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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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Running head: chimpanzee hunting vs. insectivory

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1. 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. Although there has been much debate over the putative social benefits of hunting, 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, e.g., of acquiring and consuming vertebrate relative to invertebrate (typically insect) prey. Although we lack specific nutritional data on the flesh and organs of chimpanzee prey, the macro-nutrient profiles of insects and wild vertebrate meat are generally comparable on a gram-to-gram basis. There are currently very few data on the micro-nutrient (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 favored by chimpanzees (including termites, especially alates) are effectively available only at certain times of year. In this review, we identify the critical data needed to test our hypothesis that, in terms of micro-and macronutritional values (and associated packaging benefits) 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.

2. Introduction

Early hominins likely ate more meat[1] than any extant nonhuman primate species (Balter et al. 2012; Milton 1999a). 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 (Milton 1999a, b, 2003a; Stanford 1996; Wrangham and Pilbeam 2001). 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 to our living ape counterparts. Although there is increasing evidence that bonobos eat meat more often than originally thought (Oelze et al. 2011; Surbeck and Hohmann 2008), we focus our review on chimpanzees, for whom predation upon vertebrates is well-documented (Boesch 1994; Gilby et al. 2006; 2008; Hosaka et al. 2001; Mitani and Watts 2001; Newton-Fisher et al. 2002; Stanford et al. 1994a).

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 to

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[1] Here and elsewhere in this article, we use the term 'meat' (and 'meat scrap') to refer to vertebrate tissues in general (thus brain, muscle, viscera, etc. fall under this definition).

invertebrate prey. Although there has been much debate over the putative social benefits of hunting (Gilby 2006; Gilby et al. 2010; Gomes and Boesch 2009; Stanford 1998; Stanford et al. 1994b), 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 (Mitani 2009; Uehara 1997). 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 ((by male colobus, Busse 1977; Goodall 1986) or falling (Gilby, personal observation)) and 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

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

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 macro-nutrients 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 micro-nutrients, or other variables- compared to 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 a) acquiring and b) consuming vertebrates and invertebrates is necessary. Here, we review what is currently known, emphasizing significant gaps in current knowledge.

3. Prey Acquisition

For simplicity, we start by assuming that vertebrates and invertebrates are nutritionally equivalent for chimpanzees. In other words, we will assume that one gram of monkey meat contains roughly the same nutrients (in roughly the same proportions) as one gram 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 section 4, 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 of future research.

Availability of vertebrate prey

Chimpanzees prey upon at least 32 species of mammals (Uehara 1997), 9 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 bushbuck 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, these 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 1–33 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). In this sense, infant or otherwise 'vulnerable' monkeys may be more available at certain times of 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 (Gullen and Cranston 2005), though only a few genera (termites: *Cubitermes, Macrotermes, Pseudacanthotermes*; ants: *Dorylus, Oecophylla, Camponotus, Crematogaster*; bees: *Apis*; stingless Meliponini) are sought out and eaten by African apes with any consistency (reviewed in McGrew 1992; see McGrew et al. 2007 for update). In some cases, insect consumption may be unintentional (e.g. insects contained in fruit), though Redford et al. (1984) argue that some forms of primate frugivory may actually target insects infesting ripe fruit. The consequences of rare and unintentional insect consumption are unknown and difficult to study. Therefore, we concentrate on two major taxa that chimpanzees actively consume on a regular basis across Africa – termites (Order Isoptera; primarily *Macrotermes*) and ants (Order Hymenoptera; primarily *Oecophylla* (weaver ants) and *Dorylus* (driver ants)). These are generally considered to be the most important invertebrate prey for wild chimpanzees (McGrew 1992).

At several sites across Africa, chimpanzees 'fish' for termites by inserting tools made from vegetation into a termite mound, and then extracting and eating soldiers that cling to the tool (Goodall 1963). At Gombe, termite mounds (of which at least 14.3% were occupied by *Macrotermes*) are distributed throughout the study area at a density of 9.2/ha (O'Malley 2011). Kasekela chimpanzees have successfully fished at some specific termite mounds for at least twenty years (McGrew, personal communication). However, even though termite mounds are static, the prey themselves are not always accessible. Year-round termite fishing is known from only a few sites (e.g., Ndoki (Suzuki et al. 1995), Goualougo (Sanz et al. 2004), and Rio Muni (McGrew et al. 1979)). At Gombe, termite fishing is strongly seasonal, peaking in the early wet season (Oct-Dec), when there is increased activity in the upper reaches of the termite mounds as alates (flying reproductives) prepare to disperse (Goodall 1986). At this time, workers remodel exit tunnels while soldiers gather to defend the nest, which makes termite fishing more productive. At other times of year, most termites occupy lower and more inaccessible regions of the mounds. In addition, termites may be locally depletable. In the course of a fishing bout, chimpanzees may shift from hole to hole on a mound repeatedly, particularly after several unsuccessful insertions, – or they may abandon a mound entirely and walk directly to another mound (O’Malley, pers. observation).

When the termite alates emerge, they provide a chance for chimpanzees to gather a considerable number of calorie-rich prey (see *Nutritional content*, below). At Gombe these alates are avidly consumed by many other species of mammals and birds, including humans (O’Malley personal observation).

In contrast to termites, ants (*Dorylus* and *Oecophylla*) are consumed year-round at Gombe (Goodall 1986; McGrew 1979,1974), although temporal and spatial variation has not been rigorously examined. Similarly, chimpanzees at Mahale consume ants (*Camponotus* and *Crematogaster*) throughout the year, although there is some variation by season. At Gombe, density estimates of *Dorylus* bivouacs are about 0.8/ha (O'Malley 2011). A particular bivouac may remain in the same location for several days, but typically their movements and location are not predictable over longer periods. Based on transect surveys and active searches for *Dorylus* bivouacs and trails in Gashaka, Nigeria, Schoning et al. (2007) concluded that chimpanzees are unlikely to actively search for *Dorylus* and instead simply prey on them opportunistically when encountered. Chimpanzees consume *Dorylus* ants by “dipping” long wands of vegetation into a bivouac or (less commonly) a migration trail (McGrew 1974). The ants swarm up the wand, and the chimpanzee predator either eats them off the end directly or by sweeping movements of the hand (or the mouth) along the tool. This serves to both amass ants efficiently and minimize ant bites. The end of a *Dorylus* dipping session may not be entirely the decision of a chimpanzee predator, as often the ants will spread out in three dimensions in response to repeated probing – and given the painfulness of their bites, this will drive away the chimpanzees. The chimpanzees have a counterstrategy, in which they hang from overhead vines or trees, but even then sometimes they are still driven away as the ant bites intensify (Goodall 1986; McGrew 1974).

Consumption of weaver ants (*Oecophylla longinoda*) occurs without tools; instead the woven leaf nests constructed by these ants are crushed or rolled in the hands and/or feet and their insect contents consumed. Goodall (1986) reported that Kasekela chimpanzees spent relatively more time feeding on weaver ants in the late dry season and early wet season (Aug-Oct), at least in 1978 and 1979, though the ants are present year round.

This shows that invertebrates can vary in their accessibility and predictability, with termites being more predictable prey in time and space but (usually) available only seasonally, while *Oecophylla* and *Dorylus* ants are less predictably encountered in space but are (at least potentially) available year-round. Additionally, termite fishing is absent at some sites (e.g. Mahale M-Group), even though termites are present (Whiten et al. 1999; also see Collins and McGrew 1987). One thus cannot assume that invertebrate prey is always an option for wild chimpanzees at any place and time. This varying availability may be a major factor in the decision to hunt vertebrates instead. For example, if we assume that all chimpanzee faunivory fulfills the same nutritional needs, an individual may be more inclined to hunt (or even seek out vertebrate prey (e.g. at Ngogo)) if readily accessible insects are not available at that time due to spatial, seasonal and/or depletion constraints.

Prey capture

Acquiring vertebrate prey is best described as “high-risk, high-yield”. The potential payoff can be great (e.g., an entire red colobus carcass weighing from 1-12 kg), and even non-hunters are often able to obtain appreciable amounts through scrounging, begging or active sharing (Gilby 2006; Mitani and Watts 2001). However, there are considerable costs associated with hunting (and even possessing meat). First, moving at high speeds can be energetically very costly

(Ralston 1958), which is a particularly important consideration when calories are scarce (Gilby and Wrangham 2007). Second, there are costs associated with potential injury from mobbing by male colobus (Boesch and Boesch 1989; Busse 1977; Goodall 1986) or falling. To our knowledge, no systematic data exist on injuries sustained during hunting. However, in the Mitumba community at Gombe, during a conflict over meat, alpha male Vincent (VIN) fell approximately 15 meters onto a rocky streambed, an accident which ultimately resulted in his overthrow and death (Gombe Stream Research Centre, unpublished data). Third, there are opportunity costs. An average hunt of red colobus monkeys lasts 18.1 min at Taï (Boesch and Boesch 1989) and 19 min at Ngogo (Mitani and Watts 1999), but can be considerably longer (Taï: 120 min (Boesch and Boesch 1989); Ngogo: 91 min (Mitani and Watts 1999)). Fourth, there is a real risk of hunting failure; for example, at Gombe, focal males failed to capture a monkey in 68% of the hunts they actively participated in (Gilby et al. 2006). Even if another member of the hunting party makes a kill, not all hunters may obtain a share. Finally, meat possessors often face harassment (Wrangham 1975) from other chimpanzees begging for a share of the carcass. At Gombe, this harassment typically takes the form of reaching for and pulling on the carcass, acts which slow the rate at which the possessor can consume meat (Gilby 2006).

The benefits associated with prey capture are all affected by chimpanzee party size. Hunting parties containing many adult males are most likely to make a kill (Gilby et al. 2006; Mitani and Watts 2001), which increases the probability that both hunters and non-hunters obtain at least some meat (Gilby et al. 2008; Tennie et al. 2009). Similarly, hunting costs per hunter are expected to decrease as the number of hunters increases and it becomes more difficult for colobus to either escape or defend themselves (Gilby and Connor 2010). The potential for harassment of meat possessors is higher in large parties, however this may be offset by the increased likelihood that multiple carcasses are available.

There are also sex differences in the costs and benefits of hunting vertebrate prey. Males hunt red colobus more often than females do (Mitani and Watts 1999; Stanford et al. 1994a). While some have suggested that females can more easily gain access to meat in return for mating (Stanford 1998; Stanford et al. 1994b; but see Gilby et al (2010)), thus allowing them to often forego hunting themselves, other explanations exist. Hunting may be relatively more costly for females – females carrying infants have higher travel costs than non-mothers (Pontzer and Wrangham 2004), and would seem to be less agile. However, one of us (Gilby, personal observation) observed a female chimpanzee at Gombe actively hunting red colobus monkeys while carrying infant twins. Relative to males, females may engage in more hunts of hidden prey (e.g. bushbuck fawns, bushbabies, fledglings; Goodall 1986; Pruetz and Bertolani 2007). McGrew (1979; 1983) argued that for females with dependents, insectivory is a more viable option than hunting. Indeed, females consume insects more frequently and for longer durations than males (McGrew 1979, 1992).

Compared to hunting vertebrates, it probably requires less energy per minute of effort to acquire insects. However, the gain is (in most cases) also diminished (at least when compared to the potential high-gain outcome of vertebrate hunting). McGrew (1974) reported that Dorylus ant-fishing sessions ranged from 3-48 minutes, and an average dip rate of 2.6/minute. Using these values, O'Malley and Power (2012) estimated the maximum payoffs for ant-fishing to be 56.16g of ants, 59kcal (metabolizeable energy basis), 0.82g of fat and12.87g of protein.). As noted above, the average hunt lasts approximately 18 minutes (at Taï and Ngogo), during which a hunter has a greater than 60% chance of obtaining at least a scrap of meat (at Gombe (Gilby et al. 2008)), which is typically more than 50g (Gilby 2006). Thus, the payoff is higher for hunting

– but also less secure. Therefore, in terms of minimizing risk (of failing to obtain anything), we assume that insectivory is favorable, as long as the opportunity is there. However, chimpanzees may displace others from termite mounds, particularly very productive ones (O'Malley personal obs.). Pandolfi et al. (2003) found that females are less likely to fish when in the presence of same-sex conspecifics; Lonsdorf (2006) reported that termite fishing occurred mostly when females were alone with offspring or maternal kin. With regard to injury, generally predation on invertebrates incurs smaller actual costs than the potential high costs of hunting monkeys.] These costs would include having to deal with the chemical defenses (formic acid and perhaps other irritants) of ants such as *Oecophylla* and *Camponotus* (Deblauwe & Janssens 2008), or the stings of honeybees (*Apis mellifera*; Schmidt 2013).

In sum, with regard to capturing vertebrates versus invertebrates, chimpanzees are faced with the ‘packaging problem’; “Costs and benefits – good and bad – always comes packaged together…No perfect food exists” (Altmann 2009). Based on classic optimal foraging theory (Stephens and Krebs 1986), we expect chimpanzees to feed on the prey type which offers the highest ratio of benefits to costs *at that time*. The resulting benefit-cost ratios will differ in response to various internal and external conditions, such as season (e.g., hunting may not be optimal when termite alates are present), opportunity (e.g. a hunt is likely to succeed if many adult male chimpanzees are present), and by an individual’s condition (e.g. if in negative energy balance, choose insectivory rather than expend energy on hunting (Gilby and Wrangham 2007)). Future research is needed to identify whether these patterns exist as predicted.

4. Consumption

Chewing

Apart from the time-consuming nature of acquiring invertebrates (described above), it seems unlikely that they present much of a challenge to chew. While termite-fishing, for example, there is typically very little delay between dips to suggest that chewing is the rate-limiting step. Raw meat, on the other hand, may be difficult for chimpanzees to chew. Wrangham (1975; 2009) and Wrangham and Conklin-Brittain (2003) emphasized the considerable length of time it may take for chimpanzees to consume vertebrate prey. Indeed, a meat-eating bout may last several hours (Goodall 1986). However, this is partly due to sequential bouts by several individuals. In some cases, chimpanzees can eat meat rather quickly. For example, Gilby (2004) reported that one male consumed an entire infant colobus (weighing approximately 0.5 kg) in five minutes. It is possible that chimpanzees target young colobus because they are more tender than adults (as is the case in domesticated cattle (Shorthose and Harris 1990)), although they may also (or in addition) be easier to capture. In addition to variation in chewing time across prey age classes, an important (and often overlooked) property of vertebrate prey is that there is considerable variability in texture among tissue types. Internal organs such as the liver and the intestines are extremely soft, while bones, sinew and skin are quite tough. This variation clearly affects chewing time, and must be taken into account when considering the costs of consuming vertebrate prey. Much of the easily-chewed parts are probably consumed quite quickly. Indeed, chimpanzees appear to be selective in which parts of the carcass they eat first. To our knowledge, the order of tissue consumption has not been systematically analyzed, but it appears as though the viscera are typically eaten early in a bout (Teleki 1973; Wrangham 1975, Gilby, personal observation). However, it is unclear whether this is due to ease of chewing, selection based on nutritional content (see *Nutritional Content*, below), or the fact that these organs become quickly available as a carcass is torn in two. Nevertheless, it is clear that the internal organs are more easily consumed than other tissues.

Similarly, although data specifically on chimpanzee prey is lacking, it is highly likely that different muscle types are easier to chew than others. For example, the psoas muscle (the tenderloin), which lies alongside the spine, is particularly tender in domestic animals (Shackelford et al. 1995; Stanley et al. 1971). At Gombe, one of us (Gilby, personal observation) has observed male chimpanzee Frodo (FR) remove the spine, ribcage and psoas muscle from large carcasses before discarding the remainder, suggesting that he was selecting the most tender muscle. Even so, chimpanzees typically supplement even the most tender meat with mature leaves (Goodall 1986, Wrangham 1975), which indicates that raw meat is relatively difficult to chew for them (especially since their teeth are not very well adapted to this task; Wrangham 2009). Wrangham (2009) describes an informal experiment (with humans) suggesting that adding leaves when chewing improves ‘traction’, allowing for more efficient raw meat-chewing. Since

Typically, the last parts to be eaten are the bones and skin (Goodall 1986) which appear to be the most time consuming (yet least rewarding) pieces to process. It is likely that these pieces contribute disproportionally to the total time spent consuming vertebrate prey. Often these parts are discarded by the primary (or secondary) meat-eaters, and are eaten by younger and/or lower-ranking individuals (Teleki 1973).

Digestion

Stomach volume imposes an upper limit on ingestion rates in many animals, including chimpanzees. With the exception of alate wings (which are discarded), insects are eaten whole. Insect exoskeleton, which is composed of a matrix of the carbohydrate chitin, minerals, and amino acids, is believed to be largely undigestible to chimpanzees because termite and ant head capsules often appear in feces intact (McGrew 1979). For the most common Gombe insect prey (*Macrotermes, Apis, Dorylus, Oecophylla*), the ash-corrected ADF fraction (a proxy for the exoskeleton, including chitin and bound proteins) comprises between 6.5 – 24.8% of the total mass consumed on a dry matter basis (O'Malley and Power 2012) However, even McGrew's (2001) maximum estimated fresh-weight termite mass consumed in a single meal (260g) would amount to about 14.2g of indigestible minerals and exoskeleton suggesting that the indigestible fraction of these insects is unlikely to impose serious energetic costs on a chimpanzee predator.

Chimpanzees appear to value some parts of vertebrate carcasses more than others; for example, muscle, brains and viscera are avidly consumed while bones and skin may be consumed last or even discarded for others to scrounge (Goodall 1986). While primary carcass possessors can afford to be selective, individuals lacking such priority of access to a carcass probably have more limited choices as to which body parts to consume or discard. As a result, although it is typically the case that an entire carcass is eventually consumed (Goodall 1986), the less preferred components are predicted to be those with lower digestibility and nutritional value. Not surprisingly, bones and skin are often visible in chimpanzee dung (Goodall 1986; Surbeck et al. 2009). Sizeable portions of undigested muscle tissue may be present in the feces as well (Goodall 1986)). This suggests that the chimpanzee gut, which is adapted to a primarily vegetarian, high-fiber diet, may not efficiently process raw meat, leaving some undigested and unabsorbed. The stomach is where most mechanical digestion (post-chewing) takes place, and is critical for breaking meat down into small pieces (Wrangham 2009). Stomach passage time in primates is much shorter than in carnivores ((Meyer et al. 1985; 1988, as cited by Wrangham (2009)), which presumably compromises digestion of raw meat. Reduced stomach time may also increase the risk of disease transmission (Leendertz et al. 2010), another possible cost of eating meat.

Nutrient Content

Micronutrients

We currently lack detailed comparisons of the micronutrient profiles of chimpanzee animal source foods. However, it is clear that both vertebrates and invertebrates are excellent sources of important minerals and vitamins. Wild (lean) red meat is rich in iron, zinc and Vitamin B12 as well as magnesium, copper, cobalt, phosphorus, chromium, nickel and selenium (Williamson et al. 2005). The original meat scrap hypothesis (Tennie et al. 2009) argued that chimpanzees hunt mainly to satisfy their need for such micronutrients. It is possible that meat contains important micronutrients that are *entirely* absent in the remainder of their diet (including invertebrates), and would therefore be worth high acquisition costs. However, this seems rather unlikely, as there are chimpanzee communities that rarely eat meat (e.g. Budongo, Newton-Fisher et al. 2002), and even within a community that regularly hunts, some individuals (e.g. low-ranking males) may never acquire meat. A second possibility is that vertebrates and invertebrates contain similar micronutrients in similar amounts, and are thus interchangeable on a gram-for-gram basis. However, although the data are scarce, micronutrient profiles even within taxa are highly differentiated. For example, some termite species are high in B12 relative to other insects, perhaps due to presence of symbiotic gut bacteria (Wakayama et al. 1984). Banjo et al. (2006) showed that magnesium levels in two insect species (*Zonocerus variegates* and *Cytacanthacris aeruginosus unicolor*) varied nearly one hundred-fold. Deblauwe and Janssens (2008) found considerable variation in micronutrient content among 19 sympatric insect species (termites and ants) in Cameroon; O’Malley and Power (2013; this volume) reported similar variation between species as well as *within* species between castes of social insects consumed by Kasekela chimpanzees. The former found evidence that apes select invertebrate prey, at least in part, based on their micronutrient profiles: Gorillas ate termite species that were high in iron (possibly to help detoxify plant antifeedants), and chimpanzees ate those high in manganese (Deblauwe and Janssens 2008).

It is therefore possible that with regard to micronutrients, chimpanzees can (and do) differentiate between vertebrates and invertebrates, and also between different types of invertebrates. Fully testing this hypothesis will require detailed nutritional analyses of the wide variety of animal source foods eaten by chimpanzees across Africa, data which are currently lacking. For example, there are no values of any kind for red colobus monkey tissue. In fact, to our knowledge, there are no data on the micronutrient content of any potentially comparable monkey species. Additionally, we need specific data on the micronutrient composition of different tissue types, which is likely to vary considerably. For example, raw beef brain contains less than ten µg of B12 while raw beef liver contains nearly 60 µg of B12 (National Nutrient Database for Standard Reference, USDA). The liver also has high concentrations of iron and zinc (Mann 2000).

Macronutrients

Meat is densely packed with accessible proteins (therefore freeing up gastrointestinal space for foraging on other essentials (Tennie et al. 2009)). However, the same is true for the invertebrate prey (DeFoliart 1989, 1992). O’Malley and Power (2012) compared assayed protein values of insects with published values on wild and domestic animal meat, and concluded that the protein content of insects consumed by Gombe chimpanzees was broadly comparable to that of wild mammal flesh such as vervet monkey, red river hog and bushbuck. While chimpanzees obtain considerable amounts of protein from leaves (Conklin-Brittain et al. 1998), many leaves contain antifeedant chemicals such as tannins (Takemoto 2003) and may therefore be less preferable than meat. Also, protein from vertebrates and invertebrates tends to be of higher quality, due to favorable ratios of essential amino acids relative to plant foods (Hladik 1977; Williamson et al. 2005).

Neither invertebrates nor vertebrates typically offer substantial amounts of digestible carbohydrates (see Deblauwe and Janssens 2008; but see Raubenheimer and Rothmann 2013 for an alternative view), so we do not consider them here. However, another macronutrient that is worth further consideration is fat. Typically the red meat of wild animals is very lean (on the order of 1-2% fat; (Mann 2000)). O'Malley and Power (2012) reported that worker and soldier castes of ants and termites consumed by Gombe chimpanzees contain < 1.0 – 5.2% fat on a fresh weight basis, with ants generally higher in fat then termite soldiers or workers.[3] Termite alates are exceptionally high in fat (up to 27.3%); an order of magnitude greater than other most insects and wild animals. This might point to an advantage in fat-content of some invertebrates over undomesticated vertebrates. However, bone marrow and brain tissue are also rich sources of fat (National Nutrient Database for Standard Reference) and can likewise be harvested, as needed, after a kill. Indeed, Goodall (1986) reports that when chimpanzees capture small prey (with easily breakable skulls), the brain is often one of the first parts they eat. In addition, some fruits

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[3] Hladik (1977) reported that *Macrotermes* termite soldiers collected at Gombe contain up to 53% lipids on a dry matter basis; this is a clear outlier compared to other, more recent estimates of fat content in termite major soldiers; e.g., *Macrotermes subhyalinus*: 2.6% fat (O'Malley and Power 2012); *M. lilljeborgi/renouxi*: 3% fat; *M. muelleri* 5% fat (Deblauwe and Janssens 2008). O'Malley and Power (2012) suggest this reflects differences in preservation or assay methods.

and nuts can be high in fat content – and may be more efficiently harvested (when available) than bone marrow, brain or invertebrates. For example, the fiber-free pulp of the African oil palm (*Elaeis guineensis*), a staple of the Kasekela community diet since observations on the community began in 1960 (Goodall 1986; Murray et al. 2006), is composed of >98% lipid on a fresh-weight basis, and provides an estimated 875kcal/100g in metabolizeable energy (Wu Leung et al. 1968).

Nutrient balancing

Foraging decisions by animals in part reflect an effort to balance intake ratios of particular macro- or micro-nutrients; for example protein and carbohydrates (Raubenheimer and Simpson 2004; Felton et al. 2009). Raubenheimer and Rothman (2012) argue that while insectivory by primates generally provides high yields of protein, insects consumed by humans show a broader range of protein values and tend to be high in fat as well. O'Malley and Power (2012) found that of the available and palatable insect prey, those consumed by Kasekela chimpanzees have a higher distribution of fat values on both a per-unit-mass and per-unit (insect, nest or 'dip') than those available and palatable insects that are ignored. Using observed intake rates of Kasekela chimpanzee predators, O'Malley and Power (2013; this volume) found that the two most common forms of insectivory in this community (*Macrotermes* major soldiers and *Dorylus* ants) can and do make a substantial contribution to the estimated daily intake requirements for several minerals and a non-trivial amount of fat, despite having relatively small returns in terms of metabolizeable energy. It is possible that the various patterns of faunivory (targeting invertebrates, vertebrates or both) seen within chimpanzee populations over time and across long-term research sites can be explained in terms of nutrient balancing in the context of an otherwise largely frugivorous and folivorous diet (see contributions by Raubenheimer and

Rothman, this volume). Unfortunately this hypothesis cannot be effectively evaluated until comprehensive nutritional data (including vitamin and mineral content) are available for all major foods consumed by a particular chimpanzee community. Of the long-term research studies in Africa, the nutritional composition of the major foods of the Kibale chimpanzee population has been published, along with some data on actual intake rates (Conklin-Brittain et al. 1998; 2006; Wrangham et al. 1991; 1993). Unfortunately these analyses did not include any vertebrate prey (and this population does not regularly target and consume any invertebrates apart from honey and honeybees; McGrew 1992). Hohmann et al. (2010) conducted a cross-population comparison of overall energetic and macronutritional yields for two populations of chimpanzees (Taï and Ngogo) and two populations of bonobos (Gashaka and Lui Kotal), but the actual nutritional values and intake rates for the specific foods included in the analyses were not published. Macronutrient data (though not intake rates) are also available for the major plant foods consumed by the Mahale M population (Matsumoto-Oda and Hiyashi 1999), though again this included no insects despite the fact that *Crematogaster* ants are consumed on an almost daily basis. O'Malley and Power (2012; 2013) have published macronutrient and mineral data for all major insect foods consumed by Gombe chimpanzees as well as data on intake rates, but no corresponding data are available for any other foods consumed by this population.

5. Synthesis

We have discussed the costs and benefits of feeding on vertebrate versus invertebrate prey for chimpanzees. In doing so, we have identified several areas where considerable research is needed in order to understand why chimpanzees eat meat. It is critically important to analyze the nutritional composition of all chimpanzee prey – vertebrate and invertebrate – especially at the micronutrient level. These analyses must include different tissues, ages (in vertebrates), and developmental stages (in invertebrates). Additionally, more precise data are needed on post-capture processing (i.e. chewing) costs; How long does it take to consume 50g of liver compared to 50g of tough meat or skin?

For now, our conclusions must remain tentative. We believe there is evidence that hunting vertebrates can be – at times – more efficient than gathering invertebrates especially in terms of time investment and availability. Nutrient compositions vary widely both within as well as across taxa – which still allows for the possibility that vertebrate prey is superior in some aspects (especially micronutritional) over invertebrate prey. However, at this stage, we cannot rule out the possibility that, on a gram-for-gram basis, meat and invertebrates are nutritionally comparable. However, we suggest that predation upon invertebrates in many ways may be a more reliable and less-energetically costly, but also less-efficient alternative strategy of acquiring similar important nutrients than hunting vertebrates. The latter is a more energetically costly and physically risky strategy with a greater payoff (albeit less reliable). Even a small bite of meat is equivalent to tens or hundreds of termites or ants (which take considerable time to capture; see table 1). Additionally, seasonality and depletion of resources are important restrictions for insectivory but less so for vertebrates. Chimpanzees with an opportunity to acquire even small amounts of meat (either through a capture or through subsequent begging or scrounging from others) are predicted to pursue that high-value resource to the exclusion of other foods, including insects such as termites or ants (but possibly excluding alates) which will have a much lower rate-of-return. However, we also predict that peripheral, low-ranking and/or immature individuals of either sex may have reduced opportunities to acquire meat, and therefore might engage in higher levels of insectivory despite the lower rate-of-return.

Thus, with the data currently available to us, our current view is that hunting and insectivory are different but complementary strategies to acquire a set of nutrients (macro- or micro-) that are limited in plant foods. Opportunity, seasonality and predictability, as well as nutritional yields per unit time are all critically important for evaluating chimpanzee faunivory patterns, including differences between the sexes, among populations, and over time (see table 1).

In addition to increasing our understanding of the role of meat in the diet of our ancestors (Milton 2003a), our analysis also has important implications for the evolution of group coordinated meat gathering activities in early hominins. The meat scrap hypothesis entails that hunting in groups leads to a higher likelihood that each participant obtains at least a scrap of meat. At certain times, this behavior will yield a higher benefit-cost ratio than feeding on invertebrates, thus providing selective pressure for cooperation. Importantly, our hypothesis does not require that the group activity be hunting. Detecting and defending carcasses against predators are other group activities that might have increased the likelihood of obtaining meat scraps compared to individual foraging. Thus, the meat scrap model can inform our view of meat eating by early hominins – regardless of whether it was via group hunting or group scavenging (Blumenschine et al. 1987; Dominguez-Rodrigo and Pickering 2003). The initial increase in carnivory may have been driven by the micronutrient, rather than caloric, content of vertebrate prey.

Table 1: Summary of the factors affecting chimpanzee consumption of key vertebrate and invertebrate prey.

Prey type	*Nutritional Yield (per gram)*	*Acquistion costs per minute*	*Yield per minute (in gram)*	*Local abundance (when detected)*	*Availability*
Termite soldiers	Medium	Low	Low	Medium/High	Seasonal
Termite alates	High (fat)	Low	Medium/High?	High	Seasonal
***Dorylus* ants**	Medium	Medium	Low	High	Year round
Red colobus	Medium to High (depends on tissue)	High	High	Medium	Year round

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