

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

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

3

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10 Running head: chimpanzee hunting vs. insectivory

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22 **1. Abstract**

23 Understanding the benefits and costs of acquiring and consuming different forms of animal  
24 matter by primates is critical for identifying the selective pressures responsible for increased  
25 meat consumption in the hominin lineage. Chimpanzees (*Pan troglodytes*) are unusual among  
26 primates in the amount of vertebrate prey they consume. Although there has been much debate  
27 over the putative social benefits of hunting, surprisingly little is known about the nutritional  
28 benefits of eating meat for this species. In order to understand why chimpanzees eat vertebrates,  
29 it is critical to consider the relative benefits and costs of other types of faunivory, e.g., of  
30 acquiring and consuming vertebrate relative to invertebrate (typically insect) prey. Although we  
31 lack specific nutritional data on the flesh and organs of chimpanzee prey, the macro-nutrient  
32 profiles of insects and wild vertebrate meat are generally comparable on a gram-to-gram basis.  
33 There are currently very few data on the micro-nutrient (vitamin and mineral) content of meat  
34 consumed by chimpanzees. With few exceptions, the advantages of hunting vertebrate prey  
35 include year-round availability, rapid acquisition of larger packages and reduced  
36 handling/processing time (once prey are encountered or detected). The disadvantages of hunting  
37 vertebrate prey include high potential acquisition costs per unit time (energy expenditure and risk  
38 of injury) and greater contest competition with conspecifics. Acquiring an equivalent mass of  
39 invertebrates (to match even a small scrap of meat) is possible, but typically takes more time.  
40 Furthermore, in contrast to vertebrate prey, some insect resources favored by chimpanzees  
41 (including termites, especially alates) are effectively available only at certain times of year. In  
42 this review, we identify the critical data needed to test our hypothesis that, in terms of micro-and  
43 macronutritional values (and associated packaging benefits) meat scraps may have a higher (or at  
44 least comparable) net benefit:cost ratio than insect prey. This would support the ‘meat scrap’

45 hypothesis as an explanation for why chimpanzees hunt in groups even when doing so does not  
46 maximize an individual's energetic gain.

47

## 48 **2. Introduction**

49 Early hominins likely ate more meat<sup>1</sup> than any extant nonhuman primate species (Balter et al.  
50 2012; Milton 1999a). This increase is central to hypotheses addressing the evolution of the  
51 unique suite of human traits, including large brains (Aiello and Wheeler 1995), central-place  
52 foraging (Isaac 1978) and cooperation (Tomasello et al. 2012). Understanding the relative  
53 benefits and costs of acquiring and consuming different forms of animal matter by primates is  
54 critical for identifying the selective pressures responsible for increased meat consumption in the  
55 hominin lineage. As humans' closest living relatives, chimpanzees (*Pan troglodytes*) and  
56 bonobos (*Pan paniscus*) are often used to reconstruct the diet and behavior of the last common  
57 ancestor of apes and humans (Milton 1999a, b, 2003a; Stanford 1996; Wrangham and Pilbeam  
58 2001). Therefore, detailed study of the contribution of animal source foods to the diet of the  
59 genus *Pan* promises to increase our understanding of why and how meat consumption became so  
60 frequent in the hominin lineage compared to our living ape counterparts. Although there is  
61 increasing evidence that bonobos eat meat more often than originally thought (Oelze et al. 2011;  
62 Surbeck and Hohmann 2008), we focus our review on chimpanzees, for whom predation upon  
63 vertebrates is well-documented (Boesch 1994; Gilby et al. 2006; 2008; Hosaka et al. 2001;  
64 Mitani and Watts 2001; Newton-Fisher et al. 2002; Stanford et al. 1994a).

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

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<sup>1</sup> 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).

67 invertebrate prey. Although there has been much debate over the putative social benefits of  
68 hunting (Gilby 2006; Gilby et al. 2010; Gomes and Boesch 2009; Stanford 1998; Stanford et al.  
69 1994b), surprisingly little is known about the purely nutritional net benefits of eating meat for  
70 chimpanzees. In our view, the social value of meat hinges primarily upon its nutritional value. If  
71 meat were not a valuable (and therefore desirable) food item, it would be of little use as an  
72 exchange commodity. Also, the proposal that a male's social standing is sensitive to his ability to  
73 obtain and distribute vertebrate prey (Moore 1984) is valid only if meat is desirable in its own  
74 right. Therefore, we believe that the motivation to obtain meat (by capture or scrounging) is  
75 ultimately driven by the fact that meat has inherent nutritional value.

76 Chimpanzees prey most frequently upon red colobus monkeys (*Procolobus spp.*) at most  
77 sites where the two species are sympatric (Mitani 2009; Uehara 1997). The fact that chimpanzees  
78 rarely hunt other frequently-encountered species (e.g. black-and-white colobus at Ngogo, Mitani  
79 and Watts 1999) suggests that they have evolved a preference for red colobus monkeys. This is  
80 likely because the net benefit of acquiring and consuming red colobus is particularly high,  
81 perhaps due to their ease of capture (relative to other species) and/or high nutritional value.  
82 Nevertheless, hunting arboreal prey is arguably energetically costly (Boesch 1994)<sup>2</sup> and entails  
83 considerable risk, in terms of injury ((by male colobus, Busse 1977; Goodall 1986) or falling  
84 (Gilby, personal observation)) and risk of failure (Boesch and Boesch 1989; Gilby and  
85 Wrangham 2007).

86 The meat scrap hypothesis (Gilby et al. 2008; Tennie et al. 2009) provides a simple  
87 explanation for why chimpanzees undertake such costs to hunt vertebrates. We first proposed

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<sup>2</sup> 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).

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

106

### 107 **3. Prey Acquisition**

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

111 Doing so allows us to more easily assess the costs and benefits associated with acquiring and  
112 processing the different prey types. We relax this assumption in section 4, where we focus on  
113 what is known of the nutritional content of meat and insects (and the available data do suggest  
114 that meat and invertebrate nutritional content can differ when compared on a gram-for-gram  
115 basis). This approach serves to identify critical areas of future research.

116

#### 117 *Availability of vertebrate prey*

118 Chimpanzees prey upon at least 32 species of mammals (Uehara 1997), 9 birds (Teleki 1981)  
119 and possibly small lizards and amphibians. Hunts of many of these species can best be described  
120 as opportunistic; for example, stumbling upon a bushbuck fawn hidden in the undergrowth  
121 (Goodall 1986), or finding nestlings or eggs in a tree hollow (Wrangham 1975). These events are  
122 likely to be affected by many factors, including breeding seasonality of the prey (if immature  
123 individuals are targeted) and ranging patterns of both predator and prey. However, to our  
124 knowledge, there has not been a systematic study of the frequency or regularity of encounters  
125 with such prey items. While challenging to collect, these missing data are critical for  
126 understanding the role of meat in chimpanzee diet.

127 In contrast, encounters with red colobus monkeys have been recorded at several sites. At  
128 Ngogo, chimpanzees encountered red colobus 1–33 times per month in 1998 and 1999 (Mitani  
129 and Watts 2001). Also, Mitani and Watts (1999) and Watts and Mitani (2002) describe ‘hunting  
130 patrols’ in which large parties of males travel quietly, in single file, apparently deliberately  
131 searching for monkeys. This suggests that to some extent, male chimpanzees at Ngogo may have  
132 some control over the encounter rate. It should be noted, however, that the red colobus  
133 population at Ngogo has sharply declined in recent years (Teelen 2007), most likely as a result of

134 predation by chimpanzees (Teelen 2008). Therefore, without long-term data, generalizations  
135 about prey availability should be interpreted with caution. At Tai, hunting frequency peaks in  
136 September and October (Boesch and Boesch-Achermann 2000). There is no indication that this  
137 is due to increased encounter rates, although Boesch and Boesch (1989) do report that Tai males  
138 actively search for monkeys. Instead, they attribute the increase in hunting frequency to a  
139 seasonal peak in red colobus births and increased prey vulnerability (due to reduced traction on  
140 wet branches during the rainy season; Boesch and Boesch-Achermann 2000). In this sense,  
141 infant or otherwise ‘vulnerable’ monkeys may be more available at certain times of year. At  
142 Mahale, a general increase in predation rates over time may have been linked to an overall  
143 increase in red colobus density (Hosaka et al. 2001), although encounter rates were not reported.  
144 At Gombe, red colobus encounter rate is strongly seasonal, peaking in the late dry season months  
145 of August and September (Gilby 2004; Gilby et al. 2013). A simple explanation for this pattern is  
146 that the probability of encountering colobus is positively correlated with daily travel distance,  
147 which increases during these months (Gilby 2004; Gilby et al. 2013). Additionally, the  
148 probability of encountering red colobus in woodland habitat (where hunts are more likely to  
149 occur (Gilby et al. 2006)) is correlated with daily travel distance (Gilby et al. 2013).

150

#### 151 *Availability of invertebrate prey*

152 Tropical forests exhibit extremely high insect species richness (Gullen and Cranston 2005),  
153 though only a few genera (termites: *Cubitermes*, *Macrotermes*, *Pseudacanthotermes*; ants:  
154 *Dorylus*, *Oecophylla*, *Camponotus*, *Crematogaster*; bees: *Apis*; stingless Meliponini) are sought  
155 out and eaten by African apes with any consistency (reviewed in McGrew 1992; see McGrew et  
156 al. 2007 for update). In some cases, insect consumption may be unintentional (e.g. insects



157 contained in fruit), though Redford et al. (1984) argue that some forms of primate frugivory may  
158 actually target insects infesting ripe fruit. The consequences of rare and unintentional insect  
159 consumption are unknown and difficult to study. Therefore, we concentrate on two major taxa  
160 that chimpanzees actively consume on a regular basis across Africa – termites (Order Isoptera;  
161 primarily *Macrotermes*) and ants (Order Hymenoptera; primarily *Oecophylla* (weaver ants) and  
162 *Dorylus* (driver ants)). These are generally considered to be the most important invertebrate prey  
163 for wild chimpanzees (McGrew 1992).

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

180 mound (O'Malley, pers. observation).

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

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

203 Consumption of weaver ants (*Oecophylla longinoda*) occurs without tools; instead the woven  
204 leaf nests constructed by these ants are crushed or rolled in the hands and/or feet and their insect  
205 contents consumed. Goodall (1986) reported that Kasekela chimpanzees spent relatively more  
206 time feeding on weaver ants in the late dry season and early wet season (Aug-Oct), at least in  
207 1978 and 1979, though the ants are present year round.

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

219

#### 220 *Prey capture*

221 Acquiring vertebrate prey is best described as “high-risk, high-yield”. The potential payoff can  
222 be great (e.g., an entire red colobus carcass weighing from 1-12 kg), and even non-hunters are  
223 often able to obtain appreciable amounts through scrounging, begging or active sharing (Gilby  
224 2006; Mitani and Watts 2001). However, there are considerable costs associated with hunting  
225 (and even possessing meat). First, moving at high speeds can be energetically very costly

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

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

249 increased likelihood that multiple carcasses are available.

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

263           Compared to hunting vertebrates, it probably requires less energy per minute of effort to  
264 acquire insects. However, the gain is (in most cases) also diminished (at least when compared to  
265 the potential high-gain outcome of vertebrate hunting). McGrew (1974) reported that *Dorylus*  
266 ant-fishing sessions ranged from 3-48 minutes, and an average dip rate of 2.6/minute. Using  
267 these values, O'Malley and Power (2012) estimated the maximum payoffs for ant-fishing to be  
268 56.16g of ants, 59kcal (metabolizable energy basis), 0.82g of fat and 12.87g of protein.). As  
269 noted above, the average hunt lasts approximately 18 minutes (at Tai and Ngogo), during which  
270 a hunter has a greater than 60% chance of obtaining at least a scrap of meat (at Gombe (Gilby et  
271 al. 2008)), which is typically more than 50g (Gilby 2006). Thus, the payoff is higher for hunting

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

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

292

#### 293 **4. Consumption**

294 *Chewing*

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

318 easily consumed than other tissues.

319           Similarly, although data specifically on chimpanzee prey is lacking, it is highly likely that  
320 different muscle types are easier to chew than others. For example, the psoas muscle (the  
321 tenderloin), which lies alongside the spine, is particularly tender in domestic animals  
322 (Shackelford et al. 1995; Stanley et al. 1971). At Gombe, one of us (Gilby, personal observation)  
323 has observed male chimpanzee Frodo (FR) remove the spine, ribcage and psoas muscle from  
324 large carcasses before discarding the remainder, suggesting that he was selecting the most tender  
325 muscle. Even so, chimpanzees typically supplement even the most tender meat with mature  
326 leaves (Goodall 1986, Wrangham 1975), which indicates that raw meat is relatively difficult to  
327 chew for them (especially since their teeth are not very well adapted to this task; Wrangham  
328 2009). Wrangham (2009) describes an informal experiment (with humans) suggesting that  
329 adding leaves when chewing improves ‘traction’, allowing for more efficient raw meat-chewing.  
330 Since

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

336

### 337 *Digestion*

338 Stomach volume imposes an upper limit on ingestion rates in many animals, including  
339 chimpanzees. With the exception of alate wings (which are discarded), insects are eaten whole.  
340 Insect exoskeleton, which is composed of a matrix of the carbohydrate chitin, minerals, and



341 amino acids, is believed to be largely undigestible to chimpanzees because termite and ant head  
342 capsules often appear in feces intact (McGrew 1979). For the most common Gombe insect prey  
343 (*Macrotermes*, *Apis*, *Dorylus*, *Oecophylla*), the ash-corrected ADF fraction (a proxy for the  
344 exoskeleton, including chitin and bound proteins) comprises between 6.5 – 24.8% of the total  
345 mass consumed on a dry matter basis (O'Malley and Power 2012) However, even McGrew's  
346 (2001) maximum estimated fresh-weight termite mass consumed in a single meal (260g) would  
347 amount to about 14.2g of indigestible minerals and exoskeleton suggesting that the indigestible  
348 fraction of these insects is unlikely to impose serious energetic costs on a chimpanzee predator.

349 Chimpanzees appear to value some parts of vertebrate carcasses more than others; for  
350 example, muscle, brains and viscera are avidly consumed while bones and skin may be  
351 consumed last or even discarded for others to scrounge (Goodall 1986). While primary carcass  
352 possessors can afford to be selective, individuals lacking such priority of access to a carcass  
353 probably have more limited choices as to which body parts to consume or discard. As a result,  
354 although it is typically the case that an entire carcass is eventually consumed (Goodall 1986), the  
355 less preferred components are predicted to be those with lower digestibility and nutritional value.  
356 Not surprisingly, bones and skin are often visible in chimpanzee dung (Goodall 1986; Surbeck et  
357 al. 2009). Sizeable portions of undigested muscle tissue may be present in the feces as well  
358 (Goodall 1986)). This suggests that the chimpanzee gut, which is adapted to a primarily  
359 vegetarian, high-fiber diet, may not efficiently process raw meat, leaving some undigested and  
360 unabsorbed. The stomach is where most mechanical digestion (post-chewing) takes place, and is  
361 critical for breaking meat down into small pieces (Wrangham 2009). Stomach passage time in  
362 primates is much shorter than in carnivores ((Meyer et al. 1985; 1988, as cited by Wrangham  
363 (2009)), which presumably compromises digestion of raw meat. Reduced stomach time may also

364 increase the risk of disease transmission (Leendertz et al. 2010), another possible cost of eating  
365 meat.

366

### 367 *Nutrient Content*

#### 368 Micronutrients

369 We currently lack detailed comparisons of the micronutrient profiles of chimpanzee animal  
370 source foods. However, it is clear that both vertebrates and invertebrates are excellent sources of  
371 important minerals and vitamins. Wild (lean) red meat is rich in iron, zinc and Vitamin B12 as  
372 well as magnesium, copper, cobalt, phosphorus, chromium, nickel and selenium (Williamson et  
373 al. 2005). The original meat scrap hypothesis (Tennie et al. 2009) argued that chimpanzees hunt  
374 mainly to satisfy their need for such micronutrients. It is possible that meat contains important  
375 micronutrients that are *entirely* absent in the remainder of their diet (including invertebrates), and  
376 would therefore be worth high acquisition costs. However, this seems rather unlikely, as there  
377 are chimpanzee communities that rarely eat meat (e.g. Budongo, Newton-Fisher et al. 2002), and  
378 even within a community that regularly hunts, some individuals (e.g. low-ranking males) may  
379 never acquire meat. A second possibility is that vertebrates and invertebrates contain similar  
380 micronutrients in similar amounts, and are thus interchangeable on a gram-for-gram basis.  
381 However, although the data are scarce, micronutrient profiles even within taxa are highly  
382 differentiated. For example, some termite species are high in B12 relative to other insects,  
383 perhaps due to presence of symbiotic gut bacteria (Wakayama et al. 1984). Banjo et al. (2006)  
384 showed that magnesium levels in two insect species (*Zonocerus variegates* and *Cytacanthacris*  
385 *aeruginosus unicolor*) varied nearly one hundred-fold. Deblauwe and Janssens (2008) found  
386 considerable variation in micronutrient content among 19 sympatric insect species (termites and

387 ants) in Cameroon; O'Malley and Power (2013; this volume) reported similar variation between  
388 species as well as *within* species between castes of social insects consumed by Kasekela  
389 chimpanzees. The former found evidence that apes select invertebrate prey, at least in part, based  
390 on their micronutrient profiles: Gorillas ate termite species that were high in iron (possibly to  
391 help detoxify plant antifeedants), and chimpanzees ate those high in manganese (Deblauwe and  
392 Janssens 2008).

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

404

#### 405 Macronutrients

406 Meat is densely packed with accessible proteins (therefore freeing up gastrointestinal space for  
407 foraging on other essentials (Tennie et al. 2009)). However, the same is true for the invertebrate  
408 prey (DeFoliart 1989, 1992). O'Malley and Power (2012) compared assayed protein values of  
409 insects with published values on wild and domestic animal meat, and concluded that the protein

410 content of insects consumed by Gombe chimpanzees was broadly comparable to that of wild  
411 mammal flesh such as vervet monkey, red river hog and bushbuck. While chimpanzees obtain  
412 considerable amounts of protein from leaves (Conklin-Brittain et al. 1998), many leaves contain  
413 antifeedant chemicals such as tannins (Takemoto 2003) and may therefore be less preferable than  
414 meat. Also, protein from vertebrates and invertebrates tends to be of higher quality, due to  
415 favorable ratios of essential amino acids relative to plant foods (Hladik 1977; Williamson et al.  
416 2005).

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

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<sup>3</sup> 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.

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

#### 436 Nutrient balancing

437 Foraging decisions by animals in part reflect an effort to balance intake ratios of particular  
438 macro- or micro-nutrients; for example protein and carbohydrates (Raubenheimer and Simpson  
439 2004; Felton et al. 2009). Raubenheimer and Rothman (2012) argue that while insectivory by  
440 primates generally provides high yields of protein, insects consumed by humans show a broader  
441 range of protein values and tend to be high in fat as well. O'Malley and Power (2012) found that  
442 of the available and palatable insect prey, those consumed by Kasekela chimpanzees have a  
443 higher distribution of fat values on both a per-unit-mass and per-unit (insect, nest or 'dip') than  
444 those available and palatable insects that are ignored. Using observed intake rates of Kasekela  
445 chimpanzee predators, O'Malley and Power (2013; this volume) found that the two most  
446 common forms of insectivory in this community (*Macrotermes* major soldiers and *Dorylus* ants)  
447 can and do make a substantial contribution to the estimated daily intake requirements for several  
448 minerals and a non-trivial amount of fat, despite having relatively small returns in terms of  
449 metabolizeable energy. It is possible that the various patterns of faunivory (targeting  
450 invertebrates, vertebrates or both) seen within chimpanzee populations over time and across  
451 long-term research sites can be explained in terms of nutrient balancing in the context of an  
452 otherwise largely frugivorous and folivorous diet (see contributions by Raubenheimer and

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

## 470 **5. Synthesis**

471 We have discussed the costs and benefits of feeding on vertebrate versus invertebrate prey for  
472 chimpanzees. In doing so, we have identified several areas where considerable research is  
473 needed in order to understand why chimpanzees eat meat. It is critically important to analyze the  
474 nutritional composition of all chimpanzee prey – vertebrate and invertebrate – especially at the  
475 micronutrient level. These analyses must include different tissues, ages (in vertebrates), and

476 developmental stages (in invertebrates). Additionally, more precise data are needed on post-  
477 capture processing (i.e. chewing) costs; How long does it take to consume 50g of liver compared  
478 to 50g of tough meat or skin?

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

498         Thus, with the data currently available to us, our current view is that hunting and

499 insectivory are different but complementary strategies to acquire a set of nutrients (macro- or  
500 micro-) that are limited in plant foods. Opportunity, seasonality and predictability, as well as  
501 nutritional yields per unit time are all critically important for evaluating chimpanzee faunivory  
502 patterns, including differences between the sexes, among populations, and over time (see table  
503 1).

504         In addition to increasing our understanding of the role of meat in the diet of our ancestors  
505 (Milton 2003a), our analysis also has important implications for the evolution of group  
506 coordinated meat gathering activities in early hominins. The meat scrap hypothesis entails that  
507 hunting in groups leads to a higher likelihood that each participant obtains at least a scrap of  
508 meat. At certain times, this behavior will yield a higher benefit-cost ratio than feeding on  
509 invertebrates, thus providing selective pressure for cooperation. Importantly, our hypothesis does  
510 not require that the group activity be hunting. Detecting and defending carcasses against  
511 predators are other group activities that might have increased the likelihood of obtaining meat  
512 scraps compared to individual foraging. Thus, the meat scrap model can inform our view of meat  
513 eating by early hominins – regardless of whether it was via group hunting or group scavenging  
514 (Blumenschine et al. 1987; Dominguez-Rodrigo and Pickering 2003). The initial increase in  
515 carnivory may have been driven by the micronutrient, rather than caloric, content of vertebrate  
516 prey.  
517



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

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

520

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523

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