Predation by female chimpanzees: Toward an understanding of sex differences in meat acquisition in the last common ancestor of *Pan* and *Homo*

Ian C. Gilby [a, *], Zarin P. Machanda [b, c], Robert C. O'Malley [d], Carson M. Murray [d], Elizabeth V. Lonsdorf [e], Kara Walker [f], Deus C. Mjungu [g], Emily Otali [h], Martin N. Muller [i], Melissa Emery Thompson [i], Anne E. Pusey [f, 1], Richard W. Wrangham [b, 1]

[a] School of Human Evolution and Social Change, and Institute of Human Origins, Arizona State University, Tempe, AZ 85287, USA
[b] Department of Human Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA
[c] Department of Anthropology, Tufts University, Medford, MA 02155, USA
[d] Center for the Advanced Study of Human Paleobiology, The George Washington University, Washington, DC 20052, USA
[e] Department of Psychology and Biological Foundations of Behavior Program, Franklin & Marshall College, Lancaster, PA 17603, USA
[f] Department of Evolutionary Anthropology, Duke University, Durham, NC 27708, USA
[g] Gombe Stream Research Centre, The Jane Goodall Institute, Kigoma, Tanzania
[h] Kibale Chimpanzee Project, Fort Portal, Uganda
[i] Department of Anthropology, University of New Mexico, Albuquerque, NM 87131, USA

ARTICLE INFO

ABSTRACT

Among modern foraging societies, men hunt more than women, who mostly target relatively low-quality, reliable resources (i.e., plants). This difference has long been assumed to reflect human female reproductive constraints, particularly caring for and provisioning mates and offspring. Long-term studies of chimpanzees (*Pan troglodytes*) enable tests of hypotheses about the possible origins of human sex differences in hunting, prior to pair-bonding and regular provisioning. We studied two eastern chimpanzee communities (Kasekela, Mitumba) in Gombe, Tanzania and one (Kanyawara) in Kibale, Uganda. Relative to males, females had low hunting rates in all three communities, even where they encountered red colobus monkeys (the primary prey of chimpanzees) as often as males did. There was no evidence that clinging offspring hampered female hunting. Instead, consistent with the hypothesis that females should be more risk-averse than males, females at all three sites specialized in low-cost prey (terrestrial/sedentary prey at Gombe; black and white colobus monkeys at Kanyawara). Female dominance rank was positively correlated with red colobus hunting probability only at Kasekela, suggesting that those in good physical condition were less sensitive to the costs of possible failure. Finally, the potential for carcass appropriation by males deterred females at Kasekela (but not Kanyawara or Mitumba) from hunting in parties containing many adult males. Although chimpanzees are not direct analogs of the last common ancestor (LCA) of *Pan* and *Homo*, these results suggest that before the emergence of social obligations regarding sharing and provisioning, constraints on hunting by LCA females did not necessarily stem from maternal care. Instead, they suggest that a risk-averse foraging strategy and the potential for losing prey to males limited female predation on vertebrates. Sex differences in hunting behavior would likely have preceded the evolution of the sexual division of labor among modern humans.

© 2017 Elsevier Ltd. All rights reserved.

* Corresponding author.
    E-mail addresses: ian.gilby@asu.edu (I.C. Gilby), zarin.machanda@tufts.edu (Z.P. Machanda), omalleyrc@gmail.com (R.C. O'Malley), cmmurray@gwu.edu (C.M. Murray), elonsdor@fandm.edu (E.V. Lonsdorf), kara.walker@duke.edu (K. Walker), dmjungu@janegoodall.or.tz (D.C. Mjungu), eotali@yahoo.co.uk (E. Otali), muller@unm.edu (M.N. Muller), memery@unm.edu (M. Emery Thompson), anne.pusey@duke.edu (A.E. Pusey), wrangham@fas.harvard.edu (R.W. Wrangham).
    [1] Shared senior authorship.

1. Introduction

Across modern foraging societies, men consistently hunt more often and contribute more meat to their group's diet than women do (Marlowe, 2007). For example, Hadza women acquired only 3.2% (by mass) of the prey brought back to camp (Wood and Marlowe, 2013). On average, Aché men spent 110 min per day in active pursuit of game (not including search time; Hill et al., 1985), in contrast to women's 3 min (Hurtado et al., 1985). Even in societies such as the Aka, in which women frequently participate in cooperative net hunts of small ungulates (Noss and Hewlett, 2001), they did so on only 20% of observation days, compared to 65% for men (Kitanishi, 1995). Also, unlike men, women rarely hunt alone or with projectiles, nor do they target large game (reviewed in Wood and Gilby, in press). For example, Hadza, /Gui and //Gana women typically target small, relatively immobile prey such as tortoises, young ungulates, hyrax, and nesting birds (Tanaka, 1980; Wood and Marlowe, 2013). Aché women often capture burrowing animals, but tend to call men when they locate more mobile vertebrate game (Gurven and Hill, 2009).

This ubiquitous sex difference in rates of meat acquisition among modern human foraging societies has long been assumed to be due to constraints that women face in carrying, caring for, and provisioning offspring (reviewed in Bliege Bird and Codding, 2015). Women focus on reliable, yet relatively low-quality, resources (i.e., plants) that ensure a regular supply of food for their children (Marlowe, 2007; Bliege Bird and Codding, 2015). Free from these constraints, males pursue higher-quality but less reliable resources (i.e., meat), either to complement women's contributions to the family's diet (the 'economy of scale' model, reviewed in Bliege Bird and Bird, 2008) or to elevate their status by sharing widely with the larger social group (the 'show off' hypothesis; Hawkes, 1991). Women's foraging efforts ensure that families will not go hungry when males fail to obtain meat. This scenario relies upon regular offspring provisioning, and in the case of the economy of scale model, food exchange within the pair bond. Among the great apes, these behaviors are unique to humans. Although 4—8 million years of evolution separate modern humans from their last common ancestor (LCA) with chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) (Patterson et al., 2006; Langergraber et al., 2012), morphological and behavioral data indicate that the chimpanzee is a valuable point of comparison for making inferences about the possible range of behavior exhibited by the LCA (Tanner and Zihlman, 1976; Wrangham and Pilbeam, 2001; McGrew, 2010; Wood and Harrison, 2011; Stanford, 2012; Lieberman, 2013; Muller et al., in press; but see Sayers and Lovejoy, 2008 for an alternative view). For example, Pickering (2013) uses chimpanzees as a reference when suggesting that the key to human hunting is the ability to de-couple aggression and foraging (but see Sobolewski et al., 2012; Gilby et al., 2013). Observing chimpanzees provides an opportunity to study factors affecting hunting behavior in a large-bodied, forest-dwelling hominoid faced with similar ecological challenges to those probably experienced by the LCA. It also allows for the testing of hypotheses about sex differences in meat acquisition in a species closely related to humans that lacks pair bonds and a sexual division of labor, and exhibits sex differences in a number of feeding and foraging patterns. These include the frequency and duration of tool-assisted insectivory (multiple populations, female biased; McGrew, 1979, 1992; Nishida and Hiraiwa, 1982), the frequency and efficiency of nut-cracking behavior (one population, female biased; Boesch and Boesch, 1981, 1984), the use of sticks to acquire galagos (one population, female biased; Pruetz and Bertolani, 2007; Pruetz et al., 2015), and the frequency and duration of meat consumption (multiple populations, male biased; Stanford et al., 1994a; Uehara, 1997; Mitani and Watts, 2001).

The hunting behavior of chimpanzees has been studied extensively, but the majority of this work is devoted to its most frequent context, namely male predation upon red colobus monkeys (*Procolobus [Piliocolobus]* spp.; Taï National Forest, Côte d'Ivoire: Boesch, 1994; Gombe National Park, Tanzania: Stanford et al., 1994b, Gilby et al., 2006, 2015; Mahale Mountains National Park, Tanzania: Uehara, 1997, Ngogo, Kibale National Park, Uganda: Mitani and Watts, 2001; Kanyawara, Kibale: Gilby et al., 2008). Relatively little attention has been given to predation on these or other vertebrates by female chimpanzees (but see Pruetz et al., 2015). Some of this bias is likely due to the fact that hunts of red colobus monkeys ('red colobus' hereafter) are most likely to occur in parties containing many male chimpanzees (Stanford et al., 1994b; Mitani and Watts, 2001; Gilby et al., 2006). Such large, male-biased parties are avoided by non-estrous females at some study sites (Wrangham and Smuts, 1980; Wrangham, 2000; Hashimoto et al., 2001). Since large parties are easier to find and follow, female predation rates may be underestimated if they often hunt alone or in all-female parties, and/or if they specialize in cryptic prey that require stealth or an element of surprise to capture.

In the few studies that report kills of all mammalian prey species by hunter age/sex class, female representation varies considerably across sites. Nearly one-third of all predation events at Fongoli, Senegal (30% of 99 captures or possessions; Pruetz et al., 2015) and Mahale (31% of 54 hunts or first observed possessions; Takahata et al., 1984) were made by females, compared to only 3% of 128 kills at Ngogo (Mitani and Watts, 1999). Females contributed 18% of kills at Taï (Boesch and Boesch, 1989) and 23% at Gombe (Goodall, 1986). At Gombe, males killed 26 animals during 7098 h of observation, while one female participated (jointly with a male) in a single kill in 7485 observation hours (Wrangham and Bergmann-Riss, 1990). The variation among study sites is noteworthy, and is likely due to a combination of social and ecological factors, as well as research focus and effort.

Here we use long-term data from three communities of eastern chimpanzees (*P. t. schweinfurthii*) to test three hypotheses explaining sex differences in vertebrate hunting frequency. While hunting and foraging for invertebrates occurs in many nonhuman primates, few other species have been shown to consume a significant amount of vertebrate prey (with the exception of white-faced capuchins [Fedigan, 1990; Rose, 1997; Rose et al., 2003; Perry and Ordoñez Jiménez, 2006] and baboons [Butynski, 1982]), suggesting that a specific focus on hunting of vertebrates is warranted. We do not address cannibalism, which is complicated by selection pressure favoring infanticide in the context of intrasexual competition (Arcadi and Wrangham, 1999; Pusey and Schroepfer-Walker, 2013). Bonobos, as equally related to humans as chimpanzees are, also hunt vertebrates, including arboreal monkeys (Hohmann and Fruth, 2007; Surbeck and Hohmann, 2008; Surbeck et al., 2009). However, they do so very rarely, prohibiting hypothesis-driven analyses of sex differences. Nevertheless, as the data on bonobos accumulate, a more complete understanding of why they hunt less often than chimpanzees will help us to make further inferences about the hunting behavior of the LCA of *Pan* and *Homo*.

1.1. Background and hypotheses

1.1.1. Opportunity Due to the costs of feeding competition, non-sexually receptive adult female chimpanzees at our study sites spend more time alone compared to adult males (Kanyawara: Wrangham et al., 1992; Gombe: Wrangham and Smuts, 1980; Murray et al., 2007). Because the probability of hunting (and capturing) red colobus is strongly positively correlated with male

chimpanzee party size (Mitani and Watts, 2001; Gilby et al., 2006, 2008), females in these communities may have fewer opportunities to hunt red colobus because they travel in large parties less frequently than males do. Large parties also travel greater distances relative to small parties, increasing the probability of encountering red colobus (Gilby et al., 2013). Since red colobus make up a high percentage of the prey at most long-term chimpanzee research sites (53%–92% of prey items; Newton-Fisher, 2014), the relatively low gregariousness of females compared to males provides a simple explanation for lower female predation rates at these sites. However, females may have more opportunities than males to hunt prey types that require some element of stealth or surprise to capture (e.g., cached infant bushbuck, *Tragelaphus scriptus*).

The opportunity hypothesis predicts (Table 1) that 1) chimpanzee parties will be smaller at kills of terrestrial and/or sedentary prey species (that require surprise or stealth to capture) compared to kills of arboreal monkeys; 2) females will encounter red colobus less often than males will; 3) female hunting rates of red colobus will be positively correlated with overall gregariousness; and 4) when present at a hunt attempt of red colobus, male and female chimpanzees will be equally likely to hunt.

1.1.2. Risk-sensitivity Female chimpanzees are expected to be more risk-averse than males for two reasons. First, they should be more averse to the risk of food shortage because variation in female reproductive success is determined more by calorie intake than by access to mates (Trivers, 1972). Therefore, females should be especially sensitive to the costs and benefits associated with hunting, including energy expenditure, their physical condition, and the net energetic and nutritional value of the prey. Second, females are often carrying young offspring that could be injured during a hunt. Predation upon red colobus appears risky (in terms of energy and the possibility of injury) relative to other forms of predation (e.g., snatching an infant bushbuck or duiker). It can be time consuming - the average red colobus hunt at Gombe lasts 28 min (Stanford, 1998), although there is considerable variation (Gilby, personal observation). Also, climbing through the canopy in pursuit of monkeys is likely to be energetically expensive (Gilby and Wrangham, 2007), and hunters have been mobbed, bitten, and fallen from considerable heights (Goodall, 1986; Stanford, 1998). Together, these observations suggest that risk-averse individuals should avoid hunting red colobus. Prior studies indicate that terrestrial or sedentary animals make up a substantial fraction of the prey captured by female chimpanzees (Takahata et al., 1984; Goodall, 1986; Pruetz et al., 2015), although the relative acquisition of

different prey types by males and females has not been systematically examined.

The risk-sensitivity hypothesis (Table 1) predicts sex differences in both the types of prey captured and the factors affecting the decision to pursue risky prey. It predicts that 1) females will specialize in prey species that do not involve extensive pursuit, and/or involve a lower risk of injury to the hunter. When present at a red colobus hunt attempt, the probability that a given female hunts is expected to be 2) lower if she is has a clinging infant, and 3) greater if she is high-ranking (as a proxy for physical condition, since female dominance rank was positively correlated with body mass at Gombe; Pusey et al., 2005).

1.1.3. Male appropriation When females capture a prey item, it is often immediately stolen by an adult male. For example, seven of 19 prey captured by females in mixed-sex parties at Gombe were immediately appropriated by males (Goodall, 1986). Ten of the 12 that were not stolen had been captured (and were retained) by Gigi, an unusually large female who was able to resist male attempts to steal the carcass. To our knowledge, appropriation by adult females has not been reported from any long-term site. The potential for carcass appropriation by males could in theory deter females from hunting in parties containing many adult males, as long as the likelihood of losing the carcass outweighs any net benefit to individual hunters in large groups (via by-product mutualism; West-Eberhard, 1975; Brown, 1983; Connor, 1995), as is the case for male chimpanzees (Gilby et al., 2008, 2015). This is analogous to data from obligate carnivores demonstrating that prey choice (e.g., by cheetahs) may be affected by the threat of kleptoparasitism (e.g., by hyenas; Hayward et al., 2006).

The male appropriation hypothesis (Table 1) predicts that 1) the likelihood of having one's carcass stolen will be higher for females than for males; 2) when a female makes a kill, the probability that the carcass is stolen from her will be positively associated with the number of adult males present; and 3) at a hunt, the probability that a given female participates will be negatively correlated with the number of adult male chimpanzees present.

2. Methods

2.1. Research sites

We tested our predictions using data collected over a total of 71 community-years from three chimpanzee (*P. t. schweinfurthii*) communities at two East African study sites. Gombe National Park comprises 35 km^2 of riverine forest, woodland and grassland (Clutton-Brock and Gillett, 1979) on the shore of Lake Tanganyika,

Table 1
Summary of hypotheses, predictions and results.[a]

Hypothesis	Predictions	Supported?		
		Kasekela	Mitumba	Kanyawara
Opportunity	1) Chimpanzee parties smaller at kills of terrestrial/sedentary prey	Y	N	▓▓▓▓
	2) Females encounter red colobus less often than males do	Y	N	Y
	3) Frequency of red colobus hunting correlates positively with female gregariousness	**Y**	**Y**	**Y**
	4) When present at a red colobus hunt, males and females equally likely to participate.	**N**	**N**	**N**
Risk-sensitivity	1) Females will specialize in low-cost prey	**Y**	**Y**	**Y**
	2) At a red colobus hunt, a female will be:			
	a) less likely to participate with clinging offspring	**N**	**N**	**N**
	b) more likely to participate if high-ranking	Y	N	N
Male appropriation	1) Likelihood of carcass theft higher for females	Y	▓▓▓▓	N
	2) Stealing from females will occur more often in parties with many adult males	Y	▓▓▓▓	▓▓▓▓
	3) At a hunt, the probability that a female participates will be negatively correlated with number of males present	Y	N	N

[a] Gray cells indicate that a prediction could not be tested in a particular community. Bold type highlights results that were consistent across all three study sites. Y = yes, N = no.

in western Tanzania. It contains three communities of chimpanzees: Mitumba in the north, Kasekela in the center and Kalande in the south. Research at Gombe began in 1960 (Goodall, 1986), and daily follows (see below) of chimpanzees have been conducted in Kasekela and Mitumba since the early 1970s and mid-1990s, respectively (Goodall, 1986; Wilson, 2012). The Kalande group remains relatively unhabituated and is not included in these analyses. During our study period (1976−2013), the Kasekela community consisted of an average of 11 (range: 7−14) adult males and 17 (range: 11−25) adult females. Following previous hunting studies from Gombe (Gilby et al., 2006, 2013, 2015) and Kanyawara (Gilby and Wrangham, 2007; Gilby et al., 2008), we considered males that were at least 12 years old as adults. We defined females as adult at ≥13 years of age, by which time they have settled and the earliest pregnancies have been reported (for *P. t. schweinfurthii*; Emery Thompson et al., 2007; Emery Thompson, 2013). Mean yearly community range size (98% Minimum Convex Polygon [MCP]) for Kasekela (±1 standard deviation) was 11.31 (±4.03) km^2. The Mitumba community is much smaller than Kasekela. During our study period (2000−2014), there was an average of 3 (range: 2−6) adult males and 8 (range: 6−9) adult females in Mitumba, that ranged in an area (98% MCP) of 4.05 (±1.03) km^2.

During the study period (1996−2015), the Kanyawara chimpanzee community had a yearly median home range of 16.4 km^2 (98% MCP; Wilson et al., 2012) in the northwest quadrant of Kibale National Park, Uganda. Their range consisted of approximately 60% moist deciduous forest, with small areas of swamp, grassland and colonizing forest (Chapman and Wrangham, 1993). The community has been studied continuously since 1987, and all individuals were habituated to human observers by 1993. Between 1996 and 2015 there was an average of 12 (range: 9−15) adult males and 16 (range: 12−19) adult females in Kanyawara.

2.2. Data collection

2.2.1. Gombe (Kasekela and Mitumba) For the present study, we analyzed data collected on chimpanzees in Kasekela between 1976 and 2013, and in Mitumba between 2000 and 2014. Each day, field assistants followed a focal chimpanzee in each community from night-nest to night-nest, when possible (Goodall, 1986; Wilson, 2012). Observers located focal animals by consulting nesting and party composition data from the previous day, listening for vocalizations, and/or checking recent feeding trees, and attempted to follow each adult once per month. One observer used a checksheet to continuously record party composition, the identity of any females with full ano-genital swellings (indicating sexual receptivity; Goodall, 1986), all feeding by the focal individual and the presence of other species (regardless of any interest in hunting). The second observer used all-occurrence sampling (Altmann, 1974) to record the behavior of the focal chimpanzee, as well as conspicuous group-level activities, including aggression, hunting, scavenging and piracy (theft of prey from baboons). When hunting occurred, he recorded the identity of all chimpanzees observed to pursue prey. When possible, he recorded which chimpanzee(s) made a kill (or initially obtained the carcass in the case of piracy or scavenging), and those that subsequently acquired and ate parts of the carcass.

Family follows (of mothers and dependent offspring) began in 1970 in Kasekela, and complement the individual focal data described above. Observers collected data on a target mother, her youngest dependent offspring, and next oldest offspring, when present. They recorded behaviors such as traveling, resting, feeding, and grooming at 1-min point samples, as well as collecting data on group composition. Events such as hunts, aggression and vocalizations were recorded ad libitum.

2.2.2. Kanyawara Field assistants at Kanyawara worked in teams of two and entered the forest before dawn to locate chimpanzees by returning to the nesting site from the previous night. If no nesting location was known, the assistants would listen for calls or wait at known fruiting trees. Once they located a party of chimpanzees, at 15 min intervals, one observer recorded party composition (including female sexual swellings), feeding, and (since 1996) the presence of any potential prey species within 100 m of the chimpanzees. Prior to 2009, the second field assistant took detailed narrative notes on all occurrences of conspicuous behavior, including aggression and hunting. Since 2009, these observations targeted a focal individual from the start of the follow to the end, usually all day. The assistant recorded the behavior of the focal individual at 1 min intervals, as well as all occurrences of conspicuous behavior by other group members, including aggression, submissive behavior and hunting. When the chimpanzees began hunting or were seen holding a prey item, both field assistants spread out to ensure that they had clear observations of as many party members as possible. They conferred after the hunt and recorded all details on an additional predation-specific checksheet. This included the timing and identity of any chimpanzees who hunted, killed, possessed a carcass and/or ate meat.

2.3. Data extraction

From the data collected at all three sites, we extracted the start times of all 'encounters' with red colobus from the checksheets and notes. At Kasekela and Mitumba, an encounter began when red colobus were first observed within approximately 50 m of the focal chimpanzee. At Kanyawara, we identified an encounter as any 15 min scan when the chimpanzees were within 100 m of red colobus that was not immediately preceded by another scan with red colobus. For each encounter, we calculated the number of adult males and females who were present within 15 min of the start of the encounter (Kasekela and Mitumba) or at the 15 min scan at the start of an encounter (Kanyawara). In all three communities, we matched each encounter with hunt observations to identify all 'hunt attempts'. We defined these as encounters at which there was at least one 'hunter' (any chimpanzee observed to climb in pursuit of red colobus) of either sex (Gilby et al., 2006, 2008, 2015). We excluded all encounters for which there was insufficient detail in the notes to determine whether or not at least one chimpanzee actually climbed (Gilby et al., 2006, 2008, 2015). A 'successful hunt' was any hunt attempt at which at least one monkey was killed. Whenever possible, we recorded the identity of the chimpanzee(s) that made the kill(s). On the rare occasion when two chimpanzees simultaneously captured the same prey item, we credited each captor with half of the kill.

In most cases, opportunities to acquire prey other than arboreal monkeys are difficult to identify unless the attempt is successful. For example, it is unlikely that researchers will notice the presence of nestlings in a tree hole, or a bushbuck fawn hidden in undergrowth, unless the chimpanzees make an attempt to acquire them. Usually, with these types of prey, the success rate is high, as the prey is harmless and/or easily captured. Also, while the observers note encounters with all species, it is not always clear whether a catchable prey item (e.g., an infant) is available. Therefore, we began all analyses of non-red colobus prey at acquisition. At Kanyawara, we identified non-red colobus acquisition events using the predation checksheets. At Gombe, we used several methods. First, for the whole study period in each community (Kasekela: 1976−2013, Mitumba: 2000−2014), we used the focal feeding records to identify all cases when the focal chimpanzee ate non-colobus meat. We then extracted acquisition details from the narrative notes. Second, for Kasekela between 1994 and 2013 (for

which the narrative notes had been digitally transcribed), we used keyword searches to find all instances when non-colobus animal species were mentioned. Finally, we supplemented this dataset with successful hunts and meat eating recorded during family follows (Kasekela) and by one of us (KW), who conducted 226 focal follows of adolescent and young adult female chimpanzees (ages 8—16 years) between June 2011 and May 2014 in Kasekela and Mitumba (Walker, 2015).

When meat was acquired, we recorded 1) whether a prey item was eaten (at least partially) by any member of the party, 2) the identity of the acquirer (if known), 3) chimpanzee party composition, and 4) the mode of acquisition (kill, piracy, scavenging). At Gombe, 'piracy' occurred when the chimpanzees were seen to take a carcass from baboons. In some cases the actual event was not observed, but it was clear that a theft had just occurred. For example, on 10 December, 2001, Kasekela observers heard commotion among baboons, and briefly lost their focal as the chimpanzees rushed toward the noise. When the observers caught up, the chimpanzees had a bushbuck carcass, and baboons were still close by. Piracy was not observed at Kanyawara. 'Scavenging' occurred when chimpanzees encountered and ate a prey item that was already dead, and there were no predators visible in the area. Finally, at Kasekela and Kanyawara, for every case when a chimpanzee possessed a prey item, and it was clear from the notes that the observation was complete (i.e., the possessor was the focal chimpanzee or there was sufficient detail to indicate that the entire possession was observed), we recorded whether another chimpanzee stole the carcass from him/her. We defined such 'theft' as carcass appropriation that evoked a negative reaction from the possessor (e.g., scream, retaliate). Theft data have not yet been extracted from the Swahili notes from Mitumba.

For all three communities, we used submissive pant-grunt data to calculate female Elo dominance scores (Neumann et al., 2011) using the method developed by Foerster et al. (2016) which uses maximum likelihood to determine the initial score for each individual and the weight (k) of each dominance interaction. In order to be able to compare Elo-ratings across periods and communities, we re-scaled them to fall between 0 and 1, preserving gaps among individuals. One Kanyawara female (LP) never pant-grunted to another female during the study period, which made it impossible to calculate an Elo-rating for her. Therefore, we gave her a score of 1 in the re-scaled hierarchy.

2.4. Statistical analyses

We used R version 3.2.3 (R Development Core Team, 2015) with the lme4 (Bates et al., 2014), and multcomp (Hothorn et al., 2008) packages for statistical analyses. We ran the following tests separately for each community. To test the first prediction of the opportunity hypothesis (chimpanzee party size versus prey type), we ran a Generalized Linear Model (GLM) with the number of adult chimpanzees present as the (continuous) dependent variable, and prey type (arboreal monkey, other) as a categorical independent variable, with a Gaussian error structure and identity link function. To control for changes in community size over time, we included the number of adult chimpanzees alive in the community on that date as a second factor in the model. To test the second prediction of the opportunity hypothesis (red colobus encounter rate versus sex), we ran a Generalized Linear Mixed Model (GLMM) with focal follow as the unit of analysis and red colobus encounter (Y/N) as the response variable. We included focal chimpanzee sex and follow duration as main effects, with a binomial error structure, logit link function, and focal chimpanzee ID as a random effect. Next, we tested the third prediction of the opportunity hypothesis (red colobus hunting frequency versus female gregariousness). For each adult female, we

determined the number of adults present at each 15 min interval that she was observed in a party, and then calculated the mean for each year she was an adult. We used this measure of gregariousness as a main effect in a GLMM, with red colobus hunting frequency (number of red colobus hunt attempts in a given year at which the female hunted) as the dependent variable. The models used a Poisson link function and included observation time of each female as an offset, with year and chimpanzee ID as random effects. To test the fourth prediction of the opportunity hypothesis, we asked whether, when present at a red colobus hunt attempt, focal females were less likely to hunt than focal males were. We ran a GLMM (error structure: binomial, link function: logit, random effect: focal ID) with focal hunt (Y/N) as the dependent variable and sex of the focal as the main effect. Due to the relatively small sample of focal data from Kanyawara, we ran a follow-up GLMM on the full Kanyawara dataset (1996—2015), with each adult chimpanzee present at a hunt attempt (rather than the focal individual) as the unit of analysis. We modeled the probability that a given individual hunted (Y/N) as a function of sex, with chimpanzee ID and hunt ID as random factors, using a logit link function and binomial error structure.

Next, we tested the first prediction of the risk-sensitivity hypothesis (prey type versus sex of acquirer). For each prey item acquired, we used a GLM to model the probability that the acquirer was female (Y/N), using a binomial error structure and logit link function, and included prey type (arboreal monkey, bushpig/baboon, bushbuck/other) as a main effect. To account for chance, we also included the number of adult male and adult female chimpanzees present at the acquisition as main effects.

Because of the potential confounding effects of dominance rank, clinging offspring and adult male party size, we ran a GLMM incorporating these variables, thus simultaneously testing prediction two of the risk sensitivity hypothesis and prediction three of the male appropriation hypothesis, concerning female participation in red colobus hunts. For Kasekela and Mitumba, we modeled the probability that a focal female hunted red colobus (when present at a hunt attempt), with her scaled Elo-rating on that day, dependent offspring (≤ 2 yr old, Y/N) and adult male party size as main effects. We used a binomial error structure, logit link function, and included focal ID as a random effect. Because there was only one red colobus hunt by a focal female at Kanyawara, we ran a follow-up GLMM on the entire dataset (1996—2015), with each female present at a hunt attempt (rather than the focal) as the unit of analysis and hunt ID as an additional random effect. To test prediction one of the male appropriation hypothesis (carcass theft versus sex) we performed a GLMM (steal [Y/N] versus female possessor [Y/N], error structure: binomial, link function: logit, random effect: chimpanzee ID). Finally, to test prediction two (theft probability from females versus number of adult males present), we ran a follow-up GLMM, including the number of adult males present and the female possessor × adult males interaction term.

3. Results

3.1. Summary statistics

3.1.1. *Kasekela* At Kasekela, chimpanzees were observed to feed upon 2206 vertebrate prey items (from 1292 hunts or piracy/scavenging events) between 1976 and 2013 (Table 2). Females accounted for 263 (14.5%) of the 1819 cases in which the sex of the initial acquirer was clear, although females acquired a greater percentage of the non-colobus prey (33.8% of 297). Notably, females acquired 22.5 (45.9%) of the 49 bushbuck fawns and 27 (69.2%) of the 39 birds. By contrast, females captured only 163.5 (10.7%) of the 1523 red colobus. Of the 360 non-colobus prey items for which the mode of acquisition could be ascertained,

there were 38 (10.5%) cases of piracy, in which chimpanzees stole meat (37 bushbuck fawns and one young bushpig) from baboons. In 44.4% (12/27) of the piracy cases in which the sex of the acquirer was known, it was a female. There were three cases of scavenging − on a blue monkey, a bushbuck, and a redtail monkey. The observers estimated that the bushbuck (mainly ribs and skin) had been dead for about two days based on the presence of maggots. In one case, chimpanzees retrieved a rodent that was dropped by an eagle. There were no observed cases of piracy or scavenging of red colobus.

3.1.2. Mitumba Mitumba chimpanzees were observed to feed upon 254 prey items (from 204 hunts or piracy events) between 2000 and 2014 (Table 2). Of these, 208 (81.9%) were red colobus. Females acquired 21.4% (47.5/222) of all prey. As in Kasekela, females caught a larger percentage of the non-colobus prey (33.3%; 12/36), including 45% (5/11) of the bushbuck. However, females were responsible for a greater percentage (19.1%) of the red colobus kills (35.5/186) in Mitumba than in Kasekela (10.7%; 163.5/1523). There were 10 cases of piracy, all of which were bushbuck fawns stolen from baboons. In three (37.5%) of the eight cases in which the sex of the acquirer was known, it was a female. No scavenging events were observed.

3.1.3. Kanyawara At Kanyawara, chimpanzees were observed to feed upon 349 prey items (from 213 hunts and two scavenging events) between 1996 and 2015 (Table 2). All but one of these (a red duiker, which was scavenged, see below) was an arboreal monkey. As at Gombe, the majority ($n = 288$, 82.5%) were red colobus. The second-most frequent prey ($n = 44$) were black and white colobus monkeys, which are not present at Gombe. When the killer could be identified, females at Kanyawara were responsible for 11 (5.1%) and six (16.7%) of 214 red colobus and 36 black and white colobus kills, respectively. As at Gombe, females at Kanyawara were responsible for a greater proportion of the kills of redtail monkeys (3/4, 75%) and blue monkeys (3/5, 60%) than of red colobus.

There was one case in which chimpanzees caught a red duiker which they then used in dominance displays for over an hour. The duiker eventually died and was not consumed, and is therefore not included in the above totals. In a separate incident, an adult female found a dead duiker in a tree and fed on part of the head. On 12 March, 1997, adult male KK emerged from the undergrowth with an infant red colobus that the observers noted was decomposing, emitting a strong odor. KK fed on the carcass for 120 min before relinquishing it to adult female LP, who was still eating it 15 min later when the chimpanzee party was lost. There were no cases of piracy at Kanyawara.

3.2. Opportunity hypothesis: prey type and chimpanzee party size

In Kasekela, a mean of 39.7% (standard error [S.E.] = 0.7) of community adults were present at kills of arboreal monkeys, compared to 32.4% (S.E. = 1.8) of kills of terrestrial or sedentary prey. As expected, the association between adult party size and adult community size was positive (GLM parameter estimate: 0.50, $t = 12.8$, $p < 0.0001$). With this controlled for, chimpanzee party size at kills of arboreal monkeys was significantly greater than at kills of other prey: (estimate = 1.94, $t = 3.66$, $p = 0.0003$), supporting the opportunity hypothesis (Table 1). In Mitumba, a mean of 61.5% (S.E. = 2.1), of community adults were present at kills of arboreal monkeys ($n = 145$) compared to 58.5% (S.E. = 6.5) of terrestrial or sedentary prey. This difference was not statistically significant (GLM, estimate = 0.46, $t = 0.65$, $p = 0.52$) whether or not we controlled for the number of adults in the community (which was not significant at $p = 0.42$). Therefore, in Mitumba, there was no evidence that fewer community members were present at hunts

Table 2
Predation totals by community, sex of killer and prey type.[a]

Community	Sex of Killer	All Prey	Arboreal Monkeys							Terrestrial/Active							Concealed/sedentary/other						
			Red colobus	Black & white colobus	Red-tailed monkey	Blue monkey	Grey-cheeked mangabey	Total	Bushpig	Baboon	Vervet monkey	Total	Bushbuck	Bird	Red duiker	Rodent	Egg	Galago	Lizard	Bat	Unknown	Total
Kasekela 1976–2013	M	1556	1359.5		10.5	3		1373	84.5	55	1	140.5	26.5	12		2	1					42.5
	F	263	163.5		5.5	4		173	23.5	7		30.5	22.5	27		2	7	1	1		1	60.5
	U	387	290		6	3		299	31	22		53	34	1								35
	Total	2206	1813		22	10		1845	139	84	1	224	83	40		4	8	1	1		1	138
	% by F[b]	14.5	10.7		34.4	57.1		11.2	21.8	11.3	0	17.8	45.9	69.2			87.5					58.7
Mitumba 2000–2014	M	174.5	150.5		3	1		154.5	11	3		14	6									6
	F	47.5	35.5		1	1		37.5	1			1	5	2		1	1					9
	U	32	22		2			24	2			2	6									6
	Total	254	208		6	2		216	14	3		17	17	2		1	1					21
	% by F[b]	21.4	19.1		25	50		19.5	8.3	0		6.7	45.5	100		100	100					60
Kanyawara 1996–2015	M	238	203	30	1	2	2	238							1							0
	F	23	11	6	3	3		23														0
	U	88	74	8	1	1		84							1					3	3	4
	Total	349	288	44	5	6	2	345												3	3	4
	% by F[b]	8.8	5.1	16.7	75	60	0	8.8														

[a] Sex of killer: M = Male, F = Female, U = Unknown. Decimals arise when one prey item is captured jointly by a male and a female − each was credited with half of the kill. Shaded cells indicate absence of that species at that site.
[b] Only cases when sex of acquirer is known.

of prey that may require stealth or an element of surprise to capture, a finding that does not support the opportunity hypothesis. We were unable to test this prediction at Kanyawara, where all but one of the 346 identifiable prey items were arboreal monkeys.

3.3. Opportunity hypothesis: sex differences in red colobus encounter rate

At all three sites, GLMMs demonstrated significant, positive association between follow duration and the probability of encountering red colobus (Kasekela: estimate = 0.19, Z = 21.2, $p < 0.0001$; Mitumba: estimate = 0.15, Z = 10.0, $p < 0.0001$; Kanyawara: estimate = 0.08, Z = 2.9, $p = 0.004$). With follow duration statistically controlled for, the models indicated that the probability of encountering red colobus was significantly lower if the focal chimpanzee was female at Kasekela (estimate = −0.66, Z = −5.1, $p < 0.0001$) and at Kanyawara (estimate = −0.31, Z = −2.1, $p = 0.04$), supporting the opportunity hypothesis. This was not the case at Mitumba, however (Z = 0.1, $p = 0.9$).

3.4. Opportunity hypothesis: female gregariousness and red colobus hunting frequency

There was a strong positive association between a female's gregariousness and her participation in red colobus hunting in all three communities (Kasekela: estimate = 0.34, Z = 6.17, $p < 0.0001$; Mitumba: estimate = 1.54, Z = 6.31, $p < 0.0001$, Kanyawara: estimate = 0.63, Z = 5.11, $p < 0.0001$), supporting the opportunity hypothesis.

3.5. Opportunity hypothesis: hunting probability by sex

The focal chimpanzee was less likely to participate in a hunt if female than if male at Kasekela (estimate = −1.22, Z = −6.9, $p < 0.0001$) and Mitumba (estimate = −1.01, Z = −4.08, $p < 0.0001$), but not at Kanyawara (estimate = −2.31, Z = −1.50, $p = 0.13$) (Fig. 1). However, the lack of statistical significance at Kanyawara was likely

due to the relatively small sample size (seven years of focal data, 35 hunt attempts). The follow-up GLMM on the full Kanyawara dataset (with each present adult chimpanzee as the unit of analysis) demonstrated that female chimpanzees were significantly less likely to participate than males were (estimate = −2.27, Z = −5.72, $p < 0.0001$).

3.6. Risk-sensitivity hypothesis: prey type versus sex of acquirer

At Kasekela, as expected by chance, the likelihood that a prey acquirer was female correlated negatively with the number of adult male chimpanzees (estimate = −0.21, Z = −7.7, $p < 0.0001$) and positively with the number of adult females (estimate = 0.14, Z = 6.89, $p < 0.0001$) present at a prey acquisition event. With these factors controlled for, the probability that a given prey item was acquired by a female was higher if the prey was a bushpig or baboon than if it was an arboreal monkey (estimate = 0.56, Z = 2.3, $p = 0.02$) (Fig. 2). If the prey was a bushbuck (or egg, rodent, etc.) the odds that the acquirer was female were even higher (estimate = 2.2, Z = 8.99, $p < 0.0001$).

In Mitumba, there was no effect of the number of adult male (Z = −0.28, $p = 0.07$) or female (Z = −0.06, $p = 0.41$) chimpanzees on the probability that a prey acquirer was female. However, as in Kasekela, when the prey was bushbuck/other, the probability that the acquirer was female was significantly higher than if the prey was an arboreal monkey (estimate = 1.77, Z = 3.09, $p = 0.002$), or a baboon or bushpig (estimate = 3.17, Z = 2.70, $p = 0.007$, Fig. 2). There was no sex difference in the acquisition of baboon/bushpig vs. arboreal monkeys (Z = −1.32, $p = 0.19$). Given the relatively limited prey profile, we were unable to test this prediction at Kanyawara.

3.7. Risk-sensitivity and male appropriation hypotheses: female participation in red colobus hunts

There was a significant positive association between dominance rank and focal female hunting probability at Kasekela ($n = 384$ hunt
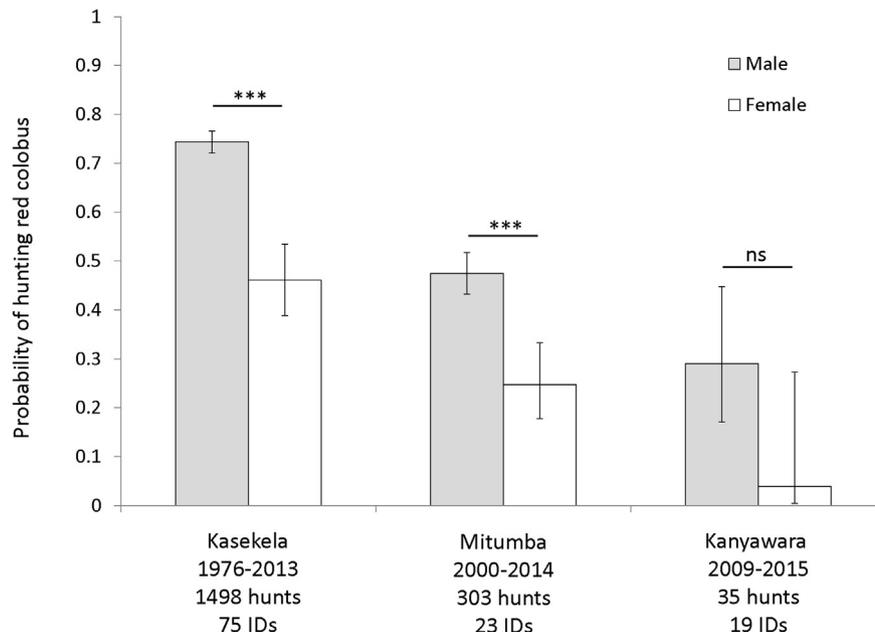

Figure 1. Relationship between the probability of hunting by a focal chimpanzee (when present at a red colobus hunt attempt) and sex of the focal. These predicted values were calculated from the GLMM described in the text, with error bars representing 1 standard error. Study period, and the number of hunts and focal chimpanzees (IDs) are reported for each community. ***$p < 0.0001$. Ns = not significant.
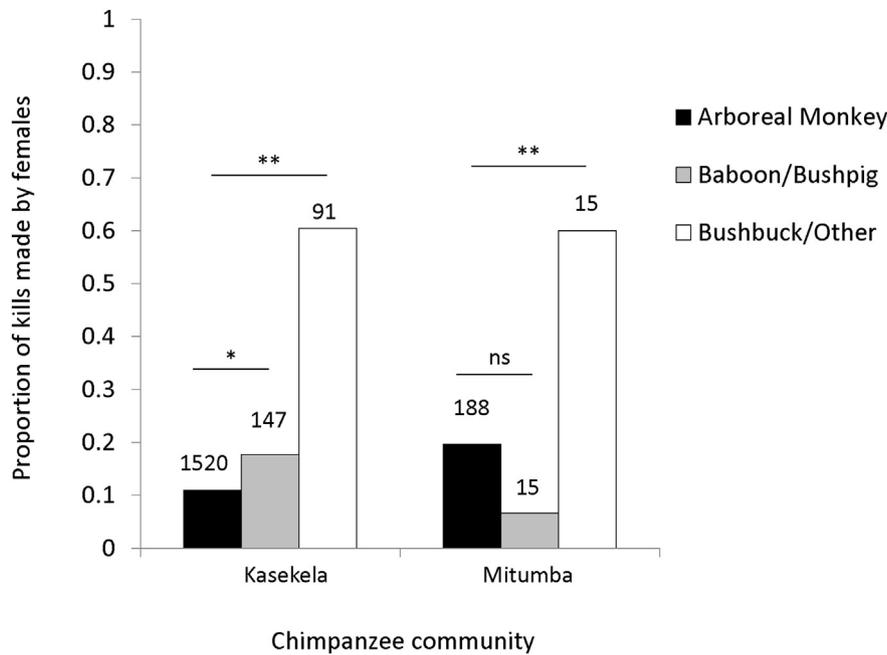
Figure 2. Prey type by sex of acquirer, Kasekela. Numbers indicate the total prey items for which the sex of the killer was known. $^*p < 0.05$; $^{**}p < 0.005$. *p*-values based on GLMs described in the text, which controlled for the number of male and female chimpanzees present at a kill. Ns = not significant.

Table 3
Summary of GLMMs of female hunting probability (Y/N) versus dominance rank (scaled Elo-rating) , presence of clinging offspring and adult male party size.[a]

Community	Fixed effect	Estimate	Z	p
Kasekela	Intercept	−4.29	−1.28	0.2
	Scaled Elo-rating	**0.93**	**2.01**	**0.04**
	Offspring ≤ 2yr	0.18	0.76	0.45
	Adult males	**−0.06**	**−2**	**0.04**
Mitumba	Intercept	−0.25	−0.39	0.7
	Scaled Elo-rating	−0.61	−0.96	0.34
	Offspring ≤ 2yr	0.08	0.18	0.86
	Adult males	−0.26	−1.25	0.21
Kanyawara	**Intercept**	**−6.4**	**−2.76**	**0.006**
	Scaled Elo-rating	−0.17	−0.19	0.85
	Offspring ≤ 2yr	**0.82**	**1.93**	**0.050**
	Adult males	0.18	1.15	0.25

[a] Bold indicates statistical significance.

attempts attended, 35 females, Table 3), supporting the risk sensitivity hypothesis. However, this was not the case at Mitumba (*n* = 123 hunt attempts attended, nine females) or Kanyawara (*n* = 135 hunt attempts attended, 18 females, mean 3.9 females per hunt).

Focal females at both Kasekela and Mitumba were equally likely to hunt red colobus whether or not they had an offspring under two years of age (Table 3), a result that does not support the risk sensitivity hypothesis. At Kanyawara, females with offspring under two years old were actually more likely to hunt than those with older (or no) offspring (Table 3). To investigate this result further, we conducted a pair-wise test on the eight adult females that were present for at least 15 red colobus hunt attempts with an offspring under two years of age, and 15 hunt attempts without. For each female, we calculated the proportion of hunt attempts in which she hunted with and without young offspring. Five females exhibited higher rates when they had young offspring, and three had lower rates, a difference that was not statistically significant (Wilcoxon Signed Ranks Test, V = 33, *p* = 0.23).

Focal females at Kasekela were less likely to hunt as the number of adult males present increased (Table 3), supporting the male

appropriation hypothesis. However, this was not the case at Mitumba or with female hunt attendees at Kanyawara (Table 3).

3.8. Male appropriation hypothesis: carcass theft versus sex and number of adult males

For each carcass possession by an adult chimpanzee, we recorded whether or not the possessor had the carcass stolen. At Kasekela, there were 220 cases for which we could be absolutely sure whether or not theft took place — e.g., the possessor was the focal individual, a theft was explicitly described, or there were multiple descriptions of a non-focal individual continually possessing meat from beginning to end. If a non-focal meat possessor was simply seen later without meat, and there was no description of a theft, we did not include the possession in the following analysis. Carcasses were stolen from adult males in 3.8% (5/131) of possessions, compared to 28.1% (25/89) for females. This difference was statistically significant — females were more likely to have their carcass stolen than males were (GLMM of steal versus female possessor: estimate = 2.29, Z = 4.45, *p* < 0.0001). In the follow-up GLMM, including the number of adult males present and the female possessor × adult males interaction term, the interaction term was significant, indicating that the probability that a female had the carcass stolen from her increased with the number of males present (Table 4, Fig. 3). These results support the male appropriation hypothesis.

At Kanyawara, there were 207 initial carcass possessions by adult chimpanzees for which it could be determined conclusively

Table 4
Output of GLMM of the probability of having a carcass stolen (Y/N) versus sex of the possessor and the number of adult males present, Kasekela.[a]

Fixed effect	Estimate	Z	p
Intercept	**−2.66**	**−2.99**	**0.003**
Female possessor (Y)	0.25	0.238	0.81
# Adult males	−0.08	−0.69	0.49
Female possessor (Y)* #Adult males	**0.29**	**2.2**	**0.03**

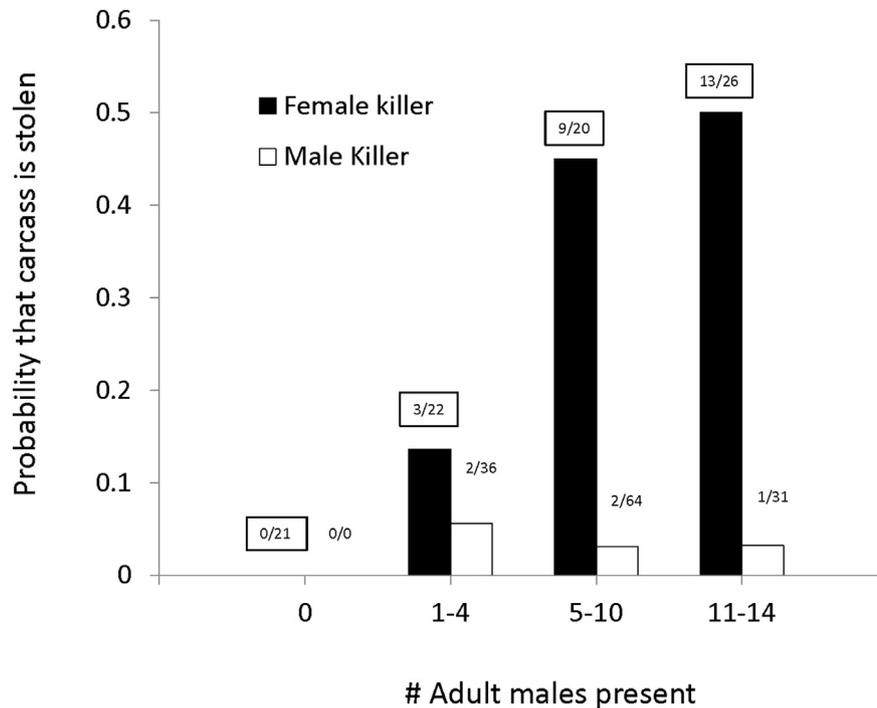[a] Bold indicates statistical significance.

Figure 3. Likelihood of carcass theft versus sex of possessor and number of adult male chimpanzees present, Kasekela. Number of adult males was divided into categories for illustration only. In parties with more males, females were more likely to have the carcass stolen than in parties with fewer males. Males rarely had carcasses stolen, and were not affected by adult male party size. Numbers indicate sample sizes.

whether or not theft occurred. Carcasses were stolen from adult females in 21.4% (3/14) of possessions, compared to 8.3% (16/193) for males. However, this difference was not statistically significant (GLMM: estimate = 1.46, Z = 1.36, p = 0.17), probably due to the relative rarity of possessions by adult females. Similarly, with the small sample, we were unable to test whether theft from females increased with adult male party size. However, of the three thefts from adult females, two occurred in relatively large groups (10 and 11 adult males).

4. Discussion

We analyzed long-term data from three eastern chimpanzee communities in order to test hypotheses explaining sex differences in hunting in one of humans' closest relatives. Female chimpanzees in all three study communities hunted less often than males did. In the Kasekela and Kanyawara communities, which were of similar mean size (28 adults) and female:male sex ratio (Kanyawara: 1.3:1, Kasekela: 1.5:1), females were responsible for only 8.8% and 14.5% of all kills, respectively. To put this in perspective, if females killed at rates based purely on their numerical representation in the population, we would expect them to be responsible for 57—60% of kills at these sites. At Mitumba, which had fewer adults (11) and a more female-biased sex ratio (2.6:1), females accounted for 21.4% of kills (compared to the expected value of 72.5%).

4.1. Opportunity hypothesis

Part of the reason for the relatively low female hunting rates at Kasekela and Kanyawara was that females at those sites had fewer opportunities to capture red colobus, the most common prey of chimpanzees. Females, which are less gregarious than males at both sites, encountered red colobus less often than males did, because large parties travel greater distances (Gilby et al., 2013). Also, party sizes at Kasekela were larger at kills of red colobus than at those of

other prey types, suggesting that relatively gregarious females have more quality chances to hunt (because larger parties are more likely to hunt red colobus; reviewed in Newton-Fisher, 2014). Indeed, in all three communities, the total number of hunts a female actively participated in was positively correlated with her gregariousness. At Kanyawara, party size was statistically similar at kills of red colobus and kills of other species, probably because this community does not hunt cryptic prey that require stealth or surprise to capture (a result that requires explanation, see below). In Mitumba, females and males were equally likely to encounter red colobus, and there was no difference in the average party size at hunts of arboreal monkeys versus other prey. This is likely because parties are more stable (in size and composition) in this smaller community, a hypothesis that can be tested in the future if this community continues to grow (Gombe Stream Research Centre, unpublished data). Mitumba is unusual in that hunting probability was positively associated with female, as well as male, party size (Gilby et al., 2015), suggesting that females may play a more active role in hunts.

In sum, the only prediction of the opportunity hypothesis that was supported in all three communities was that higher female gregariousness was associated with higher hunting rates (Table 1). By contrast, the prediction that hunt participation rates should be equal for males and females was not supported at any site. When present at a hunt of red colobus, the odds that a given female participated were 64—90% lower than they were for a male. Therefore, although the opportunity hypothesis partly explains sex differences in predation rates at Kasekela and Kanyawara, where females were less likely than males to encounter red colobus, there must be other constraints on female hunting in all three communities.

4.2. Risk-sensitivity

Relative to males, variation in female reproductive success is determined more by calorie intake than by access to mates. Females are therefore more constrained by the need to acquire enough food

to satisfy their daily nutritional requirements. Human females also forage for, and share with, their dependents. Hence, women follow a risk-averse foraging strategy, in which they seek low-variance, but often low-quality, foods (Marlowe, 2007; Bliege Bird and Codding, 2015). When they do hunt, they typically target small, sedentary prey. We found some evidence that female chimpanzees follow a similar hunting strategy. While females did participate successfully in hunts of arboreal monkeys in both Gombe communities (accounting for 11.2% and 19.5% of kills at Kasekela and Mitumba, respectively), the probability that a killer (or acquirer, in the case of piracy) was female was greater when the prey was terrestrial. Hunts of arboreal monkeys at Gombe are lengthy, energetically costly, and involve conflict with formidable males equipped with large canines. By contrast, while hunts of infant bushpigs and baboons involve confrontations with adults, they do not appear to entail the same energetic costs, and there is no risk of falling. Capturing sedentary or concealed prey appears to be even less costly, and indeed, bushbuck fawns, nestlings, eggs and rodents were captured more often by females than by males at Kasekela and Mitumba. It is important to note, however, that in 42.9% (15/35) of the cases of bushbuck piracy at Gombe, the thief was female, indicating that they frequently risk confrontation with baboons. This suggests that females at Gombe are most sensitive to the costs of arboreal pursuit, rather than risk of injury.

At Kanyawara, where the prey profile is almost exclusively arboreal monkeys, females captured 16.7% (6/36 for which the sex of the killer was known) of the black and white colobus monkeys, compared to only 5.1% (11/214) of the red colobus. Red colobus at Kanyawara actively and aggressively defend themselves, sometimes preemptively attacking chimpanzees that show no interest in hunting (Kibale Chimpanzee Project, unpublished data). By contrast, black and white colobus appear more passive and slow, are less defensive in the presence of chimpanzees, and therefore seem to be less costly to pursue. Given the rarity of terrestrial/sedentary prey at Kanyawara, we suggest that black and white colobus present a valuable low-cost option for females. However, if this is the case, why don't chimpanzees hunt them more frequently? One possibility is that their meat is somehow less desirable, a notion that is supported by observations of lower levels of excitement and conflict at kills of black and white colobus relative to red colobus (Kibale Chimpanzee Project, unpublished data).

The foraging strategies of human females must also allow for the transport and care of dependent offspring. Often this involves traveling shorter distances than men, and targeting resources that allow them to forage while carrying children while avoiding contact with dangerous prey. We expected that female chimpanzees would be constrained in similar ways. However, at all three sites female chimpanzees with young offspring (≤2 years) sometimes hunted red colobus. There are several possible explanations for this result. Perhaps females temporarily leave young offspring behind while hunting. Or, the benefits of meat for lactating females may offset the added costs of hunting with offspring. That is, lactating females may take on the added costs of hunting with offspring because they benefit disproportionately (relative to other females) by obtaining food rich in fat and micronutrients. However, O'Malley et al. (2016) found that among lower-ranking females at Kasekela, pregnancy was associated with greater meat consumption than lactation was (although this could result from differences in begging rather than hunting). Finally, in our study, 'hunt' was a binary variable, based on whether or not a chimpanzee climbed in active pursuit of prey. It is possible that females with young offspring may hunt just as often as other females, but they do so with less intensity, or they abandon a hunt more readily.

The risk-sensitivity hypothesis predicts that individuals in good physical condition (indicative of a positive energy balance), should be more willing than individuals in poor condition to target resources with some risk of failure. We are not aware of any studies in humans that examine within-sex variation in risk-averse foraging. Among chimpanzees, however, the probability that a Kasekela female hunted red colobus was positively correlated with dominance rank. In that community, high ranking females weigh more, and their mass fluctuates less than that of low-ranking females (Pusey et al., 2005), suggesting that they have access to higher quality and/or less variable resources. As such, high-ranking females may be more likely to have sufficient energy reserves required to hunt, or they are able to absorb the costs of failure more easily. A low-ranking female may forego hunting in favor of more predictably-acquired plant foods. There are, of course, many other factors associated with dominance rank that are likely to affect female hunting decisions, such as age, experience and gregariousness. This may explain why there was no statistical relationship between female rank and hunting at Kanyawara or Mitumba, although small sample sizes cannot be ruled out. Another possibility is that there simply may not be enough variance in female dominance scores at Kanyawara and Mitumba to test whether there is a relationship between rank and hunting.

In sum, there was mixed support for the risk-sensitivity hypothesis. Rather than focus on red colobus monkeys, females at all three sites specialized in prey that entail fewer costs to acquire. However, there was no indication that the existence of young offspring hampered female hunting, and dominance rank was associated with higher hunting probability at Kasekela only. More data are required to assess whether the latter result is due to low statistical power at Kanyawara and Mitumba.

4.3. Male appropriation

At Kasekela, the probability that a given female hunted red colobus was negatively correlated with the number of adult males present in the party. By contrast, previous work at several sites has shown that the likelihood of hunting by males increased with male party size (Mitani and Watts, 2001; Gilby et al., 2006; Gilby and Wrangham, 2007). Gilby et al. (2008, 2015) argued that this pattern is the result of a by-product mutualism in which the independent actions of individual hunters incidentally decrease the costs for other hunters, thus providing an incentive to join a hunt. Why does this not appear to apply to females at Kasekela? We suggest that any decrease in hunting costs associated with the presence of more male hunters is offset by a greater likelihood that a successful female hunter will immediately have the carcass stolen. Indeed, females at Kasekela were much more likely to have carcasses stolen from them than males were, and the probability of theft from a female increased with male party size.

At Kanyawara and Mitumba, however, there was no association between adult male party size and female hunting probability. At Mitumba, we suspect that this was due to the small number of males—either there was not enough variation in the number of males that could be present, or theft may be less of a threat. Unfortunately, theft data from Mitumba are not currently available. The small sample of female carcass possessions at Kanyawara prevented statistical tests of theft versus male party size.

4.4. Inter-community variation

Given that humans dwell in a wide range of habitats, it is not surprising that diets vary considerably. By comparison, chimpanzees have a relatively limited habitat range, restricted to forests, woodlands and savannas across equatorial Africa. Nevertheless, chimpanzee prey profiles and meat-eating frequency vary greatly, even among eastern African sites (Newton-Fisher, 2014). The

variation in hunting patterns is generally greater than the variation in other aspects of chimpanzee diet. For example, the percentage of feeding time spent eating fruit is remarkably consistent across our three study communities (Kanyawara: 65% [Bray et al., submitted]; Kasekela: 64%; Mitumba: 61% [Gombe Stream Research Centre, unpublished data]). The greater variability in meat consumption is perhaps not surprising given the fact that vertebrate prey are mobile and require more skill to obtain compared to most plant foods. Indeed, while chimpanzees at Kanyawara reached adult levels of fruit consumption between ages 5—10 (Bray et al., submitted), males typically did not achieve peak hunting rates until their mid-20s (Gilby et al., 2015). Our study also suggests that both ecological and demographic factors help to explain this variation. Although the communities were of similar size (~28 adults), meat eating was three times more frequent at Kasekela (~58 prey/year) than at Kanyawara (~18 prey/year), a difference that could not be explained by either red colobus encounter rate or research effort. At Mitumba, although a much smaller community (~11 adults), chimpanzees captured prey at a similar rate (17 prey/year) as at Kanyawara. For a community of its size that regularly encounters its most common prey, why do the Kanyawara chimpanzees hunt so rarely? Forest structure, grouping and travel patterns, and prey distribution are all likely factors. For example, chimpanzees are more likely to hunt red colobus in areas with broken canopy at Ngogo (Mitani and Watts, 2001) and in woodland (where trees are sparsely distributed) at Kasekela (Gilby et al., 2006). Perhaps there are relatively few low-cost options to hunt arboreal monkeys at Kanyawara. At all sites where chimpanzees hunt red colobus, larger chimpanzee parties are more likely to hunt and to succeed (reviewed by Newton-Fisher, 2014). The same is true at Kanyawara (Gilby et al., 2008), but it may be that there, large parties form relatively rarely in comparison to Kasekela. Strikingly, Kanyawara chimpanzees focused almost exclusively on arboreal monkeys. The most parsimonious explanation for this result is that alternative prey species are relatively rare within their range. While many of the types of prey targeted at Gombe (e.g., small ungulates) are present at Kanyawara, and eaten by chimpanzees elsewhere within the same forest (Ngogo: Watts and Mitani, 2002), their distribution and abundance is not well documented. If such ecological factors can be ruled out, then it is possible that these represent cultural differences in diet, as inferred at Taï (Boesch et al., 2006).

This inter-site variation should inform interpretation of the fossil record. Just as our data indicate that chimpanzee hunting decisions are sensitive to ecological and demographic variation, it is almost certain that early hominins experienced similar fluctuations in group size and ecology over time and space. Unfortunately, the resolution of the fossil record may not be sufficient to distinguish inter-population differences to the degree that we can for living primates. Nonetheless, it is important to note that among chimpanzees, explanations of when, what and why to hunt are not necessarily species-specific but instead are community-specific.

5. Conclusions

There was mixed support for three hypotheses addressing the relatively low rates of predation by female chimpanzees. In the two larger communities, females had fewer opportunities to hunt red colobus than males did. In the smaller Mitumba community, males and females were equally likely to encounter red colobus. In support of the notion that females are more risk-averse than males, females at all three sites specialized in low-cost prey. However, clinging offspring did not hamper female participation in hunts, and only Kasekela females hunted more often if they were high-ranking. Finally, female hunting probability was negatively

affected by the threat of losing the carcass to a male at Kasekela, but not Mitumba or Kanyawara.

These results highlight the variability in female hunting that exists between communities, and raise many questions about the sources of these differences. Why don't the Kanyawara chimpanzees hunt terrestrial or sedentary prey? Why did females at Mitumba encounter red colobus at the same rate as males did? Future studies must examine ecological variation, community composition, range size, and the abundance, distribution and habituation level of prey to explain these inter-community differences. Additionally, females also varied in their hunting decisions within communities. Future studies will likely identify other factors affecting individual variation, such as demography, reproductive state, and kinship.

It is important to acknowledge the possibility that small sample sizes might be affecting our results. Despite being the most comprehensive study of chimpanzee hunting to date, spanning 71 years and three communities, we were unable to test all of our predictions at Mitumba and Kanyawara. For example, over 20 years of Kanyawara data collection observers recorded over 200 initial monkey possessions by adult chimpanzees. However, only 14 of those were by females and in only three cases did a female have the carcass stolen. While it is possible that Kanyawara females are not hunting because of the fear of theft by males, at the current rate, many more years of data are needed to test this prediction. This substantiates the necessity of long-term data when studying a rare behavior performed by a long-lived species and also highlights the need for comparable datasets collected from multiple sites where animals experience different social and ecological environments.

We have shown that despite demographic and ecological variation within and between three well-studied communities, female chimpanzees hunt significantly less often than adult males and that this difference is due to a number of factors that constrain females. While these factors differ across our study groups, we believe that our results have important implications for understanding the evolution of human hunting patterns. Genetic, morphological and behavioral data indicate that the chimpanzee is a valuable point of comparison for making inferences about the possible range of behavior exhibited by the LCA of *Pan* and *Homo* (Wrangham and Pilbeam, 2001; McGrew, 2010; Wood and Harrison, 2011; Stanford, 2012; Muller et al., in press). We do not assume that chimpanzees are identical to the LCA. Rather, we use them to place human behavior in context — e.g., what key variables influence sex differences in hunting in a forest-dwelling hominoid that has changed less from the LCA than any other living species? The present study provides insight into the possible biological constraints faced by LCA females, before the development of regular offspring provisioning and food sharing within the pair bond (which are not present in either *Pan* species or in *Gorilla*, and therefore almost certainly evolved in hominins).

We suggest that before the advent of social obligations regarding sharing and provisioning, hominin females faced similar constraints as chimpanzees. An inherent sex difference in hunting behavior would therefore have preceded, and may have provided a basis for, the evolution of the sexual division of labor among modern humans. Finally, our study identifies the need to understand more fully the constraints that modem humans face. What factors other than the prospect of sharing and provisioning affect what (and when) women hunt? For example, we are not aware of data from human populations on sex differences in prey encounter rate. We suggest that it would be useful to compare sex differences in human hunting patterns using some of the measures that we have assessed here.

References

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour 49, 227–267.

Arcadi, A.C., Wrangham, R.W., 1999. Infanticide in chimpanzees: review of cases and a new within-group observation from the Kanyawara study group in Kibale National Park. Primates 40, 337–351.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., 2014. lme4: Linear mixed-effects models using Eigen and S4. http://cran.r-project.org/web/packages/lme4/index.html.

Bliege Bird, R., Codding, B.F., 2015. The sexual division of labor. In: Emerging Trends in the Social and Behavioral Sciences. John Wiley & Sons, Inc., Hoboken, pp. 1–16.

Bliege Bird, R.L., Bird, D.W., 2008. Why women hunt. Curr. Anthropol. 39, 655–683.

Boesch, C., 1994. Cooperative hunting in wild chimpanzees. Anim. Behav. 48, 653–667.

Boesch, C., Boesch, H., 1981. Sex differences in the use of natural hammers by wild chimpanzees: a preliminary report. J. Hum. Evol. 10, 585–593.

Boesch, C., Boesch, H., 1984. Possible causes of sex differences in the use of natural hammers by wild chimpanzees. J. Hum. Evol. 13, 415–440.

Boesch, C., Boesch, H., 1989. Hunting behavior of wild chimpanzees in the Taï National Park. Am. J. Phys. Anthropol. 78, 547–573.

Boesch, C., Goné Bi, Z.B., Anderson, D.P., Stahl, D., 2006. Food choice in Taï chimpanzees: Are cultural differences present? In: Hohmann, G., Robbins, M., Boesch, C. (Eds.), Feeding Ecology in Apes and Other Primates. Cambridge University Press, Cambridge, pp. 365–399.

Bray, J., Emery Thompson, M., Muller, M.N., Wrangham, R.W., Machanda, Z.P., 2017. The development of feeding behavior in wild chimpanzees (Pan troglodytes schweinfurthii). Am. J. Phys. Anthropol submitted for publication.

Brown, J.L., 1983. Cooperation – a biologist's dilemma. In: Rosenblatt, J.S. (Ed.), Advances in Behaviour. Academic Press, New York, pp. 1–37.

Butynski, T.M., 1982. Vertebrate predation by primates: a review of hunting patterns and prey. J. Hum. Evol. 11, 421–430.

Chapman, C.A., Wrangham, R.W., 1993. Range use of the forest chimpanzees of Kibale: implications for the understanding of chimpanzee social organization. Am. J. Primatol. 31, 263–273.

Clutton-Brock, T.H., Gillett, J.B., 1979. A survey of forest composition in the Gombe National Park, Tanzania. Afr. J. Ecol. 17, 131–158.

Connor, R.C., 1995. The benefits of mutualism: a conceptual framework. Biol. Rev. Camb. Phil. Soc. 70, 427–457.

Emery Thompson, M., 2013. Reproductive ecology of female chimpanzees. Am. J. Primatol. 75, 222–237.

Emery Thompson, M., Jones, J.H., Pusey, A.E., Brewer-Marsden, S., Goodall, J., Marsden, D., Matsuzawa, T., Nishida, T., Reynolds, V., Sugiyama, Y., Wrangham, R.W., 2007. Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. Curr. Biol. 17, 2150–2156.

Fedigan, L.M., 1990. Vertebrate predation in Cebus capucinus: meat eating in a Neotropical monkey. Folia Primatol. 54, 196–205.

Foerster, S., Franz, M., Murray, C.M., Gilby, I.C., Feldblum, J.T., Walker, K.K., Pusey, A.E., 2016. Chimpanzee females queue but males compete for social status. Sci. Reports 6, 35404.

Gilby, I.C., Wrangham, R.W., 2007. Risk-prone hunting by chimpanzees (Pan troglodytes schweinfurthii) increases during periods of high diet quality. Behav. Ecol. Sociobiol. 61, 1771–1779.

Gilby, I.C., Eberly, L.E., Pintea, L., Pusey, A.E., 2006. Ecological and social influences on the hunting behaviour of wild chimpanzees (Pan troglodytes schweinfurthii). Anim. Behav. 72, 169–180.

Gilby, I.C., Eberly, L.E., Wrangham, R.W., 2008. Economic profitability of social predation among wild chimpanzees: individual variation promotes cooperation. Anim. Behav. 75, 351–360.

Gilby, I.C., Wilson, M.L., Pusey, A.E., 2013. Ecology rather than psychology explains co-occurrence of predation and border patrols in male chimpanzees. Anim. Behav. 86, 61–74.

Gilby, I.C., Machanda, Z.P., Mjungu, D.C., Rosen, J., Muller, M.N., Pusey, A.E., Wrangham, R.W., 2015. "Impact hunters" catalyse cooperative hunting in two wild chimpanzee communities. Phil. Trans. Roy. Soc. B 370, 20150005.

Goodall, J., 1986. The Chimpanzees of Gombe: Patterns of Behavior. Harvard University Press, Cambridge, MA.

Gurven, M., Hill, K., 2009. Why do men hunt? A reevaluation of "Man the Hunter" and the sexual division of labor. Curr. Anthropol. 50, 51–74.

Hashimoto, C., Furuichi, T., Tashiro, Y., 2001. What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda? Examination of fruit abundance and number of estrous females. Int. J. Primatol. 22, 947–960.

Hawkes, K., 1991. Showing off: tests of a hypothesis about men's foraging goals. Ethol. Sociobiol. 12, 29–54.

Hayward, M.W., Hofmeyr, M., O'Brien, J., Kerley, G.I.H., 2006. Prey preferences of the cheetah (Acinonyx jubatus) (Felidae: Carnivora): morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? J. Zool. 270, 615–627.

Hill, K.R., Kaplan, H.S., Hawkes, K., Hurtado, A.M., 1985. Men's time allocation to subsistence work among the Ache of eastern Paraguay. Hum. Ecol. 13, 29–47.

Hohmann, G., Fruth, B., 2007. New records on prey capture and meat eating by bonobos at Lui Kotale, Salonga National Park, Democratic Republic of Congo. Folia Primatol. 79, 103–110.

Hothorn, T., Frank, B., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometrical J. 50, 346–363.

Hurtado, A.M., Hawkes, K., Hill, K.R., Kaplan, H.S., 1985. Female subsistence strategies among the Ache hunter-gatherers of eastern Paraguay. Hum. Ecol. 13, 1–28.

Kitanishi, K., 1995. Seasonal changes in the subsistence activities and food intake of the Aka hunter-gatherers in northeastern Congo. Afr. Stud. Monog. 16, 73–118.

Langergraber, K.E., Prufer, K., Rowney, C., Boesch, C., Crockford, C., Fawcett, K., Inoue, E., Inoue-Muruyama, M., Mitani, J.C., Muller, M.N., Robbins, M.M., Schubert, G., Stoinski, T.S., Viola, B., Watts, D., Wittig, R.M., Wrangham, R.W., Zuberbühler, K., Paabo, S., Vigilant, L., 2012. Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. Proc. Natl. Acad. Sci. 109, 15716–15721.

Lieberman, D.E., 2013. The Story of the Human Body: Evolution, Health, and Disease. Pantheon, New York, NY.

Marlowe, F.W., 2007. Hunting and gathering: the human sexual division of foraging labor. Cross-Cultural Res. 41, 170–195.

McGrew, W.C., 1979. Evolutionary implications of sex differences in chimpanzee predation and tool use. In: Hamburg, D.A., McCown, E.R. (Eds.), The Great Apes. Benjamin Cummings, London, pp. 441–463.

McGrew, W.C., 1992. Chimpanzee Material Culture. Cambridge University Press, Cambridge.

McGrew, W.C., 2010. In search of the last common ancestor: new findings on wild chimpanzees. Phil. Trans. Roy. Soc. B 365, 3267–3276.

Mitani, J.C., Watts, D.P., 1999. Demographic influences on the hunting behavior of chimpanzees. Am. J. Phys. Anthropol. 109, 439–454.

Mitani, J.C., Watts, D.P., 2001. Why do chimpanzees hunt and share meat? Anim. Behav. 61, 915–924.

Muller, M.N., Wrangham, R.W., Pilbeam, D. (Eds.), 2017. Chimpanzees and Human Evolution. Harvard University Press, Cambridge, MA in press.

Murray, C.M., Mane, S., Pusey, A.E., 2007. Dominance rank influences female space use in wild chimpanzees, Pan troglodytes: towards an ideal despotic distribution. Anim. Behav. 74, 1795–1804.

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A.M., Agil, M., Widdig, A., Engelhardt, A., 2011. Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. Anim. Behav. 82, 911–921.

Newton-Fisher, N.E., 2014. Chimpanzee hunting behavior. In: Henke, W., Tattersall, I. (Eds.), Handbook of Physical Anthropology, 2nd Edition. Springer-Verlag, Berlin/Heidelberg, pp. 1–19.

Nishida, T., Hiraiwa, M., 1982. Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. J. Hum. Evol. 11, 73–99.

Noss, A.J., Hewlett, B.S., 2001. The contexts of female hunting in central Africa. Am. Anthropol. 103, 1024–1040.

O'Malley, R.C., Stanton, M.A., Gilby, I.C., Lonsdorf, E.V., Pusey, A.E., Markham, A.C., Murray, C.M., 2016. Reproductive state and rank influence patterns of meat consumption in wild female chimpanzees (*Pan troglodytes schweinfurthii*). J. Hum. Evol. 90, 16–28.

Patterson, N., Richter, D.J., Gnerre, S., Lander, E.S., Reich, D., 2006. Genetic evidence for complex speciation of humans and chimpanzees. Nature 441, 1103–1108.

Perry, S., Ordoñez Jiménez, J.C., 2006. The effects of food size, rarity, and processing complexity on white-faced capuchins' visual attention to foraging conspecifics. In: Hohmann, G., Robbins, M.M., Boesch, C. (Eds.), Feeding Ecology in Apes and Other Primates: Ecological, Physical and Behavioral Aspects. Cambridge University Press, Cambridge, pp. 203–234.

Pickering, T.R., 2013. Rough and Tumble: Aggression, Hunting, and Human Evolution. University of California Press, Los Angeles, CA.

Pruetz, J.D., Bertolani, P., 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. Curr. Biol. 17, 412–417.

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. Roy. Soc. Open Sci. 2, 140507.

Pusey, A.E., Schroepfer-Walker, K., 2013. Female competition in chimpanzees. Phil. Trans. Roy. Soc. London B 368, 20130077.

Pusey, A.E., Oehlert, G.W., Williams, J.M., Goodall, J., 2005. Influence of ecological and social factors on body mass of wild chimpanzees. Int. J. Primatol 26, 3–31.

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rose, L.M., 1997. Vertebrate predation and food-sharing in *Cebus* and *Pan*. Int. J. Primatol. 18, 727–765.

Rose, L.M., Perry, S., Panger, M., Jack, K., Manson, J.H., Gros-Louis, J., Mackinnon, K.C., Vogel, E., 2003. Interspecific interactions between *Cebus capucinus* and other species: data from three Costa Rican sites. Int. J. Primatol. 24, 759–796.

Sayers, K., Lovejoy, C.O., 2008. The chimpanzee has no clothes: a critical examination of *Pan troglodytes* in models of human evolution. Curr. Anthropol. 49, 87–114.

Sobolewski, M.E., Brown, J.L., Mitani, J.C., 2012. Territoriality, tolerance and testosterone in wild chimpanzees. Anim. Behav. 84, 1469–1474.

Stanford, C.B., 1998. Chimpanzee and Red Colobus: The Ecology of Predator and Prey. Harvard University Press, Cambridge, MA.

Stanford, C.B., 2012. Chimpanzees and the behavior of *Ardipithecus ramidus*. Ann. Rev. Anthropol. 41, 139–149.

Stanford, C.B., Wallis, J., Matama, H., Goodall, J., 1994a. Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982-1991. Am. J. Phys. Anthropol. 94, 213–228.

Stanford, C.B., Wallis, J., Mpongo, E., Goodall, J., 1994b. Hunting decisions in wild chimpanzees. Behaviour 131, 1–18.

Surbeck, M., Fowler, A., Deimel, C., Hohmann, G., 2009. Evidence for the consumption of arboreal, diurnal primates by bonobos (*Pan paniscus*). Am. J. Primatol. 71, 171–174.

Surbeck, M., Hohmann, G., 2008. Primate hunting by bonobos at LuiKotale, Salonga National Park. Curr. Biol. 18, R906–R907.

Takahata, Y., Hasegawa, T., Nishida, T., 1984. Chimpanzee predation in the Mahale Mountains from August 1979 to May 1982. Int. J. Primatol. 5, 213–233.

Tanaka, J., 1980. The San, Hunter-Gatherers of the Kalahari: A Study in Ecological Anthropology. University of Tokyo Press, Tokyo.

Tanner, N., Zihlman, A., 1976. Women in evolution. Part I: Innovation and selection in human origins. Signs 1, 585–608.

Trivers, R.L., 1972. Parental investment and sexual selection. In: Campbell, B. (Ed.), Sexual Selection and the Descent of Man. Aldine, Chicago, pp. 136–179.

Uehara, S., 1997. Predation on mammals by the chimpanzee (*Pan troglodytes*). Primates 38, 193–214.

Walker, K.K., 2015. Dispersal and integration in female chimpanzees. Ph.D. Dissertation, Duke University.

Watts, D.P., Mitani, J.C., 2002. Hunting and meat sharing by chimpanzees at Ngogo, Kibale National Park, Uganda. In: Boesch, C., Hohmann, G., Marchant, L. (Eds.), Behavioural Diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge, pp. 244–255.

West-Eberhard, M.J., 1975. The evolution of social behavior by kin selection. Q. Rev. Biol. 50, 1–33.

Wilson, M.L., 2012. Long-term studies of the chimpanzees of Gombe National Park, Tanzania. In: Kappeler, P.M., Watts, D.P. (Eds.), Long-Term Field Studies of Primates. Springer-Verlag, Berlin Heidelberg, pp. 357–384.

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. Anim. Behav. 83, 277–291.

Wood, B., Gilby, I.C., 2017. From *Pan* to man the hunter: hunting and meat sharing by chimpanzees, humans, and our common ancestor. In: Muller, M.N., Wrangham, R.W., Pilbeam, D. (Eds.), Chimpanzees and Human Evolution. Harvard University Press, Cambridge, MA in press, Chapter 10.

Wood, B., Harrison, T., 2011. The evolutionary context of the first hominins. Nature 470, 347–352.

Wood, B.M., Marlowe, F.W., 2013. Household and kin provisioning by Hadza men. Hum. Nat. 24, 280–317.

Wrangham, R.W., 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: Kappeler, P.M. (Ed.), Primate Males: Causes and Consequences of Variation in Group Composition. Cambridge University Press, Cambridge, pp. 248–258.

Wrangham, R.W., Bergmann-Riss, E., 1990. Rates of predation on mammals by Gombe chimpanzees, 1972-1975. Primates 31, 157–170.

Wrangham, R.W., Pilbeam, D., 2001. African apes as time machines. In: Galdikas, B., Briggs, N., Sheeran, L., Shapiro, G., Goodall, J. (Eds.), All Apes Great and Small, Volume I: African Apes. Kluwer Academics/Plenum Publishers, New York, pp. 5–17.

Wrangham, R.W., Smuts, B., 1980. Sex differences in the behavioral ecology of chimpanzees in the Gombe National Park, Tanzania. J. Repr. Fert. Suppl. 28, 13–31.

Wrangham, R.W., Clark, A.P., Isabirye-Basuta, G., 1992. Female social relationships and social organization of Kibale forest chimpanzees. In: Nishida, T., McGrew, W.C., Marler, P., Pickford, M., de Waal, F.B.M. (Eds.), Topics in Primatology. Vol. 1. Human Origins. Tokyo University Press, Tokyo, pp. 81–98.