



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



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### 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.

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## 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 Coddling, 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 Coddling, 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; Pruett and Bertolani, 2007; Pruett 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 Pruett 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; Pruett 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

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