberbu, K., Crockford, C., Wolovich, C. K., Perea-Rodriguez, J. P., Fernandez-Duque, E., Moore, J., Jaeggi, A. V., de Groot, E., Stevens, J. M. J. R., Van Schaik, C. P., Goffe, A. S., Fischer, J., Wright, B. M., ... Gilby, I. C. (2004). Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: A phylogenetic meta-analysis. *Evolution and Human Behavior*, 23(2), 19–43. <https://doi.org/10.1098/rspb.2013.1615>
- Massen, J. J. M., Haley, S. M., & Bugnyar, T. (2020). Azure-winged magpies' decisions to share food are contingent on the presence or absence of food for the recipient. *Scientific Reports*, 10(1), 1–13. <https://doi.org/10.1038/s41598-020-73256-0>
- Matthews, J. K., Ridley, A., Niyigaba, P., et al. (2019). Chimpanzee feeding ecology and fallback food use in the montane forest of Nyungwe National Park, Rwanda. *American Journal of Primatology*, 81, e22971.
- 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.
- Mauss, M. (1960). The Gift. In *The Gift: The Form and Reason for Exchange in Archaic Societies* (6th ed.). Cohen & West. <https://doi.org/10.4324/9781912281008>
- Mazumder, J., & Kaburu, S. S. K. (2021). First report of food sharing among Nicobar long-tailed macaques. *Quaternary International*, 603, 31–39. <https://doi.org/10.1016/j.quaint.2020.11.049>
- McGrew, W. C. (2004). *The Cultured Chimpanzee: Reflections on Cultural Primatology*. Cambridge University Press. [https://doi.org/DOI: 10.1017/CBO9780511617355](https://doi.org/DOI:10.1017/CBO9780511617355)
- McGrew, William C. (1975). Patterns of plant food sharing by wild chimpanzees. *Contemporary Biology*, January 1972, 304–309.
- McGrew, W. C., Baldwin, P. J., & Tutin, C. E. G. (1988). Diet of wild chimpanzees (*Pan*

- troglydites verus*) at Mt. Assirik, Senegal: I. Composition. *American Journal of Primatology*, 16, 213-226.
- Melis, A. P., & Semmann, D. (2010). How is human cooperation different? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1553), 2663–2674. <https://doi.org/10.1098/rstb.2010.0157>
- Mitani, J. C. (2006). Demographic influences on the behavior of chimpanzees. *Primates*, 47(1), 6–13. <https://doi.org/10.1007/s10329-005-0139-7>
- Mitani, J. C. (2009). Cooperation and competition in chimpanzees: Current understanding and future challenges. *Evolutionary Anthropology*, 18(5), 215–227. <https://doi.org/10.1002/evan.20229>
- Mitani, J. C., Merriwether, D. A., & Zhang, C. (2000). Male affiliation, cooperation, and kinship in wild chimpanzees. *Animal Behaviour*, 59(4), 885–893. <https://doi.org/10.1006/anbe.1999.1389>
- Mitani, J. C., & Watts, D. P. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour*, 61(5), 915–924. <https://doi.org/10.1006/anbe.2000.1681>
- Mitani, J. C., Watts, D. P., & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, 20(12), 507–508. <https://doi.org/10.1016/j.cub.2010.04.021>
- Mitani, J. C., Watts, D. P., Pepper, J. W., & Merriwether, D. A. (2002). Demographic and social constraints on male chimpanzee behaviour. *Animal Behaviour*, 64(5), 727–737. <https://doi.org/10.1006/anbe.2002.4014>
- Moore, J. “Savanna” chimpanzees. (1992). In T. Nishida, W.C. McGrew, P. Marler, M. Pickford, F.B.M. de Waal (Eds.), *Topics in Primatology, Human Origins, vol. I*, University of Tokyo Press, Tokyo, pp. 99-118.
- 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.
- Morin, P. A., Moore, J. J., Chakraborty, R., Jin, L., Goodall, J., & Woodruff, D. S. (1994). Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science*, 265(5176), 1193–1201. <https://doi.org/10.1126/science.7915048>
- Muir, W. M. (1996). Group selection for adaptation to multiple-hen cages: Selection program and direct responses. *Poultry Science*, 75(4):447-58. <https://doi.org/10.3382/ps.0750447>
- Nakamura, M., & Itoh, N. (2001). Sharing of wild fruits among male chimpanzees: Two cases from Mahale, Tanzania. *Pan Africa News*, 8(2), 28–31. <https://doi.org/10.5134/143398>
- Nettelbeck, A. R. (1998). Observations on food sharing in wild Lar gibbons (*Hylobates lar*).

- Folia Primatologica*, 69(6), 386–391. <https://doi.org/10.1159/000021658>
- Newton-Fisher N. E. (2015). The hunting behavior and carnivory of wild chimpanzees. In Henke W., Tattersall I. (eds) *Handbook of Paleoanthropology*. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-39979-4_42
- Nishida, T. (1983). Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates*, 24(3), 318–336. <https://doi.org/10.1007/BF02381978>
- Nishida, Toshisada, Hasegawa, T., Hayaki, H., Takahata, Y., & Uehara, S. (1992). Meat-Sharing as a Coalition Strategy by an Alpha Male Chimpanzee? *Topics in Primatology, Vol. 1: Human Origins, June*, 159–174.
- Nishida, Toshisada, Hiraiwa-Hasegawa, M., Hasegawa, T., & Takahata, Y. (1985). Group Extinction and Female Transfer in Wild Chimpanzees in the Mahale National Park, Tanzania. *Zeitschrift Für Tierpsychologie*, 67(1–4), 284–301. <https://doi.org/10.1111/j.1439-0310.1985.tb01395.x>
- Nishida, Toshisada, Kano, T., Goodall, J., McGrew, W. C., & Nakamura, M. (1999). Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science*, 107(2), 141–188. <https://doi.org/10.1537/ase.107.141>
- Nolin, D. A. (2008). *Food-sharing networks in Lamalera, Indonesia: Tests of adaptive hypotheses*. Doctoral dissertation, University of Washington. <http://proxy.library.tamu.edu/login?url=https://www.proquest.com/dissertations-theses/food-sharing-networks-lamalera-indonesia-tests/docview/304440124/se-2?accountid=7082>
- Nolin, D. A. (2010). Food-sharing networks in Lamalera, Indonesia: Reciprocity, kinship, and distance. *Human Nature*, 21(3), 243–268. <https://doi.org/10.1007/s12110-010-9091-3.Food-Sharing>
- Nolin, D. A. (2012). Food-sharing networks in Lamalera, Indonesia: Status, sharing, and signaling. *Evolution and Human Behavior*, 33, 334–345. <https://doi.org/10.1016/j.evolhumbehav.2011.11.003>
- Nowak, M. A., Tarnita, C. E., & Wilson, E. O. (2010). The evolution of eusociality. *Nature*, 466(7310), 1057–1062. <https://doi.org/10.1038/nature09205>
- Ostojić, L., Shaw, R. C., Cheke, L. G., & Clayton, N. S. (2013). Evidence suggesting that desire-state attribution may govern food sharing in Eurasian jays. *Proceedings of the National Academy of Sciences of the United States of America*, 110(10), 4123–4128. <https://doi.org/10.1073/pnas.1209926110>
- Patton, J. Q. (2005). Meat sharing for coalitional support. *Evolution and Human Behavior*, 26, 137–157. <https://doi.org/10.1016/j.evolhumbehav.2004.08.008>
- Perry, S., & Rose, L. (1994). Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capucinus*. *Primates*, 35(4), 409–415. <https://doi.org/10.1007/BF02381950>
- 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.
- Potts, R. (1998). Environmental Hypotheses of Hominin Evolution. *Yearbook of Physical Anthropology*, 41, 93–136. [https://doi.org/10.1002/\(sici\)1096-8644\(1998\)107:27+<93::aid-ajpa5>3.0.co;2-x](https://doi.org/10.1002/(sici)1096-8644(1998)107:27+<93::aid-ajpa5>3.0.co;2-x)
- Price, G. (1970). Selection and Covariance. *Nature*, 227(5257), 520–521. <https://doi.org/10.1038/227520a0>
- Pruetz, J., & Bertolani, P. (2009). Chimpanzee (*Pan troglodytes verus*) Behavioral Responses to Stresses Associated with Living in a Savannah-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. (2006). Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In C. Boesch, M. Robbins, G. Hohmann (eds.). *Feeding Ecology in Apes and Other Primates*. Cambridge University Press.
- Pruetz, J. D., & Lindshield, S. (2012). Plant-food and tool transfer among savanna chimpanzees at Fongoli, Senegal. *Primates*, 53(2), 133–145. <https://doi.org/10.1007/s10329-011-0287-x>
- Queller, D.C. (1992). Quantitative genetics, inclusive fitness, and group selection. *American Naturalist*, 139, 540–558.
- 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*, 285, 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, 87-114.
- Schel, A. M., Townsend, S.W., Machanda, Z, Zuberbühler K, Slocombe KE (2013) Chimpanzee Alarm Call Production Meets Key Criteria for Intentionality. *PLOS ONE* 8(10): e76674. <https://doi.org/10.1371/journal.pone.0076674>
- Schessler, T., & Nash, L. T. (1977). Food sharing among captive gibbons (*Hylobates lar*). *Primates*, 18(3), 677-689.
- Seyfarth, R., & Cheney, D. (1984). Grooming, alliances, and reciprocal altruism in vervet monkeys. *Letters to Nature*, 308, 541–543.
- Silk, J. B. (2002). Kinship in primate groups. *International Journal of Primatology*, 23(4), 849–875.
- Silk, J. B. (2005). The Evolution of Cooperation in Primate Groups. In H. Gintis, S. Bowles, R.

- Boyd, & E. Fehr (Eds.), *Moral Sentiments and Material Interests: On the Foundations of Cooperation in Economic Life* (pp. 1–40). MIT Press.
- Silk, J. B. (2009). Nepotistic cooperation in non-human primate groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1533), 3243–3254. <https://doi.org/10.1098/rstb.2009.0118>
- Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P., & Shapiro, S. (2013). Chimpanzees share food for many reasons: The role of kinship, reciprocity, social bonds and harassment on food transfers. *Animal Behaviour*, 85(5), 941–947. <https://doi.org/10.1016/j.anbehav.2013.02.014>
- Slocombe, K. E., & Newton-Fisher, N. E. (2005). Fruit sharing between wild adult chimpanzees (*Pan troglodytes schweinfurthii*): A socially significant event? *American Journal of Primatology*, 65(4), 385–391. <https://doi.org/10.1002/ajp.20123>
- Souza-Alves, J. P., Chagas, R. R. D., & Bezerra, B. M. (2019). Food-sharing behaviour within a group of free-living Endangered Coimbra-Filho's titi monkeys. *Journal of Ethology*, 37(1), 41–46. <https://doi.org/10.1007/s10164-018-0566-8>
- Stanford, C. B. (1999). *The Hunting Apes: Meat Eating and the Origins of Human Behavior*. Princeton University Press.
- Stevens, J. R., & Gilby, I. C. (2004). A conceptual framework for nonkin food sharing: Timing and currency of benefits. *Animal Behaviour*, 67(4), 603–614. <https://doi.org/10.1016/j.anbehav.2003.04.012>
- Stevens, J. R., & Stephens, D. W. (2002). Food sharing: A model of manipulation by harassment. In *Behavioral Ecology* (Vol. 13, Issue 3, pp. 393–400). Oxford University Press. <https://doi.org/10.1093/beheco/13.3.393>
- Strassmann, J. E., Page, R. E., Robinson, G. E., & Seeley, T. D. (2011). Kin selection and eusociality. *Nature* 471, E5–E6. <https://doi.org/10.1038/nature09833>
- Sugiyama, Y. (2004). Demographic parameters and life history of chimpanzees at Bossou, Guinea. *American Journal of Physical Anthropology*, 124, 154–165. <https://doi.org/10.1002/ajpa.10345>
- Suzuki, A. (1969). An ecological study of chimpanzees in a savanna woodland. *Primates*, 10, 103–148.
- Taylor, P.D. (1990). Allele-frequency change in a class structured population. *American Naturalist*, 135, 95–106.
- 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(1), 35–57. <https://doi.org/10.1086/406755>
- Troisi, C. A. (2021). Intergroup food transfers in wild golden lion tamarins (*Leontopithecus rosalia*). *Primates*, 62(1), 223–231. <https://doi.org/10.1007/s10329-020-00846-x>
- Troisi, C. A., Hoppitt, W. J. E., Ruiz-Miranda, C. R., & Laland, K. N. (2021). The role of food

- transfers in wild golden lion tamarins (*Leontopithecus rosalia*): Support for the informational and nutritional hypothesis. *Primates*, 62(1), 207–221.
<https://doi.org/10.1007/s10329-020-00835-0>
- Turner, M. G. (1989) Landscape ecology: The effect of pattern on process. *Annual Review of Ecological Systems*, 20, 171-197.
- Van Noordwijk, M. A., & Van Schaik, C. P. (2009). Intersexual food transfer among orangutans: Do females test males for coercive tendency? *Behavioral Ecology and Sociobiology*, 63(6), 883–890. <https://doi.org/10.1007/s00265-009-0728-3>
- Wade, M. J. (1985). Soft selection, hard selection, kin selection, and group selection. *American Naturalist*, 125, 61–73.
- Watts, D., & Mitani, J. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, 138(3), 299–327. <https://doi.org/https://doi.org/10.1163/15685390152032488>
- Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, 44(1), 43–55.
<https://doi.org/10.1007/s002650050513>
- Wenseleers, T., Helanterä, H., Hart, A., & Ratnieks, F. L. (2004). Worker reproduction and policing in insect societies: an ESS analysis. *Journal of Evolutionary Biology*, 17(5), 1035-1047.
- Wessling, E.G., Deschner, T., Mundry, R., Pruetz, J. D., Wittig, R. M., & Köhl, H. S. (2018). Seasonal variation in physiology challenges the notion of chimpanzees (*Pan troglodytes verus*) as a forest-adapted species. *Frontiers in Ecology & Evolution*, 6, 1-21.
<https://doi.org/10.3389/fevo.2018.00060>
- Wessling, E.G., Oelze, V.M., Esthius, H., et al. (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.
- West, S. A., Griffin, A. S., & Gardner, A. (2007). Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, 20, 415-432. <https://doi.org/10.1111/j.1420-9101.2006.01258.x>
- Wiens, J. A. (1966). On group selection and Wynne-Edwards' hypothesis. *American Scientist*, 54(3), 273–287.
- Wiessner, P. (1977). *Hxaro, a Regional System of Reciprocity*. University of Michigan Press.
- Wiessner, P. (2002). Hunting, healing, and hxaro exchange. A long-term perspective on !Kung (Ju/'hoansi) large-game hunting. *Evolution and Human Behavior*, 23(6), 407–436.
[https://doi.org/10.1016/S1090-5138\(02\)00096-X](https://doi.org/10.1016/S1090-5138(02)00096-X)
- Wilkinson, G. S. (1984). Reciprocal food sharing in the vampire bat. *Nature*, 308(8), 181–184.
- Williams, G. C. (1966). *Adaptation and Natural Selection: A Critique of Some Current*

Evolutionary Thought. Princeton University Press.

Williams, G. C. (1971). *Group Selection*. G. C. Williams (ed.). Transaction Publishers.

Williams, J. M., Oehlert, G. W., Carlis, J. V., & Pusey, A. E. (2004). Why do male chimpanzees defend a group range? *Animal Behaviour*, 68(3), 523–532.

<https://doi.org/https://doi.org/10.1016/j.anbehav.2003.09.015>

Wilson, D. S. (1977). Structured demes and the evolution of group-advantageous traits. *The American Naturalist*, 111(977), 157–185.

Wilson, D., & Wilson, E. (2007). The use of phylogenetic diversity in conservation biology and community ecology: A common base but different approaches. *Quarterly Review of Biology*, 82(4), 327–348. <https://doi.org/10.1086/703580>

Wilson, M.L., Kahlenberg, S.M., Wells, M., & Wrangham, R.W. (2012). Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees.

Animal Behaviour, 83, 277–291. <https://doi.org/10.1016/j.anbehav.2011.11.004>

Wittig, R. M., Crockford, C., Deschner, T., Langergraber, K. E., Ziegler, T. E., Zuberbu, K., & Crockford, C. (2014). Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B*, 281, 20133096. <https://doi.org/10.1098/rspb.2013.3096>

Wolovich, C. K., Perea-Rodriguez, J. P., & Fernandez-Duque, E. (2008). Food Transfers to Young and Mates in Wild Owl Monkeys (*Aotus azarai*). *American Journal of Primatology*, 20, 211–221. <https://doi.org/10.1002/ajp.20477>

Wrangham, R. W. (1999). Evolution of coalitionary killing. *American Journal of Physical Anthropology, Suppl* 29, 1–30. [https://doi.org/10.1002/\(sici\)1096-8644\(1999\)110:29+<1::aid-ajpa2>3.3.co;2-5](https://doi.org/10.1002/(sici)1096-8644(1999)110:29+<1::aid-ajpa2>3.3.co;2-5)

Wrangham, R. W., & Glowacki, L. (2012). Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers: Evaluating the chimpanzee model. *Human Nature*, 23(1), 5–29. <https://doi.org/10.1007/s12110-012-9132-1>

Wrangham, Richard W. (1975). Feeding ecology of chimpanzees in Gombe National Park. In *Primate Ecology*. University of Cambridge.

Wrangham, Richard W, & Peterson, D. (1996). Demonic males: Apes and the origins of human violence. In *Demonic males: Apes and the origins of human violence*. (p. 350). Houghton, Mifflin and Company.

Wright, B. M., Stredulinsky, E. H., Ellis, G. M., & Ford, J. K. B. (2016). Kin-directed food sharing promotes lifetime natal philopatry of both sexes in a population of fish-eating killer whales, *Orcinus orca*. *Animal Behaviour*, 115, 81–95.

<https://doi.org/10.1016/j.anbehav.2016.02.025>

Wright, S. (1922). Coefficients of Inbreeding and Relationship. *The American Naturalist*, LVI(645), 330–338.

Wynne-Edwards, V. C. (1962). *Animal Dispersion in Relation to Social Behavior*. Oliver and

Boyd.

Wynne-Edwards, V.C. (1986). *Evolution through Group Selection*. Blackwell Scientific Publications, Oxford, UK.

Yamamoto, S., & Tanaka, M. (2010). The influence of kin relationship and reciprocal context on chimpanzees' other-regarding preferences. *Animal Behaviour*, 79(3), 595–602.
<https://doi.org/https://doi.org/10.1016/j.anbehav.2009.11.034>

Yoshikawa, M., & Ogawa, H. (2015). Diet of savanna chimpanzees in the Ugalla area, Tanzania. *African Study Monographs*, 36, 189-209.

Young, M. W. (1971). *Fighting with Food: Leadership, Values and Social Control in a Massim Society*. Cambridge University Press.