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Why do chimpanzees hunt? Considering the benefits and costs of acquiring and consuming vertebrate versus invertebrate prey



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ABSTRACT

Understanding the benefits and costs of acquiring and consuming different forms of animal matter by primates is critical for identifying the selective pressures responsible for increased meat consumption in the hominin lineage. Chimpanzees (*Pan troglodytes*) are unusual among primates in the amount of vertebrate prey they consume. Still, surprisingly little is known about the nutritional benefits of eating meat for this species. In order to understand why chimpanzees eat vertebrates, it is critical to consider the relative benefits and costs of other types of faunivory – including invertebrates. Although we lack specific nutritional data on the flesh and organs of chimpanzee prey, the macronutrient profiles of insects and wild vertebrate meat are generally comparable on a gram-to-gram basis. There are currently very few data on the micronutrient (vitamin and mineral) content of meat consumed by chimpanzees. With few exceptions, the advantages of hunting vertebrate prey include year-round availability, rapid acquisition of larger packages and reduced handling/processing time (once prey are encountered or detected). The disadvantages of hunting vertebrate prey include high potential acquisition costs per unit time (energy expenditure and risk of injury) and greater contest competition with conspecifics. Acquiring an equivalent mass of invertebrates (to match even a small scrap of meat) is possible, but typically takes more time. Furthermore, in contrast to vertebrate prey, some insect resources are effectively available only at certain times of the year. Here we identify the critical data needed to test our hypothesis that meat scraps may have a higher (or at least comparable) net benefit:cost ratio than insect prey. This would support the 'meat scrap' hypothesis as an explanation for why chimpanzees hunt in groups even when doing so does not maximize an individual's energetic gain.

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Introduction

Early hominins likely ate more meat¹ than any extant nonhuman primate species (Milton, 1999a; Balter et al., 2012). This increase is central to hypotheses addressing the evolution of the unique suite of human traits, including large brains (Aiello and Wheeler, 1995), central-place foraging (Isaac, 1978) and cooperation (Tomasello et al., 2012). Understanding the relative benefits and costs of acquiring and consuming different forms of animal matter by primates is critical for identifying the selective pressures responsible for increased meat consumption in the hominin lineage. As humans' closest living relatives, chimpanzees (*Pan*

troglodytes) and bonobos (*Pan paniscus*) are often used to reconstruct the diet and behavior of the last common ancestor of apes and humans (Stanford, 1996; Milton, 1999a, b; Wrangham and Pilbeam, 2001; Milton, 2003a). Therefore, detailed study of the contribution of animal source foods to the diet of the genus *Pan* promises to increase our understanding of why and how meat consumption became so frequent in the hominin lineage compared with our living ape counterparts. Although there is increasing evidence that bonobos eat meat more often than originally thought (Surbeck and Hohmann, 2008; Oelze et al., 2011), we focus our review on chimpanzees, for whom predation upon vertebrates is well documented (Boesch, 1994; Stanford et al., 1994a; Hosaka et al., 2001; Mitani and Watts, 2001; Newton-Fisher et al., 2002; Gilby et al., 2006, 2008).

In order to understand why chimpanzees eat vertebrates, it is particularly important to consider the relative costs and benefits of capturing and consuming vertebrate compared with invertebrate

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¹ Here we use the term 'meat' (and 'meat scrap') to refer to vertebrate tissue in general (including brain, muscle, viscera, etc.).

prey. Although there has been much debate over the putative social benefits of hunting (Stanford et al., 1994b; Stanford, 1998; Gilby, 2006; Gomes and Boesch, 2009; Gilby et al., 2010), surprisingly little is known about the purely nutritional net benefits of eating meat for chimpanzees. In our view, the social value of meat hinges primarily upon its nutritional value. If meat were not a valuable (and therefore desirable) food item, it would be of little use as an exchange commodity. Also, the proposal that a male's social standing is sensitive to his ability to obtain and distribute vertebrate prey (Moore, 1984) is valid only if meat is desirable in its own right. Therefore, we believe that the motivation to obtain meat (by capture or scrounging) is ultimately driven by the fact that meat has inherent nutritional value.

Chimpanzees prey most frequently upon red colobus monkeys (*Procolobus* spp.) at most sites where the two species are sympatric (Uehara, 1997; Mitani, 2009). The fact that chimpanzees rarely hunt other frequently encountered species (e.g., black-and-white colobus at Ngogo, Mitani and Watts, 1999) suggests that they have evolved a preference for red colobus monkeys. This is likely because the net benefit of acquiring and consuming red colobus is particularly high, perhaps due to their ease of capture (relative to other species) and/or high nutritional value. Nevertheless, hunting arboreal prey is arguably energetically costly (Boesch, 1994)² and entails considerable risk, in terms of injury (Busse, 1977; Goodall, 1986; Gilby, Personal observation), not to mention a risk of failure (Boesch and Boesch, 1989; Gilby and Wrangham, 2007).

The meat scrap hypothesis (Gilby et al., 2008; Tennie et al., 2009) provides a simple explanation for why chimpanzees undertake such costs to hunt vertebrates. We first proposed this hypothesis to explain why chimpanzees hunt in groups, even when larger hunting parties fail to return more meat per capita (Gombe: Gilby et al., 2006; Ngogo: Mitani and Watts, 2001; but see Boesch, 1994). On a per-unit-mass basis, meat is a highly concentrated source of valuable and readily-accessible micro- and macronutrients relative to most plant foods (Milton, 2003a,b). The meat scrap hypothesis proposes that there is a net benefit to obtaining a mere scrap of meat, even when there is a net energetic cost. Therefore, if a male chimpanzee is more likely to obtain meat (in nearly any amount) by hunting with others, then there will be selection for hunting in groups. Consistent with the meat scrap hypothesis, the probability that a hunter obtained a piece of meat (regardless of size) at a red colobus hunt was positively correlated with the number of hunters in the party at both Kanyawara (Gilby et al., 2008) and Gombe (Tennie et al., 2009). However, the validity of the meat scrap hypothesis also hinges on the expectation that despite the difficulty in acquiring prey, eating vertebrates has some advantage(s), e.g., in terms of efficiency, predictability, net yield of macro- or micronutrients, or other variables, compared with eating invertebrates, especially if we assume that vertebrates and invertebrates have similar nutritional profiles, as McGrew (2010) has suggested. In order to test this hypothesis, a full survey of the costs and benefits of acquiring and consuming vertebrates and invertebrates is necessary. Here, we review what is currently known, emphasizing significant gaps in current knowledge.

Prey acquisition

For simplicity, we start by assuming that vertebrates and invertebrates are nutritionally equivalent for chimpanzees. In other

words, we will assume that 1 g of monkey meat contains roughly the same nutrients (in roughly the same proportions) as 1 g of insects. Doing so allows us to more easily assess the costs and benefits associated with acquiring and processing the different prey types. We relax this assumption in the section on consumption below, where we focus on what is known of the nutritional content of meat and insects (and the available data do suggest that meat and invertebrate nutritional content can differ when compared on a gram-for-gram basis). This approach serves to identify critical areas for future research.

Availability of vertebrate prey

Chimpanzees prey upon at least 32 species of mammals (Uehara, 1997), nine birds (Teleki, 1981) and possibly small lizards and amphibians. Hunts of many of these species can best be described as opportunistic; for example, stumbling upon a bush-buck fawn hidden in the undergrowth (Goodall, 1986), or finding nestlings or eggs in a tree hollow (Wrangham, 1975). These events are likely to be affected by many factors, including breeding seasonality of the prey (if immature individuals are targeted) and ranging patterns of both predator and prey. However, to our knowledge, there has not been a systematic study of the frequency or regularity of encounters with such prey items. While challenging to collect, such missing data are critical for understanding the role of meat in chimpanzee diet.

In contrast, encounters with red colobus monkeys have been recorded at several sites. At Ngogo, chimpanzees encountered red colobus one to 33 times per month in 1998 and 1999 (Mitani and Watts, 2001). Also, Mitani and Watts (1999) and Watts and Mitani (2002) describe 'hunting patrols' in which large parties of males travel quietly, in single file, apparently deliberately searching for monkeys. This suggests that to some extent, male chimpanzees at Ngogo may have some control over the encounter rate. It should be noted, however, that the red colobus population at Ngogo has sharply declined in recent years (Teelen, 2007), most likely as a result of predation by chimpanzees (Teelen, 2008). Therefore, without long-term data, generalizations about prey availability should be interpreted with caution. At Taï, hunting frequency peaks in September and October (Boesch and Boesch-Achermann, 2000). There is no indication that this is due to increased encounter rates, although Boesch and Boesch (1989) do report that Taï males actively search for monkeys. Instead, they attribute the increase in hunting frequency to a seasonal peak in red colobus births and increased prey vulnerability (due to reduced traction on wet branches during the rainy season; Boesch and Boesch-Achermann, 2000). From this perspective, infant/'vulnerable' monkeys may be more available at certain times of the year. At Mahale, a general increase in predation rates over time may have been linked to an overall increase in red colobus density (Hosaka et al., 2001), although encounter rates were not reported. At Gombe, red colobus encounter rate is strongly seasonal, peaking in the late dry season months of August and September (Gilby, 2004; Gilby et al., 2013). A simple explanation for this pattern is that the probability of encountering colobus is positively correlated with daily travel distance, which increases during these months (Gilby, 2004; Gilby et al., 2013). Additionally, the probability of encountering red colobus in woodland habitat (where hunts are more likely to occur, Gilby et al., 2006) is correlated with daily travel distance (Gilby et al., 2013).

Availability of invertebrate prey

Tropical forests exhibit extremely high insect species richness (Gullan and Cranston, 2005), though only a few genera (termites:

² We assume here that energy is a limited resource for chimpanzees, but note that under special circumstances energetically inefficient food sources may still become beneficial if intake of a particular macronutrient, e.g., protein or fat, is driving foraging decisions (Raubenheimer and Simpson, 1997).

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