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1 Chimpanzee vertebrate consumption: savanna and forest chimpanzees compared

2

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22 **Keywords:** *Pan troglodytes*, Meat eating, Early hominins, Ugalla, Predation, Faunivory

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24 **Abstract**

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

**46 Introduction***47 Chimpanzees and the origins of hunting by hominins*

48 The origin, nature, and significance of hominin consumption of vertebrates have been  
49 foci of research and debate in anthropology for nearly a century. The transition from an  
50 ape-like frugivore/folivore to a more carnivorous hominin has been linked to a shift from  
51 more forested to more open, savanna environments since before the first African fossil  
52 hominin was found (e.g., Barrell, 1917). This was thought to be either because  
53 environmental change put earliest hominins into marginal savanna habitats, forcing them  
54 to broaden their diet, or because abundant prey in savannas enabled them to expand into a  
55 vacant niche (Cartmill, 1993). To explore whether consumption of vertebrates and  
56 adaptation to savanna habitats were functionally linked in hominin evolution, it may be  
57 informative to look at meat-eating among extant chimpanzees and investigate whether  
58 adaptation to savanna habitats influences their consumption of vertebrates. Because  
59 chimpanzees and early hominins (e.g., *Ardipithecus*; Stanford, 2012) are broadly similar  
60 (e.g., body size and structure, degree of encephalization, habitat), ecological and social  
61 adaptations exhibited by savanna-dwelling chimpanzees relative to forest populations  
62 may shed light on that transition in the hominin lineage. That light may take the form of a  
63 heuristic framework for thinking about early hominins; more usefully, it may generate  
64 middle-range tests of hypotheses or discover unrecognized problems with interpretation  
65 of paleontological data (Moore, 1996; Stanford, 1996; Pickering and Domínguez-  
66 Rodrigo, 2012; Mitani, 2013). We agree with Sayers and Lovejoy (2008) that using  
67 modern panins to help understand extinct hominins can lead to erroneous conclusions and  
68 that such an approach must be applied with care. Using the one to help understand the

69 other ('referential modeling') is a method that, like any other method, must be applied  
70 carefully or error can result—for example, theoretical ('strategic') modeling resulted in  
71 the now disproved single-species hypothesis (Wolpoff, 1971).

72 Judging from the excitement that generally surrounds chimpanzee hunting (Gilby et  
73 al., 2013), the acquisition of meat is important to them. Surprisingly, there is not a  
74 consensus as to why that is. While meat is calorically dense, the energetic cost of hunting  
75 can be high and individual yields from a divided carcass low, suggesting to some that the  
76 primary function of hunting is social (Stanford et al., 1994; Mitani and Watts, 2001). This  
77 view is supported by the observation that hunting frequencies may be higher during  
78 seasons of abundant food, contrary to what one would expect if meat were making up a  
79 nutritional shortfall (Mitani and Watts, 2005). Others emphasize that, unless carcasses  
80 were intrinsically valuable, they would have little value in social exchanges and point to  
81 ecological explanations and non-caloric nutritional benefits (Gilby et al., 2006; Tennie et  
82 al., 2009; Newton-Fisher, 2015; O'Malley et al., 2016). As noted by Newton-Fisher  
83 (2015), the uncertainty about the adaptive function of chimpanzee hunting is problematic  
84 for attempts to use chimpanzees as referential models for early hominins. A better  
85 understanding of causes of variation in hunting frequency, seasonality, and prey choice  
86 among chimpanzees is needed (Newton-Fisher, 2015).

87 We report here on observational and fecal data collected at the Issa, Nguye, and  
88 Bhukalai study sites, Ugalla (Tanzania), and place them in the context of published  
89 quantitative information on the prevalence of vertebrate remains in chimpanzee feces  
90 from other wild chimpanzee populations. Fecal data indicate consumption only; however,

91 scavenging by chimpanzees is rare (Watts, 2008), such that it is therefore likely that most  
92 vertebrates consumed were hunted.

93

94 *Fecal analysis and rates of faunivory*

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

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

114 communities at Gombe averaged about 204 prey/year between 1972–1975. Between  
115 1965–1967, the Kasekela/Kahama community averaged about 42 adult and adolescent  
116 individuals (Goodall, 1986). Teleki (1973) reported that an average of eight individual  
117 chimpanzees obtained portions per predation event (range 4–15). Wild chimpanzees  
118 defecate about 3 to 3.5 times per day (calculated from Phillips and McGrew, 2014 and  
119 Nishida et al., 1979, respectively). Finally, Lambert (2002) found that markers fed to  
120 captive chimpanzees were detected between 23–63 hours following consumption (mean  
121 transit time and mean time of last appearance, respectively), a span of 40 hours. Using the  
122 above defecation rates, this would translate into about five defecations following a meal  
123 that might contain its residue. However, inspection of Lambert (2002:Fig. 1) suggests  
124 that most markers appeared between 20 and 50 hours, roughly bimodally. We therefore  
125 consider three defecations post-consumption to potentially contain identifiable residue,  
126 though recognizing that combining captive passage rates with wild defecation rates is  
127 problematic.

128 Based on these figures, the 42 Gombe chimpanzees described above would generate  
129 about 45,990 to 53,655 defecations/year, of which about  $204 * 8 * 3 = 4,896$  might be  
130 expected to contain evidence of vertebrate consumption (about 9–10%)<sup>1</sup>. This is a  
131 maximum figure, since meat and organs may not be detectable (Phillips and McGrew,  
132 2013). The observed prevalence at Gombe in a sample of 1963 feces examined between  
133 1964–1967 was 5.8% (McGrew, 1983). Such calculation can represent only a very crude

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

134 ‘test’ of the reliability of fecal data. Wrangham and van Zinnicq Bergmann Riss (1990)  
135 and Stanford et al. (1994) documented significant changes in community predation rates  
136 over time, and more than five years separate the periods of fecal sampling and  
137 observational data on predations. Basing the calculation on adult and adolescent  
138 individuals, as we have done, assumes that juvenile and infant feces were rarely sampled  
139 for dietary analysis (including them would change the expected prevalence to about 7–  
140 8%). Finally, the calculation is sensitive to the average number of consumers/episode;  
141 published estimates range from 5.6 (Mahale; Takahata et al., 1984) to 10 (Taï; Boesch  
142 and Boesch, 1989). Nevertheless, we consider the correspondence between calculated  
143 and observed values to be close enough to challenge the assertion that fecal evidence is  
144 an unreliable indication of meat consumption by chimpanzees.

145 Why then did Boesch and Boesch (1989) conclude that fecal data are unreliable? They  
146 found evidence of vertebrate consumption in only one of 381 feces examined over two  
147 years “in the early part of the study” (Boesch and Boesch-Achermann, 2000:159; the  
148 study began in 1979). Boesch and Boesch (1989) estimated roughly 72 kills/year (120  
149 hunts/year \* 60% success rate) during 22 months in 1984–1986, 35 adults (79 individuals  
150 total) and 10 consumers/episode ( $N = 52$  kills). Combining these figures from (probably)  
151 non-overlapping time periods, the expected maximum prevalence in feces would be about  
152 5.6% considering only adults, and including immatures would reduce it to 2.5%, still  
153 much greater than the observed 0.3%. If one treats these samples as independently drawn  
154 from a population with a true prevalence of 2.5%, the probability of finding only one  
155 positive sample is  $<0.005^2$ . Does that mean fecal analysis is unreliable? No, the biological

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<sup>2</sup> Because of sharing, samples from the same party are not independent. Average party



156 reality of ‘what (undigestible) goes in, must come out’ is hard to deny, and the Gombe  
157 example suggests that the method can reflect actual diet well within an order of  
158 magnitude. The low prevalence reported for Tai is a puzzle. Assuming that it is not an  
159 artifact of non-independent samples and does not simply reflect a failure to detect  
160 bone/hair that was present, it suggests either that the Tai chimpanzees were fastidious  
161 eaters, consuming meat and organs but not bone and hair; that the figure of 10  
162 consumers/episode is too high by a substantial margin; that there were dramatic  
163 fluctuations in predation rate between the period of fecal collection and behavioral  
164 observations; or some other potentially interesting and informative difference between  
165 the behavior of Tai and Gombe chimpanzees.

166 Given the amount of attention paid to behavioral sampling methods (e.g., Altmann,  
167 1974), it is surprising that fecal sampling has generally not been thought of as a sampling  
168 problem; i.e., little attention has been given to sample sizes, confidence limits, statistical  
169 independence, etc. (but see Hohmann and Fruth, 2008). Wrangham and van Zinnicq  
170 Bergmann Riss (1990:166) considered sample sizes of at least 500 to be “adequate” for  
171 intersite comparisons, without explanation; that is the closest we have found to an explicit  
172 consideration of the sample size problem. Figure 1 illustrates the sample sizes required to  
173 be confident of detecting vertebrate remains for expected prevalence values under 5%.  
174 The 95% confidence intervals (CI) are shown; following the recommendation of Naing et  
175 al. (2006), these are based on setting precision ( $d$ ) to 50% of expected prevalence ( $P$ ).  
176 Thus, for expected prevalence  $P = 1\%$ , we set  $d = (0.5 * 0.01) = 0.005$  and find that a

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size at Tai is 10 (Boesch and Boesch-Achermann, 2000), so the appropriate  $N$  might be  
closer to 38 than to 381; one in 38 is 2.6%.

177 sample of  $N \geq 1,521$  is required to be 95% confident of detection (i.e., for the CI to not  
178 include 0). Note that, while a sample size of 500 should detect faunivory if it is present at  
179 expected prevalences over 1%, much larger samples are needed to distinguish statistically  
180 between different observed prevalence values.

181 There is an important caveat to the use of Figure 1 to estimate desired sample sizes for  
182 using feces to study chimpanzee diets: it is based on the assumption that samples are  
183 independent, but chimpanzees feed in parties and share meat. Consequently, evidence of  
184 vertebrate consumption may be highly clustered (McGrew et al., 1979; e.g., Anderson et  
185 al., 1983; Alp, 1993). Sampling strategies can be designed to avoid such non-  
186 independence (Hohmann and Fruth, 2008), but no published chimpanzee study has  
187 explicitly followed such a protocol. Another bias that needs to be considered when  
188 interpreting small published samples is that, for some, it is unlikely that fecal diet data  
189 would have been presented at all had vertebrate remains not been found; i.e., there is a  
190 ‘publication bias’ (see below). For example, Nishida (1989) reported that mammal hair  
191 was found in one of two feces examined.

192 Despite these issues, we believe that the problem with fecal analysis is not inherent in  
193 the method itself, but in frequent reliance on small sample sizes and failure to specify  
194 precisely what was done (were immature individuals included? if unhabituated, was fecal  
195 size used as a criterion for collection? were samples collected opportunistically with  
196 respect to party, time, and season, or according to a formal design? etc.), let alone  
197 standardize methods across sites (Uehara, 1997). Given some attention to methodology,  
198 we agree with Phillips and McGrew (2014:539) that “macroscopic inspection of feces can  
199 be a valuable tool to provide a generalized overview of dietary composition for primate

200 populations.” It is not possible to extrapolate from vertebrate remains in feces to mass of  
201 meat consumed on an individual basis, because prey often are shared unevenly: a scrap of  
202 hide might be all that remains of a large portion, or it may be the entire portion consumed  
203 by that chimpanzee. Given accurate identification of prey species and age/size class, it  
204 may however be possible to estimate at least relative amounts of meat consumed by a  
205 community using fecal prevalence data (Wrangham and van Zinnicq Bergmann Riss,  
206 1990).

207

## 208 **Methods**

### 209 *Field methods*

210 Ugalla is a region of about 3000 km<sup>2</sup> of primarily savanna woodland with narrow  
211 strips of riverine forest and has been described elsewhere (Hernandez-Aguilar, 2009;  
212 Stewart et al., 2011; Moore and Vigilant, 2014; Fig. 2). Rainfall at Issa averages about  
213 1150 mm/year (range 955–1275,  $N = 4$  complete years; one incomplete year totaled 1490  
214 mm) with a dry season (<60 mm/month) lasting from May through October; in a typical  
215 year, no rain at all falls during June–August (Fig. 3). Data come from three distinct  
216 locations: Nguye and Bhukalai (Yoshikawa and Ogawa, 2015), which are about 40 km  
217 apart, and Issa, which lies between them. Research at Issa has taken place in two phases,  
218 with one camp (October 2001–June 2003; Hernandez-Aguilar, 2009) about 9 km north of  
219 the other (October 2008–ongoing; Stewart et al., 2011). We believe that the two Issa  
220 studies have looked at the same large community of about 70 individuals with a home  
221 range >100 km<sup>2</sup> (Rudicell et al., 2011), but neither the community size nor the range have  
222 been positively confirmed. In addition to being about 9 km apart (comparable to the

223 distance between Kanyawara and Ngogo at Kibale), Hernandez-Aguilar's camp was  
224 about 400 m lower in elevation than the current, permanent camp.

225 We report on fecal samples collected at Issa from October 2001 to June 2003  
226 (Hernandez-Aguilar, 2006) and from mid-2008 through August 2015 (Piel et al., in  
227 press). We collected all fresh (estimated < 12 hours old) feces encountered in clean  
228 plastic bags and returned them to camp for sluicing through a 1 mm mesh screen and  
229 examination following the recommendations of McGrew et al. (2009) and McGrew and  
230 Phillips (2013). We tried to collect whole feces, but some samples were undoubtedly  
231 incomplete due to splatter effects (Phillips and McGrew, 2013) and, for samples from  
232 2009, we noted this as either partial or whole. During sluicing, researchers checked for  
233 any bone, hair, feathers, or flesh, in addition to plant and insect parts. Exact collection  
234 dates are not available for some Ugalla samples, so while prevalence is based on  
235 examination of 2481 samples, only 1665 were used for the seasonality analysis.

236

### 237 *Literature review*

238 For the comparative analysis, we attempted to locate all published information on  
239 prevalence of vertebrate remains in chimpanzee feces that also provided sample size.  
240 Bonobos are included for comparison but are not considered further other than to note  
241 that the popular belief that bonobos are less predatory than chimpanzees (e.g., Gilby et  
242 al., 2013) is not supported by the fecal prevalence data (Table 2). Interestingly, female  
243 bonobos may be relatively more involved in hunting than are female chimpanzees  
244 (Gruber and Clay, 2016; see also Tokuyama et al., 2017; Gilby et al., 2017). Although  
245 dichotomizing sites into 'forest' and 'savanna' masks potentially important quantitative

246 differences in vegetation, we have followed general usage and done so for this analysis.  
247 At savanna sites, evergreen forest typically makes up 1–10% of the habitat, with the rest  
248 being primarily deciduous open grassy woodland to wooded grassland; rainfall is usually  
249 under 1200 mm/yr and there are > 4 dry months. Most forest sites are predominantly  
250 evergreen forest with rainfall over 1400 mm and shorter dry seasons. Gombe, sometimes  
251 referred to as ‘woodland,’ is about 25% evergreen forest overall, although the proportion  
252 of forest is much greater within the range of the main study community (Foerster et al.,  
253 2016). See Moore (1992) and Domínguez-Rodrigo (2013) for further discussion. Note  
254 that descriptions of the paleoenvironment of *Ardipithecus ramidus* as grassy woodland  
255 mosaic savanna (Domínguez-Rodrigo, 2013:Table 3) fit Ugalla well. Because predation  
256 rates are known to vary over time, we treated published studies, not sites, as the unit of  
257 analysis in the meta-analysis and figures (i.e., we did not pool the results of multiple  
258 studies at Mahale, Kanyawara, and Ugalla). We then looked for evidence of publication  
259 bias. Because chimpanzee meat-eating is of theoretical interest to anthropologists, there  
260 may be a tendency to publish positive results even when sample sizes are small. We did a  
261 funnel plot (following Nakagawa and Santos, 2012) of sample size as a function of  
262 reported prevalence of vertebrate remains and found three distinct outlier studies with  
263 high prevalence values and small samples (Fig. 4): Anderson et al. (1983), Nishida  
264 (1989), and Alp (1993). These three studies were removed from the analysis and a second  
265 funnel plot was constructed with the remaining studies (Fig. 5). Forested sites show a  
266 rough inverted funnel with the peak between 1–2% prevalence, as is expected in the  
267 absence of publication bias, except for two outlying points representing Gombe and  
268 Mahale. Both of those samples are large enough ( $N > 1,000$ ) such that we do not believe

269 publication bias to be responsible for their reporting.

270 If taken separately, savanna sites exhibit a negative relationship between sample size  
271 and fecal prevalence, which is consistent with publication bias (Fig. 5). However, this  
272 slope is not significant. Furthermore, we are investigating whether or not there is a  
273 savanna-forest difference in faunivory and there is no a priori reason to treat savanna sites  
274 separately. Additionally, all the savanna prevalence values fall well within the  
275 distribution of those of forested sites. For these reasons, the negative slope alone does not  
276 justify discounting any of the remaining savanna studies, although we note the possibility  
277 that the data may overestimate faunivory in the ‘savanna’ category. Only the publication  
278 of additional large sample sets can resolve this problem.

279

#### 280 *Data analysis*

281 The comparison of effects across multiple studies requires meta-analytic techniques  
282 (e.g., Hedges and Olkin, 1985; Hox, 2002; McDonald, 2014). Here, we use meta-analysis  
283 to compare the prevalence of vertebrate remains in chimpanzee feces using data from  
284 multiple studies and sites. Because meta-analyses include data from studies that are by  
285 nature heterogeneous, with differences at the level of study design, purpose, data  
286 collection, time frame, and so forth, the differences between studies may confound the  
287 systematic summary of the same effect across studies and may add random error variance  
288 to any between group comparisons. Different levels of analyses (within-study cases,  
289 when available; study or site; region) make meta-analysis a special case of multilevel or  
290 hierarchical linear regression analyses (e.g., Bryk and Raudenbush, 2001; Hox, 2002).

291 SAS 9.3 (PROC GLIMMIX) was used to model the data. PROC GLIMMIX fits  
292 generalized linear mixed models when the outcome variable is not normally distributed.  
293 Count data (quantity of fecal samples containing vertebrate remains) and sample size  
294 were used as the dependent variable (events/trials syntax to specify a binomial response  
295 distribution) in a mixed model, with habitat (forest vs. savanna) as a fixed between  
296 groups variable. Study site nested in habitat was entered as a random variable (including  
297 intercept; unstructured covariance matrix). When necessary, proportion was used to  
298 estimate either sample size or count according to the information provided by the original  
299 study, and where only a minimum sample size was given, we used that (e.g., for Fongoli  
300 we estimated count as 0.4% of 1,400 = 5.6). Maximum likelihood estimation (LaPlace  
301 method) provided fit indices. We present estimates for mean percentage of vertebrate  
302 remains from the mixed model; these take into account sample size, the hierarchical  
303 nature of the dataset, and the variance between sites.

304 All research complied with ethical policies, regulation, and guidelines from the  
305 Tanzanian Wildlife Research Institute (TAWIRI) and Commission for Science and  
306 Technology (COSTECH).

307

## 308 **Results**

309 Table 1 lists all evidence of vertebrate consumption by the chimpanzees of Ugalla. At  
310 least 11, and probably 12, separate instances have been recorded (two positive samples  
311 collected by GI two days and 4 km apart conceivably could represent a single episode of  
312 consumption, but we consider them separately here). In five cases, the evidence was hair  
313 judged to belong to a small mammal, possibly a squirrel, and a sixth was a vertebra of a

314 squirrel-sized mammal. Accurate field identification of hair in feces is difficult, and we  
315 cannot exclude the possibility that some were galagos (*Galago senegalensis*, *Galago*  
316 *moholi*, or *Otolemur crassicaudatus*). Four small ungulates were consumed; in one case,  
317 a hoof (possibly klipspringer, *Oreotragus oreotragus*) was found in feces; in two,  
318 chimpanzees were observed feeding on blue duiker (*Philantomba monticola*); and in one,  
319 the prey resembled a small blue duiker but the identification was not positive.

320 The Issa community is not fully habituated and observations are incomplete. In all  
321 three observed cases, the parties were large (6, 9, and 'large'). Passive sharing by an adult  
322 male was seen in one case (Ramirez-Amaya et al., 2015), but in another an adult male  
323 monopolized the prey for several hours. In the third case, more than one individual had  
324 portions, but the sex of the primary holder could not be determined.

325 Vertebrate consumption at Ugalla appears to be strongly seasonal, with 11 of 12  
326 occurrences falling during the dry season and eight of them during the late dry season,  
327 August-October. The single rainy season occurrence, on 22 November 2016, is the  
328 'exception that proves the rule'—rainfall for August to mid-November that year was 99.6  
329 mm, only 60% of average for the period (169.2 mm, range 99.6–381.5;  $N = 7$  years). The  
330 degree of seasonality needs to be corrected for observational effort, which has been  
331 biased to summer months. Combining fecal collection dates from Issa, Nishida (1989)  
332 and Yoshikawa and Ogawa (2015), 41% of 1665 samples come from August-October  
333 and account for 4 of 5 (80%) of the datable vertebrate-positive samples. Correcting that  
334 80% figure for the sampling bias, 65% of positive fecal samples would have come from  
335 these three months.

336 Table 2 lists all the published results that describe prevalence of vertebrate remains in



337 chimpanzee and bonobo feces, with 95% CI. For forested sites, all prevalence values  
338 <0.25% come from sites where significant human disturbance was notable or recent at the  
339 time of sample collection, or sample size was small (<75). For savanna sites, small  
340 sample sizes (<75) were associated with higher, not lower, prevalence values (consistent  
341 with the possibility of publication bias, noted above). Only three studies, all in forest,  
342 reported no vertebrate remains in feces. Chimpanzee predation on vertebrates has been  
343 observed at two of them, Bossou and Rubondo (Sugiyama and Koman, 1987; Moscovice  
344 et al., 2007). The third, Belinga, is represented by only 25 feces.

345 Samples from savanna sites tended to have slightly less evidence of vertebrate remains  
346 ( $M = 0.68\%$ , 95% CI = 0.26%, 1.78%) than did those from forest sites ( $M = 1.17\%$ , CI =  
347 0.63%, 2.17%), but the difference was not statistically significant ( $F(1, 24) = 0.96$ ,  $p =$   
348 0.337, odds ratio = 0.58, 95% CI = 0.18, 1.84). Removing the studies from Bossou,  
349 Rubondo, and Belinga made little difference: mean proportion for savanna ( $M = 0.68\%$ ,  
350 95% CI = 0.27%, 1.71%) remained less than that for forest ( $M = 1.47\%$ , 95% CI =  
351 0.81%, 2.66%), but not significantly so ( $F(1, 21) = 2.13$ ,  $p = 0.159$ , odds ratio = 0.46,  
352 95% CI = 0.15, 1.39).

353 Vertebrates consumed at savanna sites tend to be small and solitary. At Mt. Assirik, all  
354 known cases of meat-eating were of prosimians (galago and potto; McGrew, 1983;  
355 McGrew et al., 1988); at Fongoli, galagos made up nearly 60% of observed prey  
356 captures, with monkeys (vervets, patas, and baboons) making up 37% (Pruetz et al.,  
357 2015); and at Ugalla, 67% were thought to be squirrel/galago-sized small mammals or  
358 fledgling birds. In contrast, predation on galagos is remarkably rare at Gombe and  
359 Mahale (O'Malley, 2010). While sample sizes at Tenkere and Semliki are small, they

360 suggest a more typical emphasis on eating monkeys. At Tenkere, the four independent  
361 predation/consumption episodes reported by Alp (1993) consist of two monkeys, a  
362 duiker, and a scaly-tailed flying squirrel, and at Semliki the only mammal consumed was  
363 black and white colobus (*Colobus guereza*; two observed captures and two fecal remains;  
364 Hunt and McGrew, 2002).

365

### 366 **Discussion**

367 The prevalence of vertebrate remains in large ( $\geq 1,000$ ) samples of chimpanzee feces  
368 varies about 60-fold, from 0.1% to 5.9%. Somewhat surprisingly, given the extreme  
369 ecological and demographic differences between so-called ‘forest’ and ‘savanna’  
370 chimpanzee populations, there is no significant difference in prevalence of fecal evidence  
371 of vertebrate consumption, echoing the apparent absence of a savanna chimpanzee  
372 pattern in insectivory (Webster et al., 2014). It is notable, however, that the two largest  
373 savanna samples, for Fongoli and Ugalla, have very low prevalence values and that the  
374 negative slope in a funnel plot analysis suggests the possibility of publication bias toward  
375 higher prevalences. Regardless of whether there is a savanna pattern in overall frequency  
376 of vertebrate consumption, savanna populations appear to consume vertebrates more  
377 seasonally and to eat more smaller, solitary prey. These findings are relevant to the  
378 debate over why chimpanzees hunt (see below), and thus may have implications for  
379 understanding why early hominins consumed vertebrates.

380 We emphasize that, because chimpanzees typically share meat, the prevalence of  
381 vertebrate remains in feces should not be confused with the frequency of hunting. At  
382 Gombe, with fecal prevalence of 5.81% (Table 2), Teleki (1973) reported an average of

383 eight consumers/kill. If there were no sharing, then one might expect fecal prevalence of  
384  $5.81/8 = 0.73\%$ . Reduced sharing is likely where prey tend to be small, such as squirrels  
385 or galagos (cf. Pruettz and Bertolani, 2007). By this logic, the frequency of hunting at Mt.  
386 Assirik might in fact be greater than at Gombe or Mahale (multiplying, rather than  
387 dividing, Mt. Assirik's prevalence by 8 = 14.3%). Only observational data can address  
388 the frequency of hunting.

389

#### 390 *Intersite variation*

391 McGrew (1983) reviewed possible ecological explanations for intersite variation in  
392 chimpanzee vertebrate consumption rates. Firstly, of course, the absence of suitable prey  
393 taxa might explain low rates. Newton-Fisher (2015) listed 32 mammalian taxa reported to  
394 have been consumed by chimpanzees (excluding chimpanzees, i.e., cannibalism); pooling  
395 allopatric variants (e.g., lumping yellow and olive baboons as 'baboons') reduces this to  
396 27. Twenty of the 27 are reported to be present at savanna sites; Ugalla alone has 16,  
397 including favorite chimpanzee prey, red colobus (*Procolobus badius tephrosceles*), blue  
398 duiker, bushbuck (*Tragelaphus scriptus*), and bushpig (*Potamochoerus porcus*). In fact,  
399 the Issa study area at Ugalla has the largest number (40) of medium/large mammal genera  
400 (this excludes rodents, bats, and elephant shrews) reported for any chimpanzee study site  
401 (Johnson, 2014; cf. 37 for Kibale: Russak and McGrew, 2008). Secondly, McGrew  
402 (1983) suggested that abundant predators might inhibit chimpanzee hunting by cropping  
403 sick or injured prey, as well as making hunting on the ground more dangerous for  
404 chimpanzees. Ugalla has a full complement of mammalian predators, which do interact  
405 with chimpanzees (e.g., McLester et al., 2016): lion (*Panthera leo*), leopard (*Panthera*

406 *pardus*), spotted hyena (*Crocuta crocuta*), and wild dog (*Lycaon pictus*), as well as  
407 smaller carnivores. The possible impact of predator competition/threat on Ugalla  
408 chimpanzee vertebrate consumption is hard to evaluate, but high rates of hunting at sites  
409 with healthy predator populations (e.g., leopard at Taï and leopard, lion, hyena, and wild  
410 dog at Mahale) suggest that competition with carnivores is unlikely to explain low meat  
411 consumption at Ugalla.

412 Habitat structure may explain differences in hunting rates, with broken, uneven  
413 canopies facilitating capture of arboreal prey such as monkeys (McGrew, 1983; Gilby et  
414 al., 2006). Such factors should strongly favor hunting monkeys at savanna sites where  
415 forest may be patchily distributed, as well as having uneven canopy. At Ugalla, red-tailed  
416 monkeys (*Cercopithecus ascanius*) are regularly seen in narrow strips of riverine forest of  
417 only a few trees in width and a few kilometers in length (see Fig. 2).

418 Demographic factors influence chimpanzees' hunting behavior and success (Mitani  
419 and Watts, 1999). Predation success is correlated with the number of males hunting  
420 (Boesch, 1994; Stanford, 1996; Mitani and Watts, 1999; Gilby et al., 2015), and low rates  
421 of vertebrate consumption by Mahale's K Group could have been due to there being only  
422 1–3 adult males in the community (Uehara, 1986). Bossou has had only one or two adult  
423 males for many years (Sugiyama, 2004), possibly contributing to the low rate of  
424 predation there (Table 2). However, study communities at Fongoli and Semliki contain  
425 11 and at least 29 adult males, respectively (Bogart and Pruetz, 2011; Webster et al.,  
426 2014; see the original papers for specific years covered), and the community at Issa  
427 appears to have at least 67 members (Rudicell et al., 2011), suggesting a large number of  
428 adult males.

429 Finally, low densities of suitable prey species might result in such low encounter rates  
430 that chimpanzees do not learn that they are in fact suitable or do not have the opportunity  
431 to learn how best to hunt them (McGrew, 1983). Densities of larger prey are indeed low  
432 at Ugalla. Red colobus densities range from about 1–4 groups/km<sup>2</sup> at Gombe, Mahale,  
433 and Ngogo (Stanford, 1995; Boesch et al., 2002; Uehara, 2003; Teelen, 2007). It is  
434 difficult to calculate a meaningful density at Ugalla, but we know of only one troop  
435 within the ca. 85 km<sup>2</sup> of the Issa main study area and are aware of only three troops  
436 within the ca. 3000 km<sup>2</sup> Ugalla region, despite extensive surveys. The Issa troop is small,  
437 probably under a dozen adults, which may be a result of ecological factors or chimpanzee  
438 (or other) predation (cf. Stanford, 1995). Densities of red-tailed monkeys and bushbuck  
439 in the woodlands at Mahale are about 33–63 and 1.5–7 individuals/km<sup>2</sup>, respectively  
440 (Boesch et al., 2002; Uehara, 2003); our estimates for Issa are about 0.7 and 0.35  
441 individuals/km<sup>2</sup>, respectively (Piel et al., 2015; woodland and forest are pooled).  
442 Preliminary estimates suggest galago (*G. senegalensis* and *O. crassicaudatus*) densities  
443 are around 20 individuals/km<sup>2</sup> (both species combined); this is at the low end for both  
444 taxa (Nash and Harcourt, 1986; Off et al., 2008; Bearder and Svoboda, 2013).

445 It is not clear what ecological or cognitive mechanisms are behind the (putative)  
446 association between low prey density and low rate of vertebrate consumption. Savanna  
447 chimpanzees do consume vertebrates, and arguably the patchiness of forest fragments  
448 would make it possible for even inexperienced hunters to capture arboreal prey. If  
449 vertebrate consumption by chimpanzees is primarily about nutrition, it is somewhat  
450 surprising that chimpanzees in marginal habitats have not learned to exploit available  
451 prey to a greater degree.

452       Alternatively, chimpanzee hunting may be driven more by social than nutritional  
453 factors (Stanford et al., 1994; Mitani and Watts, 2001; Gilby et al., 2006; Newton-Fisher,  
454 2015). Two aspects of savanna chimpanzee vertebrate consumption may be relevant here.  
455 First, most of the observed cases (fecal or direct observation) have involved small  
456 animals like squirrels, prosimians, and birds (McGrew, 1983; Pruetz and Bertolani, 2007;  
457 Table 1), which are unlikely to be shared widely (cf. Pruetz and Bertolani, 2007). While  
458 consumption of larger animals does occur (Pruetz and Marshack, 2009; Ramirez-Amaya  
459 et al., 2015), it appears to be rare except at Semliki and Tenkere—which have the highest  
460 reported fecal prevalence values (as well as small sample sizes; Hunt and McGrew, 2002;  
461 Table 2). The second is that the low density of larger (shareable) prey may inhibit the  
462 triggering of hunting ‘binges’ during which hunting may occur daily for several weeks  
463 (Stanford et al., 1994; Watts and Mitani, 2002). Whether such binges derive from tactical  
464 reciprocal sharing (Moore, 1984) or simpler processes of stimulus enhancement in larger  
465 social parties, their occurrence would likely be depressed by low encounter rates with  
466 prey.

467

468 *Seasonality*

469       While the sample remains small, vertebrate consumption at Ugalla appears to be  
470 highly clumped in time with eight of 12 cases falling during August-October, the late dry  
471 season; corrected for sampling effort, 65% of positive fecal samples come from these  
472 months. In the following we refer to such clumping as ‘seasonality,’ while noting that the  
473 clumping does not correspond neatly with ‘dry’ or ‘wet’ rainfall seasons. At Kasakati  
474 (near Ugalla and with similar seasons), dates are available for two episodes: May

475 (Suzuki, 1966; fecal) and October (Kawabe, 1966; observed hunt)—early dry and end dry  
476 season, respectively. At Fongoli, three of three observed predations occurred in July and  
477 August (Bogart et al., 2008; Pruetz and Marshack, 2009). A fourth instance occurred in  
478 June (Gaspersic and Pruetz, 2004), but capture was not observed and it is possible that  
479 the chimpanzees interrupted a carnivore. Pruetz and Bertolani (2007) discussed 22 galago  
480 hunting episodes, of which one (unspecified) was successful; 13 occurred during June  
481 and July. While not strictly comparable with fecal prevalence data, pooling these gives 17  
482 of 26 episodes during June-August (65%). The single rainy season is June-September,  
483 with May and October being ‘transitional’ months (Pruetz and Bertolani, 2009); 23 of 26  
484 (88%) episodes occurred between May-October, the rainy season. Pruetz et al. (2015)  
485 reported that 95% of tool-assisted hunting for galagos occurs during May-October. This  
486 proportion is not corrected for observation effort and so may overestimate seasonality. At  
487 Tenkere, evidence of vertebrate consumption comes from three independent sets of fecal  
488 samples and an observed predation; all occurred in February-April (the dry season), but  
489 the distribution of sampling effort is not given and the sample is small, so the degree to  
490 which this indicates seasonality is unclear (Alp, 1993). No comparable data on  
491 seasonality are available for Mt. Assirik or Semliki. In sum, 60% or more of vertebrate  
492 consumption at savanna sites appears to occur during the three consecutive peak  
493 consumption months. Those three months are either mainly dry season (Ugalla, Kasakati,  
494 Tenkere) or mainly wet season (Fongoli).

495 For comparison with non-savanna sites, at Gombe about 39% of all predations  
496 occurred during the peak three months of July-September (dry season, calculated from  
497 Stanford et al. [1994]), and at Mahale, about 45% in August-October (late dry season,

498 calculated from Hosaka et al. [2001]). At Tai, the three peak months for successful  
499 predations are non-consecutive: June and September-October, with no data available for  
500 July. Thirty-three percent of prey captures occurred during September-October and 44%  
501 in August-October (calculated from Boesch and Boesch-Achermann, 2000:Fig. 8.1).  
502 These are the three rainiest months (Boesch and Boesch-Achermann, 2000:Fig. 1.3).  
503 Based on the available evidence, vertebrate consumption appears more strongly seasonal  
504 at savanna sites.

505 Pickering and Domínguez-Rodrigo (2010, 2012) have argued that chimpanzee hunting  
506 is motivated at least in part by seasonal nutritional shortfalls (but not energetic ones;  
507 Mitani and Watts, 2001; Tennie et al., 2014), and thus that vertebrate consumption should  
508 be more sharply seasonal at savanna sites, which are more seasonal than forested sites  
509 (Moore, 1992). This prediction seems to be upheld. However, the peak vertebrate  
510 consumption months correspond with annual increases in average party size at Fongoli  
511 (Pruetz and Bertolani, 2009) and Ugalla (Ugalla Primate Project [UPP], unpublished  
512 data), consistent with social hypotheses for chimpanzee hunting (e.g., Stanford et al.,  
513 1994; Mitani and Watts, 2001). Existing data are not adequate to distinguish between  
514 these nutritional shortfall and social facilitation hypotheses, but we note that most of the  
515 prey at Fongoli, Mt. Assirik, and Ugalla are small, hole-dwelling prosimians and squirrels  
516 (McGrew 1983; Pruetz et al., 2015). Isaac and Crader (1981:101) argued that while the  
517 pursuit of large mobile prey is clearly hunting, “as the quarry becomes smaller and less  
518 mobile, the pursuit becomes less and less like hunting” — and they excluded from  
519 “hunting” the capture of nestling birds and “the digging up of small burrowing animals.”  
520 While this conflates size and mobility, it does get at an important feature of ‘hunting’ that



521 is central to hypotheses that chimpanzees hunt for social reasons: although capture of  
522 galagos and squirrels may carry some risk (Pickering and Domínguez-Rodrigo, 2012;  
523 Pruett et al., 2015), it is unlikely to be a venue for display (Bliege Bird and Bird, 2005)  
524 or acquiring meat to use as a social currency (Moore, 1984; Nishida et al., 1992; Mitani  
525 and Watts, 2001) because the risk is slight and there is little to share. This conclusion is  
526 supported by behavioral observations at Fongoli, which show that about half of galago  
527 captures are by females and immatures, and sharing of these vertebrate prey is limited  
528 (Pruett and Bertolani, 2007; Bogart et al., 2008; Pruett and Marshack, 2009; Pruett et al.,  
529 2015). Although seasonal peaks in meat-eating and party size are correlated at Fongoli  
530 and Ugalla, the association is not likely related to male social strategies.

531 Gilby et al. (2015) concluded that the association between male party size and hunting  
532 of red colobus monkeys at Kasekela and Kanyawara is due to the effect of ‘impact  
533 hunters,’ individuals who are unusually willing to initiate hunts. By diluting the colobus’  
534 defenses, these individuals reduce the cost of hunting for other males, and an overall  
535 increase in the rate of colobus capture results through by-product mutualism. Again, such  
536 a mechanism is unlikely to be behind the season/party size/vertebrate consumption  
537 association seen at Ugalla and Fongoli, where prey are mainly solitary and small. This  
538 leaves the ‘beater effect’ (Takahata et al., 1984): larger chimpanzee parties might be  
539 more likely to disturb small prey, and the prey’s escape is more difficult with more  
540 chimpanzees around. Although such a passive mechanism is possible, observations at  
541 Fongoli indicate a seasonal increase in galago hunting effort (Pruett et al., 2015), which  
542 suggests an active increase in motivation rather than simply a passive increase in  
543 opportunity.

544 Whether this evidence from savanna sites has bearing on the debate over hunting at  
545 forested sites remains to be seen; it is consistent with the conclusion of Gilby et al. (2006)  
546 that energetic and ecological factors, not social ones, underlie red colobus hunting at  
547 Gombe.

548 If the observed seasonal pattern has an underlying nutritional/ecological basis, the  
549 question arises whether meat consumption peaks during a time of food scarcity or of  
550 abundance. While Pickering and Domínguez-Rodrigo (2012) suggested that savanna  
551 chimpanzees might seasonally consume vertebrates during the late dry season because it  
552 is a time of (protein) scarcity, there is evidence that forest chimpanzees tend to hunt more  
553 during periods of resource (fruit) abundance. This might be because nutrient surplus  
554 enables males to adopt risky foraging tactics for primarily social reasons (Mitani and  
555 Watts, 2001, 2005), or because the costs of failure are reduced (Gilby and Wrangham,  
556 2007). At Issa, non-fig fruit abundance (NFF, an index of resource abundance; Gilby and  
557 Wrangham, 2007) peaks during the early dry season, begins to fall in August, and is low  
558 by October (Piel et al., in press). Although more data are needed to improve temporal  
559 resolution of both vertebrate consumption and NFF abundance before we can determine  
560 whether Issa chimpanzees consume more vertebrates when fruit resources are abundant,  
561 the available data suggest they do not. Data on seasonal food abundance at Fongoli are  
562 similarly preliminary, but Pruett (2006:173–174) reported that “the greatest percentage  
563 of fruiting plants was available during the late dry season,” preceding the wet-season  
564 peak in (galago) hunting (Pruett et al., 2015). We do not yet have data to speak to the  
565 obvious potential distinction between fruit and protein abundance/scarcity in analysis of  
566 seasonality at savanna sites.

567

568 **Conclusions**

569 Chimpanzees may be informative to paleoanthropologists as referential/analogical  
570 models for early hominins, though (as with any analytical method) care must be utilized  
571 when used as such (Moore, 1996; Mitani, 2013). One approach is to compare categories  
572 of chimpanzees: if the differences observed between forest and savanna chimpanzees  
573 resemble those observed between early and later hominins, the factors underlying the  
574 former difference may help to illuminate the reasons for the latter one (Moore, 1996).  
575 Alternatively, lack of resemblance can help focus attention on elements of the  
576 disanalogy—that is, ways in which the model and its referent differ.

577 Our examination of vertebrate consumption rates at forest and savanna chimpanzee  
578 sites leads to a number of conclusions relevant to understanding both the reason(s) for  
579 hunting by chimpanzees and consideration of the increase in vertebrate consumption by  
580 early hominins:

581 1) It is not clear whether there is a ‘savanna chimpanzee pattern’ in the consumption  
582 of vertebrates, but when compared with forest-living populations, savanna chimpanzees  
583 tend to consume smaller vertebrates, more seasonally. While they do not consume  
584 significantly less vertebrates, they certainly do not consume more of them than do forest  
585 chimpanzees. However, because smaller prey are less likely to be shared and thus show  
586 up in the feces of multiple individuals, conclusions about actual hunting frequency cannot  
587 reliably be drawn from these data without quantitative observational data on numbers of  
588 consumers per episode.

589 2) Whether the seasonal increase in vertebrate consumption is better explained by

590 social mechanisms—most likely a ‘beater effect’ at savanna sites, since theories  
591 developed to explain patterns of red colobus hunting seem unlikely to apply in such  
592 environments—or by nutritional shortfall is unknown. That the degree of seasonality is  
593 greater in savannas, where rainfall seasonality is greater, is consistent with nutritional  
594 hypotheses, but so far this is only an association.

595 3) The seasonality in largely solitary consumption of small vertebrates observed at  
596 savanna sites is unlikely to be explained by hypotheses developed to account for  
597 seasonality of red colobus hunting at forested sites in terms of social strategies. Whether  
598 the difficulty with explaining seasonality at savanna sites constitutes a challenge to the  
599 validity of those social hypotheses for addressing patterns observed at forest sites should  
600 be considered.

601 4) Because chimpanzees rarely scavenge and strongly prefer red colobus where they  
602 are available, there is a strong tendency in the literature to see chimpanzee vertebrate  
603 consumption through the lens of hunting red colobus. This has led to an important body  
604 of literature on monkey hunting by chimpanzees, but from the perspective of  
605 understanding faunivory in hominin evolution, this narrow focus may be misleading.

606 5) The population density of prey (not the availability of prey taxa) appears to have a  
607 strong effect on vertebrate consumption. This may complicate our understanding of the  
608 origins of increased hominin faunivory, because it is easier to determine taxonomic  
609 presence than absolute population densities from paleontological data.

610 6) The comparison of forest and savanna dwelling chimpanzees performed here  
611 provides no support for the idea that the adaptation of an early hominin to more arid  
612 environments would have required increased faunivory. Our results suggest that the

613 explanation for increased hominin consumption of vertebrates is unrelated to the  
614 transition to open habitats, or involves either a relevant difference between chimpanzees  
615 and early hominins, or a difference between ancient and modern open environments. Two  
616 obvious possibilities are bipedalism (Lovejoy et al., 2009) and the greater abundance of  
617 megafauna and their predators (reviewed in Pobiner, 2015), but full exploration of those  
618 differences is beyond the scope of this paper.

619

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637

638

639 **References**

640

641 Alp, R., 1993. Meat eating and ant dipping by wild chimpanzees in Sierra Leone.

642 Primates 34, 463–468.

643 Altmann, J., 1974. Observational study of behavior: Sampling methods. Behaviour 49,

644 227–267.

645 Anderson, J.R., Williamson, E.A., Carter, J., 1983. Chimpanzees of Sapo Forest, Liberia:

646 Density, nests, tools and meat-eating. Primates 24, 594–601.

647 Badrian, N., Badrian, A., Susman, R.L., 1981. Preliminary observations on the feeding

648 behavior of *Pan paniscus* in the Lomako Forest of central Zaire. Primates 22, 173–

649 181.

650 Barrell, J., 1917. Probable relations of climatic change to the origin of the Tertiary ape-

651 man. Sci. Monthly 4, 16–26.

652 Basabose, K., Yamagiwa, J., 1997. Predation on mammals by chimpanzees in the

653 montane forest of Kahuzi, Zaire. Primates 38, 45–55.

654 Bearder, S.K., Svoboda N.S., 2013. *Otolemur crassicaudatus*, large-eared greater galago.

655 In: Butynski, T.M., Kingdon, J., Kalina, J. (Eds.), Mammals of Africa. Volume 2—

656 Primates. Bloomsbury Publishing, London, pp. 409–413.

657 Bliege Bird, R., Bird, D.W., 2005. Human hunting seasonality. In: Brockman, D.E., van

658 Schaik, C.P. (Eds.), Seasonality in Primates: Studies of Living and Extinct Human and

659 Non-human Primates. Cambridge University Press, Cambridge, pp. 243–266.

660 Boesch, C., Boesch, H., 1989. Hunting behavior of wild chimpanzees in the Tai National

661 Park. Am. J. Phys. Anthropol. 78, 547–573.

- 662 Boesch, C., Boesch-Achermann, H., 2000. The Chimpanzees of the Tai Forest:  
663 Behavioural Ecology and Evolution. Oxford University Press, Oxford.
- 664 Boesch, C., Uehara, S., Ihobe, H., 2002. Variations in chimpanzee–red colobus  
665 interactions. In: Boesch, C., Hohmann, G., Marchant, L.F. (Eds.), Behavioural  
666 Diversity in Chimpanzees and Bonobos. Cambridge University Press, New York, pp.  
667 221–230.
- 668 Bogart, S.L., Pruett, J.D., 2011. Insectivory of savanna chimpanzees (*Pan troglodytes*  
669 *veus*) at Fongoli, Senegal. *Am. J. Phys. Anthropol.* 145, 11–20.
- 670 Bryk, A.S., Raudenbusch, S.W., 2001. Hierarchical Linear Models: Applications and  
671 Data Analysis Methods, 2<sup>nd</sup> edition. Sage, Newbury Park.
- 672 Cartmill, M., 1993. *A View to a Death in the Morning*. Harvard University Press,  
673 Cambridge.
- 674 Chancellor, R.L., Rundus, A.S., Nyandwi, S., 2012. The influence of seasonal variation  
675 on chimpanzee (*Pan troglodytes schweinfurthii*) fallback food consumption, nest  
676 group size, and habitat use in Gishwati, a montane rain forest fragment in Rwanda.  
677 *Intl. J. Primatol.* 33, 115–133.
- 678 Dart, R.A., 1925. *Australopithecus africanus*: The man-ape of South Africa. *Nature* 115,  
679 195–199.
- 680 Domínguez-Rodrigo, M., 2014. Is the “savanna hypothesis” a dead concept for  
681 explaining the emergence of the earliest hominins? *Curr. Anthropol.* 55, 59–81.
- 682 Duvall, C.S., 2008. Chimpanzee diet in the Bafing area, Mali. *Afr. J. Ecol.* 46, 679–683.
- 683 Ferraro, J.V., Plummer, T.W., Pobiner, B.L., Oliver, J.S., Bishop, L.C., Braun, D.R.,  
684 Ditchfield, P.W., Seaman III, J.W., Binetti, K.M., Seaman Jr., J.W., Hertel, F., Potts,



- 685 R., 2013. Earliest archaeological evidence of persistent hominin carnivory. *PLoS One*  
686 8, e62174.
- 687 Foerster, S., Zhong, Y., Pintea, L., Murray, C.M., Wilson, M.L., Mjungu, D.C., Pusey,  
688 A.E., 2016. Feeding habitat quality and behavioral trade-offs in chimpanzees: a case  
689 for species distribution models. *Behav. Ecol.* 27, 1004–1016.
- 690 Gilby, I.C., Eberly, L.E., Pintea, L., Pusey, A.E., 2006. Ecological and social influences  
691 on the hunting behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii*. *Anim.*  
692 *Behav.* 72, 169–180.
- 693 Gilby, I.C., Wilson, M.L., Pusey, A.E., 2013. Ecology rather than psychology explains  
694 co-occurrence of predation and border patrols in male chimpanzees. *Anim. Behav.* 86,  
695 61–74.
- 696 Gilby, I.C., Machanda, Z.P., Mjungu, D.C., Rosen, J., Muller, M.N., Pusey, A.E.,  
697 Wrangham, R.W., 2015. ‘Impact hunters’ catalyse cooperative hunting in two wild  
698 chimpanzee communities. *Phil. Trans. R. Soc. B* 370, 20150005.
- 699 Gilby, I.C., Machanda, Z.P., O’Malley, R.C., Murray, C.M., Lonsdorf, E.V., Walker, K.,  
700 Mjungu, D.C., Otali, E., Muller, M.N., Emery Thompson, M., Pusey, A.E. Wrangham,  
701 R.W., 2017. Predation by female chimpanzees: Toward an understanding of sex  
702 differences in meat acquisition in the last common ancestor of *Pan* and *Homo*. *J. Hum.*  
703 *Evol.* 110, 82–94.
- 704 Gruber, T., Clay, Z., 2016. A comparison between bonobos and chimpanzees: A review  
705 and update. *Evol. Anthropol.* 25, 239–252.
- 706 Hashimoto, C., Furuichi, T., Tashiro, Y., 2000. Ant dipping and meat eating by wild  
707 chimpanzees in the Kalinzu Forest, Uganda. *Primates* 41, 103–108.

- 708 Hedges, L.V., Olkin, I., 1985. *Statistical Methods for Meta-analysis*. Academic Press,  
709 London.
- 710 Hernandez-Aguilar, R.A., 2006. Ecology and nesting patterns of chimpanzees (*Pan*  
711 *troglodytes*) in Issa, Ugalla, Western Tanzania. PhD. Dissertation, University of  
712 Southern California, Los Angeles.
- 713 Hernandez-Aguilar, R.A., 2009. Chimpanzee nest distribution and site reuse in a dry  
714 habitat: implications for early hominin ranging. *J. Hum. Evol.* 57, 350–364.
- 715 Hohmann, G., Fruth, B., 2008. New records on prey capture and meat eating by bonobos  
716 at Lui Kotale, Salonga National Park, Democratic Republic of Congo. *Folia Primatol.*  
717 79, 103–110.
- 718 Hox, J., 2002. *Multilevel Analysis: Techniques and Applications*. Lawrence Erlbaum  
719 Associates, New Jersey.
- 720 Hunt, K.D., McGrew W.C., 2002. Chimpanzees in the dry habitats of Assirik, Senegal  
721 and Semliki Wildlife Reserve, Uganda. In: Boesch, C., Hohmann, G., Marchant, L.F.  
722 (Eds.), *Behavioural Diversity in Chimpanzees and Bonobos*. Cambridge University  
723 Press, New York, pp. 35–51.
- 724 Isaac, G.Ll., Crader, D.C., 1981. To what extent were early hominids carnivorous? An  
725 archeological perspective. In: Harding, R.S.O., Teleki, G. (Eds.), *Omnivorous*  
726 *Primates: Gathering and Hunting in Human Evolution*. Columbia University Press,  
727 New York, pp. 37–103.
- 728 Johnson, C., 2014. The feeding and movement ecology of yellow baboons (*Papio*  
729 *cynocephalus*) in a primate rich habitat: The Issa valley of western Tanzania. PhD.  
730 Dissertation, Swansea University.

- 731 Kano T., Mulavwa, M. 1984. Feeding ecology of the pygmy chimpanzees (*Pan paniscus*)  
732 of Wamba. In: Susman, R.L. (Ed.), *The Pygmy Chimpanzee*. Plenum Press, New  
733 York, pp. 233–274.
- 734 Kawabe, M., 1966. One observed case of hunting behavior among wild chimpanzees  
735 living in the savanna woodland of western Tanzania. *Primates* 7, 393–396.
- 736 Kuroda, S., Suzuki, S., Nishihara, T., 1996. Preliminary report on predatory behavior and  
737 meat sharing in Tschego chimpanzees (*Pan troglodytes troglodytes*) in the Ndoki  
738 Forest, Northern Congo. *Primates* 37, 253–259.
- 739 Lovejoy, C.O, Suwa, G., Spurlock, L., Asfaw, B., White, T.D., 2009. The pelvis and  
740 femur of *Ardipithecus ramidus*: the emergence of upright walking. *Science* 326, 71e1–  
741 71e6.
- 742 McDonald, J.H., 2014. *Handbook of Biological Statistics*. 3rd ed. Sparky House  
743 Publishing, Baltimore.
- 744 McGrew, W.C., 1983. Animal foods in the diets of wild chimpanzees (*Pan troglodytes*):  
745 Why cross-cultural variation? *J. Ethol.* 1, 46–61.
- 746 McGrew, W.C., Tutin, C.E.G., Baldwin, P., 1979. New data on meat eating by wild  
747 chimpanzees. *Curr. Anthropol.* 20, 238–239.
- 748 McGrew, W.C., Baldwin, P.J., Tutin, C.E.G., 1988. Diet of wild chimpanzees (*Pan*  
749 *troglodytes verus*) at Mt. Assirik, Senegal: I. Composition. *Am. J. Primatol.* 16, 213–  
750 226.
- 751 McLester, E., Stewart, F.A., Piel, A.K., 2016. Observation of an encounter between  
752 African wild dogs (*Lycaon pictus*) and a chimpanzee (*Pan troglodytes schweinfurthii*)  
753 in the Issa Valley, Tanzania. *Afr. Primates* 11, 27–36.

- 754 Mitani, J.C., 2013. Chimpanzee models of human behavioral evolution. In: Sponheimer,  
755 M., Lee-Thorp, J.A., Reed, K.E., Ungar, P. (Eds.), *Early Hominin Paleoecology*.  
756 University Press of Colorado, Boulder, pp. 397–435.
- 757 Mitani, J.C., Watts, D.P., 1999. Demographic influences on the hunting behavior of  
758 chimpanzees. *Am. J. Phys. Anthropol.* 109, 439–454.
- 759 Mitani, J.C., Watts, D.P., 2001. Why do chimpanzees hunt and share meat? *Anim. Behav.*  
760 61, 915–924.
- 761 Mitani, J.C., Watts, D.P., 2005. Seasonality in hunting by non-human primates. In:  
762 Brockman, D.E., van Schaik, C.P. (Eds.), *Seasonality in Primates: Studies of Living*  
763 *and Extinct Human and Non-human Primates*. Cambridge University Press,  
764 Cambridge, pp. 215–241.
- 765 Moore, D., Vigilant, L., 2014. A population estimate of chimpanzees (*Pan troglodytes*  
766 *schweinfurthii*) in the Ugalla region using standard and spatially explicit genetic  
767 capture-recapture methods. *Am. J. Primatol.* 76, 335–346.
- 768 Moore, J., 1984. The evolution of reciprocal sharing. *Ethol. Sociobiol.* 5, 5–14.
- 769 Moore, J., 1992. “Savanna” chimpanzees. In: Nishida, T., McGrew, W.C., Marler, P.,  
770 Pickford, M., de Waal, F.B.M. (Eds.), *Topics in Primatology, Vol. I: Human Origins*.  
771 University of Tokyo Press, Tokyo, pp. 99–118.
- 772 Moore, J., 1996. Savanna chimpanzees, referential models and the last common ancestor.  
773 In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*.  
774 Cambridge University Press, Cambridge, pp. 275–292.

- 775 Moscovice, L.R., Issa, M.H., Petrzalkova, K.J., Keuler, N.S., Snowdon, C.T., Huffman,  
776 M.A., 2007. Fruit availability, chimpanzee diet, and grouping patterns on Rubondo  
777 Island, Tanzania. *Am. J. Primatol.* 69, 487–502.
- 778 Naing, L., Winn, T., Rusli, B.N., 2006. Practical issues in calculating the sample size for  
779 prevalence studies. *Arch. Orofacial Sci.* 1, 9–14.
- 780 Nash, L.T., Harcourt, C.S., 1986. Social organization of galagos in Kenyan coastal  
781 forests: II. *Galago garnettii*. *Am. J. Primatol.* 10, 357–369.
- 782 Newton-Fisher, N.E., 2015. The hunting behavior and carnivory of wild chimpanzees. In  
783 Henke, W., Tattersall, I. (Eds.), *Handbook of Paleoanthropology*. Springer Verlag,  
784 Berlin, pp. 1661–1691.
- 785 Nishida, T., 1989. A note on the chimpanzee ecology of the Ugalla area, Tanzania.  
786 *Primates* 30, 129–138.
- 787 Nishida, T., Uehara, S., Nyundo, R., 1979. Predatory behavior among wild chimpanzees  
788 of the Mahale Mountains. *Primates* 20, 1–20.
- 789 Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y., Uehara, S., 1992. Meat sharing as a  
790 coalition strategy by an alpha male chimpanzee. In: Nishida, T., McGrew, W.C.,  
791 Marler, P., Pickford, M., de Waal, F.B.M. (Eds.), *Topics in Primatology*, Vol. 1.  
792 University of Tokyo Press, Tokyo, pp. 159–174.
- 793 Off, E.C., Isbell, L.A., Young, T.P., 2008. Population density and habitat preferences of  
794 the Kenya lesser galago (*Galago senegalensis braccatus*) along the Ewaso Nyiro  
795 River, Laikipia, Kenya. *J. E. Afr. Nat. Hist.* 97, 109–116.

- 796 Ogawa, H., Idani, G., Moore, J., Pintea, L. Hernandez-Aguilar, A., 2007. Sleeping parties  
797 and nest distribution of chimpanzees in the savanna woodland, Ugalla, Tanzania. Intl.  
798 J. Primatol. 28, 1397–1412.
- 799 O'Malley, R.C., 2010. Two observations of galago predation by the Kasakela  
800 chimpanzees of Gombe Stream National Park, Tanzania. Pan Afr. News 17, 17–19.
- 801 O'Malley, R.C., Stanton, M.A., Gilby, I.C., Lonsdorf, E.V., Pusey, A., Markham, A.C.,  
802 Murray, C.M., 2016. Reproductive state and rank influence patterns of meat  
803 consumption in wild female chimpanzees (*Pan troglodytes schweinfurthii*). J. Hum.  
804 Evol. 90, 16–28.
- 805 Phillips, C.A., McGrew, W.C., 2013. Identifying species in chimpanzee (*Pan*  
806 *troglodytes*) feces: A methodological lost cause? Intl. J. Primatol. 34, 792–807.
- 807 Phillips C.A., McGrew, W.C., 2014. Macroscopic inspection of ape feces: What's in a  
808 quantification method? Am. J. Primatol. 76, 539–550.
- 809 Phillips, C.A., Wrangham, R.W., McGrew, W.C., 2017. Non-dietary analytical features  
810 of chimpanzee scats. Primates 58, 393–402.
- 811 Pickering, T.R., Domínguez-Rodrigo, M., 2012. Can we use chimpanzee behavior to  
812 model early hominin hunting? In: Domínguez-Rodrigo, M. (Ed.), Stone Tools and  
813 Fossil Bones: Debates in the Archaeology of Human Origins. Cambridge University  
814 Press, Cambridge, pp. 174–197.
- 815 Piel, A.K., Lenoel, A., Johnson, C., Stewart, F.A., 2015. Deterring poaching in western  
816 Tanzania: The presence of wildlife researchers. Global Ecol. Conserv. 3, 188–199.

- 817 Piel, A.K., Strampelli, P., Greathead, E., Hernandez-Aguilar, R.A., Moore, J., Stewart,  
818 F.A., in press. The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*)  
819 in the Issa valley, western Tanzania. *J. Hum. Evol.*
- 820 Pobiner, B.L., 2015. New actualistic data on the ecology and energetics of hominin  
821 scavenging opportunities. *J. Hum. Evol.* 80, 1–16.
- 822 Pruetz, J.D., 2006. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at  
823 Fongoli, Senegal. In: Hohmann, G., Robbins, M.M., Boesch, C. (Eds.), *Feeding*  
824 *Ecology in Apes and Other Primates*. Cambridge University Press, Cambridge, pp.  
825 161–182.
- 826 Pruetz, J.D., Bertolani, P., 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with  
827 tools. *Curr. Biol.* 17, 412–417.
- 828 Pruetz, J.D., Marshack, J.L., 2009. Savanna chimpanzees (*Pan troglodytes verus*) prey on  
829 patas monkeys (*Erythrocebus patas*) at Fongoli, Senegal. *Pan Afr. News* 16, 15–17.
- 830 Pruetz J.D., Bertolani P., Boyer Ontl K., Lindshield S., Shelley M., Wessling E.G., 2015.  
831 New evidence on the tool-assisted hunting exhibited by chimpanzees (*Pan troglodytes*  
832 *verus*) in a savannah habitat at Fongoli, Sénégal. *R. Soc. Open Sci.* 2, 140507.
- 833 Ramirez-Amaya, S., McLester, E., Stewart, F.A., Piel, A.K., 2015. Savanna chimpanzees  
834 (*Pan troglodytes schweinfurthii*) consume and share blue duiker meat in the Issa  
835 Valley, Ugalla, Western Tanzania. *Pan Afr. News* 22, 17–21.
- 836 Rudicell, R.S., Piel, A.K., Stewart, F., Moore, D.L., Learn, G.H., Li, Y., Takehisa, J.,  
837 Pintea, L., Shaw, G.M., Moore, J., Sharp, P.M., Hahn, B.H., 2011. High prevalence of  
838 simian immunodeficiency virus infection in a community of savanna chimpanzees. *J.*  
839 *Virol.* 85, 9918–9928.

- 840 Russak, S.M., McGrew, W.C., 2008. Chimpanzees as fauna: Comparisons of sympatric  
841 large mammals across long-term study sites. *Am. J. Primatol.* 70, 1–8.
- 842 Rutter, C.M., Gatsonis, C.A., 2001. A hierarchical regression approach to meta-analysis  
843 of diagnostic test accuracy evaluations. *Stat. Med.* 20, 2865–2884.
- 844 Sayers, K., Lovejoy, C.O., 2008. The chimpanzee has no clothes: a critical examination  
845 of *Pan troglodytes* in models of human evolution. *Curr. Anthropol.* 49, 87–114.
- 846 Stanford, C.B., 1995. The influence of chimpanzee predation on group size and anti-  
847 predator behaviour in red colobus monkeys. *Anim. Behav.* 49, 577–587.
- 848 Stanford, C.B., 1996. The hunting ecology of wild chimpanzees: implications for the  
849 evolutionary ecology of Pliocene hominids. *Am. Anthropol.* 98, 96–113.
- 850 Stanford, C.B., 2012. Chimpanzees and the behavior of *Ardipithecus ramidus*. *Annu.*  
851 *Rev. Anthropol.* 41, 139–149.
- 852 Stanford, C.B., Nukurunungi, J.B., 2003. Behavioral ecology of sympatric chimpanzees  
853 and gorillas in Bwindi Impenetrable National Park, Uganda: Diet. *Intl. J. Primatol.* 24,  
854 901–918.
- 855 Stanford, C.B., Wallis, J.W., Mpongo, E., Goodall, J., 1994. Hunting decisions in wild  
856 chimpanzees. *Behaviour* 131, 1–18.
- 857 Stewart, F.A., Piel, A.K., McGrew, W.C., 2011. Living archaeology: Artefacts of specific  
858 nest site fidelity in wild chimpanzees. *J. Hum. Evol.* 61, 388–395.
- 859 Sugiyama, Y., 2004. Demographic parameters and life history of chimpanzees at Bossou,  
860 Guinea. *Am. J. Phys. Anthropol.* 124, 154–165.
- 861 Sugiyama, Y., Koman, J., 1987. A preliminary list of chimpanzees alimentation at  
862 Bossou, Guinea. *Primates* 28, 133–147.



- 863 Suzuki, A., 1966. On the insect-eating habits among wild chimpanzees living in the  
864 savanna woodland of western Tanzania. *Primates* 7, 481–487.
- 865 Takahata, Y., Hasegawa, T., Nishida, T., 1984. Chimpanzee predation in the Mahale  
866 Mountains from August 1979 to May 1982. *Intl. J. Primatol.* 5, 213–233.
- 867 Teelen, S., 2007. Primate abundance along five transect lines at Ngogo, Kibale National  
868 Park, Uganda. *Am. J. Primatol.* 69, 1030–1044.
- 869 Teleki, G., 1973. *The Predatory Behavior of Wild Chimpanees*. Bucknell University  
870 Press, Lewisburg.
- 871 Tennie, C., Gilby, I.C., Mundry, R., 2009. The meat-scrap hypothesis: Small quantities of  
872 meat may promote cooperative hunting in wild chimpanzees (*Pan troglodytes*). *Behav.*  
873 *Ecol. Sociobiol.* 63, 421–431.
- 874 Tennie, C., O'Malley, R.C., Gilby, I.C., 2014. Why do chimpanzees hunt? Considering  
875 the benefits and costs of acquiring and consuming vertebrate versus invertebrate prey.  
876 *J. Hum. Evol.* 71, 38–45.
- 877 Thompson, S.G., Turner, R.M., Warn, D.E., 2001. Multilevel models for meta-analysis,  
878 and their application to absolute risk differences. *Stat. Methods Med. Res.* 10, 375–  
879 392.
- 880 Tokuyama, N., Moore, D.L., Graham, K.E., Lokasola, A., Furuichi, T., 2017. Cases of  
881 maternal cannibalism in wild bonobos (*Pan paniscus*) from two different field sites,  
882 Wamba and Kokolopori, Democratic Republic of the Congo. *Primates* 58, 7–12.
- 883 Tutin, C.E.G., Fernandez, M., 1985. Foods consumed by sympatric populations of  
884 *Gorilla g. gorilla* and *Pan t. troglodytes* in Gabon: Some preliminary data. *Intl. J.*  
885 *Primatol.* 6, 27–43.

- 886 Tutin, C.E.G., Fernandez, M., 1993. Composition of the diet of chimpanzees and  
887 comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. *Am.*  
888 *J. Primatol.* 30, 195–211.
- 889 Uehara, S., 1986. Sex and group differences in feeding on animals by wild chimpanzees  
890 in the Mahale Mountains National Park, Tanzania. *Primates* 27, 1–3.
- 891 Uehara, S., 1997. Predation on mammals by the chimpanzee (*Pan troglodytes*). *Primates*  
892 38, 193–214.
- 893 Uehara, S., 2003. Population densities of diurnal mammals sympatric with the  
894 chimpanzees of the Mahale Mountains, Tanzania: Comparison between the census  
895 data of 1996 and 2000. *Afr. Stud. Monogr.* 24, 169–179.
- 896 Watts, D.P., 2008. Scavenging by chimpanzees at Ngogo and the relevance of  
897 chimpanzee scavenging to early hominin behavioral ecology. *J. Hum. Evol.* 54, 125–  
898 133.
- 899 Watts, D.P., Mitani, J.C., 2002. Hunting behavior of chimpanzees at Ngogo, Kibale  
900 National Park, Uganda. *Intl. J. Primatol.* 23, 1–28.
- 901 Webster, T.H., McGrew, W.C., Marchant, L.F., Payne, C.L.R., Kevin D. Hunt, K.D.,  
902 2014. Selective insectivory at Toro-Semliki, Uganda: Comparative analyses suggest  
903 no ‘savanna’ chimpanzee pattern. *J. Hum. Evol.* 71, 20–27.
- 904 Wolpoff, M.H., 1971. Competitive exclusion among Lower Pleistocene hominids: the  
905 single species hypothesis. *Man* 6, 601–614.
- 906 Wrangham, R.W., van Zinnicq Bergmann Riss, E., 1990. Rates of predation on mammals  
907 by Gombe chimpanzees, 1972–1975. *Primates* 31, 157–170.

- 908 Wrangham, R.W., Conklin, N.L., Chapman, C.A., Hunt, K.D., 1991. The significance of  
909 fibrous foods for Kibale Forest chimpanzees. *Phil. Trans. R. Soc. Lond. B* 334, 171–  
910 178.
- 911 Yoshikawa, M., Ogawa, H., 2015. Diet of savanna chimpanzees in the Ugalla area,  
912 Tanzania. *Afr. Stud. Monogr.* 36, 189–209.
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- 914

915 **Figure legends**

916

917 **Figure 1.** Recommended sample sizes to detect vertebrate remains (i.e., to exclude 0  
918 from the 95% confidence interval) given expected prevalence under 5%.

919

920 **Figure 2.** Central portion of Issa study area, Ugalla. The area shown is approximately 42  
921 km<sup>2</sup> (cf. Gombe National Park  $\approx$ 36 km<sup>2</sup>); it is about half the area currently monitored on a  
922 regular basis. Width of the riverine evergreen forest strip at 'A' is  $\approx$ 120 m.

923

924 **Figure 3.** Monthly rainfall at Issa. Solid line = mean, minimum, and maximum monthly  
925 rainfall at permanent camp, 2009–2015. Intermittent failures of HOBO Data Logging  
926 Rain Gauge resulted in lost data; number of months used indicated in parentheses.  
927 Dashed line = mean monthly rainfall at RAHA's camp, March 2002–May 2003.

928

929 **Figure 4.** Prevalence of vertebrate remains in feces as a function of sample size, all  
930 studies. The three chimpanzee studies with prevalence >10% appear to be outliers.  
931 Bonobos included for comparison only (note negative slope suggesting publication bias).

932

933 **Figure 5.** Funnel plot of prevalence of vertebrate remains in chimpanzee feces, outliers  
934 excluded. Dashed line = forest populations, solid line = Savanna populations.











