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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

23

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%)¹. 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

¹ 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

² 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

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 km² 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 km² (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/km² 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 km² of the Issa main study area and are aware of only three troops
436 within the ca. 3000 km² 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/km², respectively
440 (Boesch et al., 2002; Uehara, 2003); our estimates for Issa are about 0.7 and 0.35
441 individuals/km², 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/km² (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; Pruettz and Bertolani, 2007;
457 Table 1), which are unlikely to be shared widely (cf. Pruettz and Bertolani, 2007). While
458 consumption of larger animals does occur (Pruettz 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

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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 km² (cf. Gombe National Park \approx 36 km²); 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.









