

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

11

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19

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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 meat¹ 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

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).

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)² 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

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).

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.³ 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

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.

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>		
Termite soldiers	Medium	Low	Low	Medium/High	Seasonal
Termite alates	High (fat)	Low	Medium/High?	High	Seasonal
<i>Dorylus</i> ants	Medium	Medium	Low	High	Year round
Red colobus	Medium to High (depends on tissue)	High	High	Medium	Year round

520

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523

524 REFERENCES

525 Aiello LC, Wheeler P (1995) The expensive tissue hypothesis: the brain and digestive system in
 526 human and primate evolution. *Current Anthropology* 36(2):199-221

527 Altmann SA (2009) Fallback Foods, Eclectic Omnivores, and the Packaging Problem. *Am J*
 528 *Phys Anthropol* 140(4):615-629

529 Balter V, Braga J, Telouk P, Thackeray JF (2012) Evidence for dietary change but not landscape
 530 use in South African early hominins. *Nature* 489(7417):558-560

531 Banjo AD, Lawal OA, Songonuga EA (2006) The nutritional value of fourteen species of edible
532 insects in southwestern Nigeria. *African Journal of Biotechnology* 5(3):298-301

533 Blumenschine RJ, Bunn HT, Geist V, Ikawa-Smith F, Marean CW, Payne AG, Tooby J, Merwe
534 NJvd (1987) Characteristics of an Early Hominid Scavenging Niche. *Current*
535 *Anthropology* 28(4):383-407

536 Boesch C (1994) Cooperative hunting in wild chimpanzees. *Anim Behav* 48:653-667

537 Boesch C, Boesch-Achermann H (2000) *The Chimpanzees of the Taï Forest. Behavioural*
538 *Ecology and Evolution*. Oxford University Press, Oxford

539 Boesch C, Boesch H (1989) Hunting behavior of wild chimpanzees in the Taï National Park. *Am*
540 *J Phys Anthropol* 78:547-573

541 Busse CD (1977) Chimpanzee predation as a possible factor in the evolution of red colobus
542 monkey social organization. *Evolution* 31:907-911

543 Conklin-Brittain NL, Wrangham RW, Hunt KD (1998) Dietary response of chimpanzees and
544 cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *Int J Primatol*
545 19(6):971-998

546 Conklin-Brittain NL, Knott CD, Wrangham RW (2006) Energy intake by wild chimpanzees and
547 orangutans: methodological considerations and a preliminary comparison. In: Hohmann
548 G, Robbins MM, Boesch C. (Eds.), *Feeding Ecology in Apes and Other Primates:*
549 *Ecological, Physical and Behavioral Aspects*. Cambridge University Press, Cambridge,
550 pp. 445-465.

551 Deblauwe I, Janssens GPJ (2008) New insights in insect prey choice by chimpanzees and
552 gorillas in southeast Cameroon: The role of nutritional value. *Am J Phys Anthropol*
553 135(1):42-55

554 DeFoliart GR (1989) The human use of insects as food and as animal feed. *Bulletin of the*
555 *Entomological Society of America* 35(1):22-35

556 DeFoliart GR (1992) Insects as human food. *Crop Protection* 11(5):395-399

557 Dominguez-Rodrigo M, Pickering T (2003) Early hominid hunting and scavenging: a
558 zooarcheological review. *Evolutionary Anthropology* 12:275–282.

559 Gilby IC (2004) *Hunting and meat sharing among the chimpanzees of Gombe National Park,*
560 *Tanzania.* University of Minnesota

561 Gilby IC (2006) Meat sharing among the Gombe chimpanzees: harassment and reciprocal
562 exchange. *Anim Behav* 71(4):953-963

563 Gilby IC, Connor RC (2010) The role of intelligence in group hunting: Are chimpanzees
564 different from other social predators? In: Lonsdorf EV, Ross SR, Matsuzawa T (eds) *The*
565 *Mind of the Chimpanzee: Ecological and Experimental Perspectives.* University of
566 Chicago Press, Chicago, IL, pp 220-233

567 Gilby IC, Eberly LE, Pintea L, Pusey AE (2006) Ecological and social influences on the hunting
568 behaviour of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Anim Behav* 72(1):169-
569 180

570 Gilby IC, Eberly LE, Wrangham RW (2008) Economic profitability of social predation among
571 wild chimpanzees: individual variation promotes cooperation. *Anim Behav* 75:351-360

572 Gilby IC, Emery Thompson M, Ruane J, Wrangham RW (2010) No evidence of short-term
573 exchange of meat for sex among chimpanzees. *J Hum Evol* 59:44-53

574 Gilby IC, Wilson ML, Pusey AE (2013) Ecology rather than psychology explains co-occurrence
575 of predation and border patrols in male chimpanzees. *Anim Behav* (*In Press*)

576 Gilby IC, Wrangham RW (2007) Risk-prone hunting by chimpanzees (*Pan troglodytes*

577 schweinfurthii) increases during periods of high diet quality. *Behav Ecol Sociobiol*
578 61(11):1771-1779

579 Gomes CM, Boesch C (2009). Wild chimpanzees exchange meat for sex on a long-term basis.
580 *PLoS One*, 4(4): e5116

581 Goodall J (1963) Feeding behaviour of wild chimpanzees. A preliminary report. *Symposium of*
582 *the Zoological Society of London* 10:39-47

583 Goodall J (1986) *The chimpanzees of Gombe: patterns of behavior*. Harvard University Press,
584 Cambridge, MA.

585 Hladik CM (1977) Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data
586 on the diet. In: Clutton-Brock TH (ed) *Primate Ecology: Studies of Feeding and Ranging*
587 *Behaviour in Lemurs, Monkeys and Apes*. Academic Press, London, pp 481-501

588 Hohmann G, Potts K, N'Guessan A, Fowler A, Mundry R, Ganzhorn JU, & Ortmann S (2010)
589 Plant foods consumed by Pan: exploring the variation of nutritional ecology across
590 Africa. *Am J Phys Anthropol* 141(3): 476-485

591 Hosaka K, Nishida T, Hamai M, Matsumoto-Oda A, Uehara S (2001) Predation of mammals by
592 the chimpanzees of the Mahale Mountains, Tanzania. In: Galdikas B, Briggs N, Sheeran
593 L, Shapiro G, Goodall J (eds) *All Apes Great and Small, Volume I African Apes*. Kluwer
594 Academic Publishers, New York, pp 107-130

595 Isaac G (1978) The food-sharing behavior of protohuman hominoids. *Scientific American*
596 238(4):90-108

597 Leendertz SAJ, Junglen S, Hedemann C, Goffe A, Calvignac S, Boesch C, Leendertz FH (2010)
598 High Prevalence, Coinfection Rate, and Genetic Diversity of Retroviruses in Wild Red
599 Colobus Monkeys (*Piliocolobus badius badius*) in Tai National Park, Cote d'Ivoire.

600 Journal of Virology 84(15):7427-7436

601 Lonsdorf EV (2006) What is the role of mothers in the acquisition of termite-fishing behaviors in
602 wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition* 9(1):36-46

603 Mann N (2000) Dietary lean red meat and human evolution. *Eur J Nutr* 39:71-79

604 Matsumoto-Oda A, Hayashi Y (1999) Nutritional aspects of fruit choice by chimpanzees. *Folia*
605 *Primatol* 70(3): 154-162

606 McGrew WC (1974) Tool use by wild chimpanzees in feeding upon driver ants. *J Hum Evol*
607 3(6):501-508

608 McGrew WC (1979) Evolutionary implications of sex differences in chimpanzee predation and
609 tool use. In: Hamburg DA, McCown ER (eds) *The Great Apes*. Benjamin Cummings,
610 London, pp 441-463

611 McGrew WC (1983) The female chimpanzee as a human evolutionary prototype. In: Dahlberg F
612 (ed) *Woman the gatherer*. Yale University Press, New Haven, pp 35-73

613 McGrew WC (1992) *Chimpanzee material culture*. Cambridge University Press, Cambridge

614 McGrew WC, Marchant LF, Beuerlein MM, Vrancken D, Fruth B, & Hohmann G. (2007).
615 Prospects for Bonobo Insectivory: Lui Kotal, Democratic Republic of Congo. *Int J*
616 *Primatol* 28(6), 1237-1252

617 McGrew WC (2010) In search of the last common ancestor: new findings on wild chimpanzees.
618 *Philos Trans R Soc B-Biol Sci* 365(1556):3267-3276

619 McGrew WC, Tutin CEG, Baldwin PJ (1979) Chimpanzees, tools, and termites: Cross-cultural
620 comparisons of Senegal, Tanzania, and Rio-Muni. *Man* 14(2):185-214

621 Meyer JH, Dressman J, Fink A, Amidon G (1985) Effect of size and density on canine gastric-
622 emptying of nondigestible solids. *Gastroenterology* 89(4):805-813

623 Meyer JH, Elashoff J, Porterfink V, Dressman J, Amidon GL (1988) Human postprandial
624 gastric-emptying of 1-3 millimeter spheres. *Gastroenterology* 94(6):1315-1325

625 Milton K (1999a) A hypothesis to explain the role of meat-eating in human evolution.
626 *Evolutionary Anthropology* 8(1):11-21

627 Milton K (1999b) Nutritional characteristics of wild primate foods: Do the diets of our closest
628 living relatives have lessons for us? *Nutrition* 15(6):488-498

629 Milton K (2003a) The critical role played by animal source foods in human (*Homo*) evolution.
630 *Journal of Nutrition* 133(11):3886S-3892S

631 Milton K (2003b) Micronutrient intakes of wild primates: are humans different? *Comparative*
632 *Biochemistry and Physiology Part A* 136:47-59

633 Mitani JC (2009) Cooperation and competition in chimpanzees: Current understanding and
634 future challenges. *Evolutionary Anthropology* 18(5):215-227

635 Mitani JC, Watts DP (1999) Demographic influences on the hunting behavior of chimpanzees.
636 *Am J Phys Anthropol* 109:439-454

637 Mitani JC, Watts DP (2001) Why do chimpanzees hunt and share meat? *Anim Behav* 61(5):915-
638 924

639 Murray CM, Eberly LE, Pusey AE (2006) Foraging strategies as a function of season and rank
640 among wild female chimpanzees (*Pan troglodytes*). *Behav Ecol*, 17(6): 1020-1028

641

642 Newton-Fisher NE, Notman H, Reynolds V (2002) Hunting of mammalian prey by Budongo
643 Forest chimpanzees. *Folia Primatologica* 73:281-283

644 O'Malley RC (2011) Environmental, nutritional and social aspects of insectivory by Gombe
645 chimpanzees. University of Southern California

646 O'Malley RC, Power ML (2012) Nutritional composition of actual and potential insect prey for
647 the Kasekela chimpanzees of Gombe National Park, Tanzania. *Am J Phys Anthropol*
648 149(4): 493-503

649 O'Malley RC, Power ML (2013) The energetic and nutritional yields from insectivory for
650 Kasekela chimpanzees. *J Hum Evol*

651 Oelze VM, Fuller BT, Richards MP, Fruth B, Surbeck M, Hublin JJ, Hohmann G (2011)
652 Exploring the contribution and significance of animal protein in the diet of bonobos by
653 stable isotope ratio analysis of hair. *Proceedings of the National Academy of Sciences of*
654 *the United States of America* 108(24):9792-9797

655 Pandolfi S, van Schaik C, Pusey A (2003) Sex differences in termite fishing among Gombe
656 chimpanzees. In: De Waal FBM, Tyack PL (eds) *Animal social complexity: intelligence,*
657 *culture, and individualized societies.* Harvard University Press, Cambridge, MA, pp 414-
658 418

659 Pontzer H, Wrangham RW (2004) Climbing and the daily energy cost of locomotion in wild
660 chimpanzees: implications for hominoid locomotor evolution. *J Hum Evol* 46:317-335

661 Pruetz JD, Bertolani P (2007) Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools.
662 *Current Biology* 17(5):412-417

663 Ralston, HJ (1958). Energy-speed relation and optimal speed during level walking. *Internationale*
664 *Zeitschrift für angewandte Physiologie einschließlich Arbeitsphysiologie* 17:277-283

665 Raubenheimer D, Simpson SJ (1997) Integrative models of nutrient balancing: application to
666 insects and vertebrates. *Nutrition Research Reviews* 10:151-179

667 Raubenheimer D, Rothman JM (2013) Nutritional ecology of entomophagy in humans and other
668 primates. *Annual Review of Entomology* 58:141-160

669 Redford KH, Bouchardet da Fonseca GA, Lacher TE (1984) The relationship between frugivory
670 and insectivory in primates. *Primates* 25(4):433-440

671 Sanz C, Morgan D, Gulick S (2004) New insights into chimpanzees, tools, and termites from the
672 Congo basin. *Am Nat* 164(5):567-581

673 Schmidt, JO (this volume) Fighting back: how solitary and social insects have responded to
674 attacks by insectivores and overwhelmingly powerful predators.

675 Shackelford SD, Wheeler TL, Koohmaraie M (1995) Relationship between shear force and
676 trained sensory panel tenderness ratings of 10 major muscles from *Bos indicus* and *Bos*
677 *taurus* cattle. *Journal of Animal Science* 73(11):3333-3340

678 Shorthose WR, Harris PV (1990) Effect of animal age on the tenderness of selected beef
679 muscles. *J Food Sci* 55:1-14

680 Stanford CB (1996) The hunting ecology of wild chimpanzees: Implications for the evolutionary
681 ecology of Pliocene hominids. *American Anthropologist* 98:96-113

682 Stanford CB (1998) Chimpanzee and red colobus. Harvard University Press, Cambridge, MA

683 Stanford CB, Wallis J, Matama H, Goodall J (1994a) Patterns of predation by chimpanzees on
684 red colobus monkeys in Gombe National Park, 1982-1991. *Am J Phys Anthropol* 94:213-
685 228

686 Stanford CB, Wallis J, Mpongo E, Goodall J (1994b) Hunting decisions in wild chimpanzees.
687 *Behaviour* 131(1-2):1-18

688 Stanley DW, Pearson GP, Coxworth VE (1971) Evaluation of certain physical properties of meat
689 using a universal testing machine. *Journal of Food Science* 36:256-260

690 Stephens DW, Krebs JR (1986) *Foraging Theory*. Princeton University Press, Princeton, NJ

691 Surbeck M, Fowler A, Deimel C, Hohmann G (2009) Evidence for the Consumption of

692 Arboreal, Diurnal Primates by Bonobos (*Pan paniscus*). *Am J Primatol* 71(2):171-174
693 Surbeck M, Hohmann G (2008) Primate hunting by bonobos at LuiKotale, Salonga National
694 Park. *Current Biology* 18:R906-R907
695 Suzuki S, Kuroda S, Nishihara T (1995) Tool-set for termite-fishing by chimpanzees in the
696 Ndoki Forest, Congo. *Behaviour* 132:219-235
697 Takemoto H (2003) Phytochemical determination for leaf food choice by wild chimpanzees in
698 Guinea, Bossou. *Journal of Chemical Ecology* 29(11):2551-2573
699 Teelen S (2007) Primate abundance along five transect lines at Ngogo, Kibale National Park,
700 Uganda. *Am J Primatol* 69(9):1030-1044
701 Teelen S (2008) Influence of chimpanzee predation on the red colobus population at Ngogo,
702 Kibale National Park, Uganda. *Primates* 49(1):41-49
703 Teleki G (1973) The predatory behavior of wild chimpanzees. Bucknell University Press,
704 Lewisburg, PA
705 Teleki G (1981) The omnivorous diet and eclectic feeding habits of chimpanzees in Gombe
706 National Park, Tanzania. In: Harding RSO, Teleki G (eds) *Omnivorous Primates*
707 *Gathering and hunting in human evolution*. Columbia University Press, New York, pp
708 303-343
709 Tennie C, Gilby IC, Mundry R (2009) The meat-scrap hypothesis: small quantities of meat may
710 promote cooperation in wild chimpanzees (*Pan troglodytes*). *Behav Ecol Sociobiol*
711 63(3):421-431
712 Tomasello M, Melis AP, Tennie C, Wyman E, Herrmann E (2012) Two key steps in the
713 evolution of human cooperation: the interdependence hypothesis. *Current Anthropology*
714 53: 673-692.

715 Uehara S (1997) Predation on mammals by the chimpanzee (*Pan troglodytes*). *Primates*
716 38(2):193-214

717 Wakayama EJ, Dillwith JW, Howard RW, Blomquist GJ (1984) Vitamin B12 levels in selected
718 insects. *Insect Biochemistry* 14(2):175-179

719 Watts DP, Mitani JC (2002) Hunting behavior of chimpanzees at Ngogo, Kibale National Park,
720 Uganda. *Int J Primatol* 23(1):1-28

721 Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG,
722 Wrangham RW, Boesch C (1999) Cultures in chimpanzees. *Nature* 399:682-685

723 Williamson CS, Foster RK, Stanner SA, Buttriss JL (2005) Red meat in the diet. *Nutrition*
724 *Bulletin* 30:323-355

725 Wrangham RW (1975) The behavioural ecology of chimpanzees in Gombe National Park,
726 Tanzania. Cambridge University

727 Wrangham, RW, Conklin, NL, Chapman CA, Hunt KD, Milton K, Rogers E, ... , Barton RA
728 (1991) The significance of fibrous foods for Kibale Forest chimpanzees [and Discussion].
729 *Phil Transactions R Soc London. Series B: Biological Sciences*, 334(1270): 171-178.

730 Wrangham R, Etot G, Obua J, Hunt KD, Hauser MD, Clark AP (1993) The value of figs to
731 chimpanzees. *Int J Primatol* 14(2): 243-256 Wrangham RW (2009) *Catching Fire - How*
732 *cooking made us human*. Basic Books, New York

733 Wrangham RW, Conklin-Brittain N (2003) Cooking as a biological trait. *Comparative*
734 *Biochemistry and Physiology - Part A: Molecular & Integrative Physiology* 136(1):35-46

735 Wrangham RW, Pilbeam D (2001) African apes as time machines. In: Galdikas B, Briggs N,
736 Sheeran L, Shapiro G, Goodall J (eds) *All apes great and small, Volume I: African apes*.
737 Kluwer Academics / Plenum Publishers, New York, pp 5-17

738 Wu Leung WT, Busson F, Jardin C (1968) Food composition table for use in Africa. FAO-
739 Nutrition Information Documents Series, (3).
740