



Chimpanzee vertebrate consumption: Savanna and forest chimpanzees compared



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ABSTRACT

There is broad consensus among paleoanthropologists that meat-eating played a key role in the evolution of *Homo*, but the details of where, when, and why are hotly debated. It has been argued that increased faunivory was causally connected with hominin adaptation to open, savanna habitats. If savanna-dwelling chimpanzees eat meat more frequently than do forest chimpanzees, it would support the notion that open, dry, seasonal habitats promote hunting or scavenging by hominoids. Here we present observational and fecal analysis data on vertebrate consumption from several localities within the dry, open Ugalla region of Tanzania. Combining these with published fecal analyses, we summarize chimpanzee vertebrate consumption rates, showing quantitatively that savanna chimpanzee populations do not differ significantly from forest populations. Compared with forest populations, savanna chimpanzees consume smaller vertebrates that are less likely to be shared, and they do so more seasonally. Analyses of chimpanzee hunting that focus exclusively on capture of forest monkeys are thus difficult to apply to chimpanzee faunivory in open-country habitats and may be misleading when used to model early hominin behavior. These findings bear on discussions of why chimpanzees hunt and suggest that increases in hominin faunivory were related to differences between hominins and chimpanzees and/or differences between modern and Pliocene savanna woodland environments.

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1. Introduction

1.1. Chimpanzees and the origins of hunting by hominins

The origin, nature, and significance of hominin consumption of vertebrates have been foci of research and debate in anthropology for nearly a century. The transition from an ape-like frugivore/folivore to a more carnivorous hominin has been linked to a shift from more forested to more open, savanna environments since before the first African fossil hominin was found (e.g., Barrell, 1917). This was thought to be either because environmental change put earliest hominins into marginal savanna habitats, forcing them to

broaden their diet, or because abundant prey in savannas enabled them to expand into a vacant niche (Cartmill, 1993). To explore whether consumption of vertebrates and adaptation to savanna habitats were functionally linked in hominin evolution, it may be informative to look at meat-eating among extant chimpanzees and investigate whether adaptation to savanna habitats influences their consumption of vertebrates. Because chimpanzees and early hominins (e.g., *Ardipithecus*; Stanford, 2012) are broadly similar (e.g., body size and structure, degree of encephalization, habitat), ecological and social adaptations exhibited by savanna-dwelling chimpanzees relative to forest populations may shed light on that transition in the hominin lineage. That light may take the form of a heuristic framework for thinking about early hominins; more usefully, it may generate middle-range tests of hypotheses or discover unrecognized problems with interpretation of paleontological data (Moore, 1996; Stanford, 1996; Pickering and

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Domínguez-Rodrigo, 2012; Mitani, 2013). We agree with Sayers and Lovejoy (2008) that using modern panins to help understand extinct hominins can lead to erroneous conclusions and that such an approach must be applied with care. Using the one to help understand the other ('referential modeling') is a method that, like any other method, must be applied carefully or error can result—for example, theoretical ('strategic') modeling resulted in the now disproved single-species hypothesis (Wolpoff, 1971).

Judging from the excitement that generally surrounds chimpanzee hunting (Gilby et al., 2013), the acquisition of meat is important to them. Surprisingly, there is not a consensus as to why that is. While meat is calorically dense, the energetic cost of hunting can be high and individual yields from a divided carcass low, suggesting to some that the primary function of hunting is social (Stanford et al., 1994; Mitani and Watts, 2001). This view is supported by the observation that hunting frequencies may be higher during seasons of abundant food, contrary to what one would expect if meat were making up a nutritional shortfall (Mitani and Watts, 2005). Others emphasize that, unless carcasses were intrinsically valuable, they would have little value in social exchanges and point to ecological explanations and non-caloric nutritional benefits (Gilby et al., 2006; Tennie et al., 2009; Newton-Fisher, 2015; O'Malley et al., 2016). As noted by Newton-Fisher (2015), the uncertainty about the adaptive function of chimpanzee hunting is problematic for attempts to use chimpanzees as referential models for early hominins. A better understanding of causes of variation in hunting frequency, seasonality, and prey choice among chimpanzees is needed (Newton-Fisher, 2015).

We report here on observational and fecal data collected at the Issa, Nguye, and Bhukalai study sites, Ugalla (Tanzania), and place them in the context of published quantitative information on the prevalence of vertebrate remains in chimpanzee feces from other wild chimpanzee populations. Fecal data indicate consumption only; however, scavenging by chimpanzees is rare (Watts, 2008), such that it is therefore likely that most vertebrates consumed were hunted.

1.2. Fecal analysis and rates of faunivory

To compare rates of vertebrate consumption across sites requires the use of indirect evidence (fecal contents), because observational data on meat eating among savanna chimpanzees are scarce. This, in turn, requires a methodological digression, because the use of fecal analysis to detect carnivory has been categorically challenged: "feces do not appear to provide a reliable indicator of hunting: while the presence of remains can confirm that consumption does occur, little can be said about its frequency" (Newton-Fisher, 2015:1665). Both Newton-Fisher (2015) and Uehara (1997) based their reticence about fecal analysis on the rejection of such data by Boesch and Boesch (1989:551): "our experience of collecting feces during 2 years showed that such a method is not reliable as it does not match with the visual observations." Uehara (1997) also cited McGrew (1983) as calling for caution when interpreting fecal data. However, although caution is always important, in fact, McGrew (1983:47) advocated the use of fecal analysis as a "more standardized alternative" to observational data.

Is fecal analysis actually unreliable, or can it be used to estimate frequency of vertebrate consumption? To answer this question definitively, we would need concurrent quantitative data on meat consumption, defecation rates, and fecal prevalence of vertebrate remains; such data are not available. However, non-concurrent data from several sites allow us to make a crude approximate test of the method. Wrangham and van Zinnicq Bergmann Riss (1990)

concluded that the Kasekela and Kahama communities at Gombe averaged about 204 prey/year between 1972 and 1975. Between 1965 and 1967, the Kasekela/Kahama community averaged about 42 adult and adolescent individuals (Goodall, 1986). Teleki (1973) reported that an average of eight individual chimpanzees obtained portions per predation event (range 4–15). Wild chimpanzees defecate about 3–3.5 times per day (calculated from Phillips and McGrew, 2014 and Nishida et al., 1979, respectively). Finally, Lambert (2002) found that markers fed to captive chimpanzees were detected between 23 and 63 h following consumption (mean transit time and mean time of last appearance, respectively), a span of 40 h. Using the above defecation rates, this would translate into about five defecations following a meal that might contain its residue. However, inspection of Lambert (2002:Fig. 1) suggests that most markers appeared between 20 and 50 h, roughly bimodally. We therefore consider three defecations post-consumption to potentially contain identifiable residue, though recognizing that combining captive passage rates with wild defecation rates is problematic.

Based on these figures, the 42 Gombe chimpanzees described above would generate about 45,990 to 53,655 defecations/year, of which about $204 \times 8 \times 3 = 4896$ might be expected to contain evidence of vertebrate consumption (about 9–10%).¹ This is a maximum figure, since meat and organs may not be detectable (Phillips and McGrew, 2013). The observed prevalence at Gombe in a sample of 1963 feces examined between 1964 and 1967 was 5.8% (McGrew, 1983). Such calculation can represent only a very crude 'test' of the reliability of fecal data. Wrangham and van Zinnicq Bergmann Riss (1990) and Stanford et al. (1994) documented significant changes in community predation rates over time, and more than five years separate the periods of fecal sampling and observational data on predations. Basing the calculation on adult and adolescent individuals, as we have done, assumes that juvenile and infant feces were rarely sampled for dietary analysis (including them would change the expected prevalence to about 7–8%). Finally, the calculation is sensitive to the average number of consumers/episode; published estimates range from 5.6 (Mahale; Takahata et al., 1984) to 10 (Taï; Boesch and Boesch, 1989). Nevertheless, we consider the correspondence between calculated and observed values to be close enough to challenge the assertion that fecal evidence is an unreliable indication of meat consumption by chimpanzees.

Why then did Boesch and Boesch (1989) conclude that fecal data are unreliable? They found evidence of vertebrate consumption in only one of 381 feces examined over two years "in the early part of the study" (Boesch and Boesch-Achermann, 2000:159; the study began in 1979). Boesch and Boesch (1989) estimated roughly 72 kills/year (120 hunts/year \times 60% success rate) during 22 months in 1984–1986, 35 adults (79 individuals total) and 10 consumers/episode ($N = 52$ kills). Combining these figures from (probably) non-overlapping time periods, the expected maximum prevalence in feces would be about 5.6% considering only adults, and including immatures would reduce it to 2.5%, still much greater than the observed 0.3%. If one treats these samples as independently drawn from a population with a true prevalence of 2.5%, the probability of finding only one positive sample is <0.005 .² Does that mean fecal analysis is unreliable? No, the biological reality of 'what

¹ Phillips et al. (2017) reported a median defecation rate of 6.4/day; approximately doubling both defecations/year and the number expected to contain vertebrate remains does not change the expected prevalence.

² Because of sharing, samples from the same party are not independent. Average party size at Taï is 10 (Boesch and Boesch-Achermann, 2000), so the appropriate N might be closer to 38 than to 381; one in 38 is 2.6%.

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