Chimpanzee vertebrate consumption: savanna and forest chimpanzees compared

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Abstract

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.

Introduction

Chimpanzees and the origins of hunting by hominins

The origin, nature, and significance of hominin consumption of vertebrates have been foci of research and debate in anthropology for nearly a century. The transition from an ape-like frugivore/folivore to a more carnivorous hominin has been linked to a shift from more forested to more open, savanna environments since before the first African fossil hominin was found (e.g., Barrell, 1917). This was thought to be either because environmental change put earliest hominins into marginal savanna habitats, forcing them to broaden their diet, or because abundant prey in savannas enabled them to expand into a vacant niche (Cartmill, 1993). To explore whether consumption of vertebrates and adaptation to savanna habitats were functionally linked in hominin evolution, it may be informative to look at meat-eating among extant chimpanzees and investigate whether adaptation to savanna habitats influences their consumption of vertebrates Because chimpanzees and early hominins (e.g., *Ardipithecus*; Stanford, 2012) are broadly similar (e.g., body size and structure, degree of encephalization, habitat), ecological and social adaptations exhibited by savanna-dwelling chimpanzees relative to forest populations may shed light on that transition in the hominin lineage. That light may take the form of a heuristic framework for thinking about early hominins; more usefully, it may generate middle-range tests of hypotheses or discover unrecognized problems with interpretation of paleontological data (Moore, 1996; Stanford, 1996; Pickering and Domínguez-Rodrigo, 2012; Mitani, 2013). We agree with Sayers and Lovejoy (2008) that using modern panins to help understand extinct hominins can lead to erroneous conclusions and that such an approach must be applied with care. Using the one to help understand the other (‘referential modeling’) is a method that, like any other method, must be applied carefully or error can result—for example, theoretical (‘strategic’) modeling resulted in the now disproved single-species hypothesis (Wolpoff, 1971).

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

We report here on observational and fecal data collected at the Issa, Nguye, and Bhukalai study sites, Ugalla (Tanzania), and place them in the context of published quantitative information on the prevalence of vertebrate remains in chimpanzee feces from other wild chimpanzee populations. Fecal data indicate consumption only; however, scavenging by chimpanzees is rare (Watts, 2008), such that it is therefore likely that most vertebrates consumed were hunted.

Fecal analysis and rates of faunivory

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

Is fecal analysis actually unreliable, or can it be used to estimate frequency of vertebrate consumption? To answer this question definitively, we would need concurrent quantitative data on meat consumption, defecation rates, and fecal prevalence of vertebrate remains; such data are not available. However, non-concurrent data from several sites allow us to make a crude approximate test of the method. Wrangham and van Zinnicq Bergmann Riss (1990) concluded that the Kasekela and Kahama communities at Gombe averaged about 204 prey/year between 1972–1975. Between 1965–1967, the Kasekela/Kahama community averaged about 42 adult and adolescent individuals (Goodall, 1986). Teleki (1973) reported that an average of eight individual chimpanzees obtained portions per predation event (range 4–15). Wild chimpanzees defecate about 3 to 3.5 times per day (calculated from Phillips and McGrew, 2014 and Nishida et al., 1979, respectively). Finally, Lambert (2002) found that markers fed to captive chimpanzees were detected between 23–63 hours following consumption (mean transit time and mean time of last appearance, respectively), a span of 40 hours. Using the above defecation rates, this would translate into about five defecations following a meal that might contain its residue. However, inspection of Lambert (2002:Fig. 1) suggests that most markers appeared between 20 and 50 hours, roughly bimodally. We therefore consider three defecations post-consumption to potentially contain identifiable residue, though recognizing that combining captive passage rates with wild defecation rates is problematic.

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

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[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.

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

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

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[2] Because of sharing, samples from the same party are not independent. Average party

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

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

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

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

Despite these issues, we believe that the problem with fecal analysis is not inherent in the method itself, but in frequent reliance on small sample sizes and failure to specify precisely what was done (were immature individuals included? if unhabituated, was fecal size used as a criterion for collection? were samples collected opportunistically with respect to party, time, and season, or according to a formal design? etc.), let alone standardize methods across sites (Uehara, 1997). Given some attention to methodology, we agree with Phillips and McGrew (2014:539) that “macroscopic inspection of feces can be a valuable tool to provide a generalized overview of dietary composition for primate populations." It is not possible to extrapolate from vertebrate remains in feces to mass of meat consumed on an individual basis, because prey often are shared unevenly: a scrap of hide might be all that remains of a large portion, or it may be the entire portion consumed by that chimpanzee. Given accurate identification of prey species and age/size class, it may however be possible to estimate at least relative amounts of meat consumed by a community using fecal prevalence data (Wrangham and van Zinnicq Bergmann Riss, 1990).

Methods

Field methods

Ugalla is a region of about 3000 km^2 of primarily savanna woodland with narrow strips of riverine forest and has been described elsewhere (Hernandez-Aguilar, 2009; Stewart et al., 2011; Moore and Vigilant, 2014; Fig. 2). Rainfall at Issa averages about 1150 mm/year (range 955–1275, $N = 4$ complete years; one incomplete year totaled 1490 mm) with a dry season (<60 mm/month) lasting from May through October; in a typical year, no rain at all falls during June–August (Fig. 3). Data come from three distinct locations: Nguye and Bhukalai (Yoshikawa and Ogawa, 2015), which are about 40 km apart, and Issa, which lies between them. Research at Issa has taken place in two phases, with one camp (October 2001-June 2003; Hernandez-Aguilar, 2009) about 9 km north of the other (October 2008-ongoing; Stewart et al., 2011). We believe that the two Issa studies have looked at the same large community of about 70 individuals with a home range >100 km^2 (Rudicell et al., 2011), but neither the community size nor the range have been positively confirmed. In addition to being about 9 km apart (comparable to the distance between Kanyawara and Ngogo at Kibale), Hernandez-Aguilar's camp was about 400 m lower in elevation than the current, permanent camp.

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

Literature review

For the comparative analysis, we attempted to locate all published information on prevalence of vertebrate remains in chimpanzee feces that also provided sample size. Bonobos are included for comparison but are not considered further other than to note that the popular belief that bonobos are less predatory than chimpanzees (e.g., Gilby et al., 2013) is not supported by the fecal prevalence data (Table 2). Interestingly, female bonobos may be relatively more involved in hunting than are female chimpanzees (Gruber and Clay, 2016; see also Tokuyama et al., 2017; Gilby et al., 2017). Although dichotomizing sites into 'forest' and 'savanna' masks potentially important quantitative differences in vegetation, we have followed general usage and done so for this analysis. At savanna sites, evergreen forest typically makes up 1–10% of the habitat, with the rest being primarily deciduous open grassy woodland to wooded grassland; rainfall is usually under 1200 mm/yr and there are > 4 dry months. Most forest sites are predominantly evergreen forest with rainfall over 1400 mm and shorter dry seasons. Gombe, sometimes referred to as 'woodland,' is about 25% evergreen forest overall, although the proportion of forest is much greater within the range of the main study community (Foerster et al., 2016). See Moore (1992) and Domínguez-Rodrigo (2013) for further discussion. Note that descriptions of the paleoenvironment of *Ardipithecus ramidus* as grassy woodland mosaic savanna (Domínguez-Rodrigo, 2013:Table 3) fit Ugalla well. Because predation rates are known to vary over time, we treated published studies, not sites, as the unit of analysis in the meta-analysis and figures (i.e., we did not pool the results of multiple studies at Mahale, Kanyawara, and Ugalla). We then looked for evidence of publication bias. Because chimpanzee meat-eating is of theoretical interest to anthropologists, there may be a tendency to publish positive results even when sample sizes are small. We did a funnel plot (following Nakagawa and Santos, 2012) of sample size as a function of reported prevalence of vertebrate remains and found three distinct outlier studies with high prevalence values and small samples (Fig. 4): Anderson et al. (1983), Nishida (1989), and Alp (1993). These three studies were removed from the analysis and a second funnel plot was constructed with the remaining studies (Fig. 5). Forested sites show a rough inverted funnel with the peak between 1–2% prevalence, as is expected in the absence of publication bias, except for two outlying points representing Gombe and Mahale. Both of those samples are large enough ($N > 1{,}000$) such that we do not believe publication bias to be responsible for their reporting.

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

Data analysis

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

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

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

Results

Table 1 lists all evidence of vertebrate consumption by the chimpanzees of Ugalla. At least 11, and probably 12, separate instances have been recorded (two positive samples collected by GI two days and 4 km apart conceivably could represent a single episode of consumption, but we consider them separately here). In five cases, the evidence was hair judged to belong to a small mammal, possibly a squirrel, and a sixth was a vertebra of a squirrel-sized mammal. Accurate field identification of hair in feces is difficult, and we cannot exclude the possibility that some were galagos (*Galago senegalensis*, *Galago moholi*, or *Otolemur crassicaudatus*). Four small ungulates were consumed; in one case, a hoof (possibly klipspringer, *Oreotragus oreotragus*) was found in feces; in two, chimpanzees were observed feeding on blue duiker (*Philantomba monticola*); and in one, the prey resembled a small blue duiker but the identification was not positive.

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

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

Table 2 lists all the published results that describe prevalence of vertebrate remains in chimpanzee and bonobo feces, with 95% CI. For forested sites, all prevalence values <0.25% come from sites where significant human disturbance was notable or recent at the time of sample collection, or sample size was small (<75). For savanna sites, small sample sizes (<75) were associated with higher, not lower, prevalence values (consistent with the possibility of publication bias, noted above). Only three studies, all in forest, reported no vertebrate remains in feces. Chimpanzee predation on vertebrates has been observed at two of them, Bossou and Rubondo (Sugiyama and Koman, 1987; Moscovice et al., 2007). The third, Belinga, is represented by only 25 feces.

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

Vertebrates consumed at savanna sites tend to be small and solitary. At Mt. Assirik, all known cases of meat-eating were of prosimians (galago and potto; McGrew, 1983; McGrew et al., 1988); at Fongoli, galagos made up nearly 60% of observed prey captures, with monkeys (vervets, patas, and baboons) making up 37% (Pruetz et al., 2015); and at Ugalla, 67% were thought to be squirrel/galago-sized small mammals or fledgling birds. In contrast, predation on galagos is remarkably rare at Gombe and Mahale (O'Malley, 2010). While sample sizes at Tenkere and Semliki are small, they suggest a more typical emphasis on eating monkeys. At Tenkere, the four independent predation/consumption episodes reported by Alp (1993) consist of two monkeys, a duiker, and a scaly-tailed flying squirrel, and at Semliki the only mammal consumed was black and white colobus (*Colobus guereza*; two observed captures and two fecal remains; Hunt and McGrew, 2002).

Discussion

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

We emphasize that, because chimpanzees typically share meat, the prevalence of vertebrate remains in feces should not be confused with the frequency of hunting. At Gombe, with fecal prevalence of 5.81% (Table 2), Teleki (1973) reported an average of eight consumers/kill. If there were no sharing, then one might expect fecal prevalence of 5.81/8 = 0.73%. Reduced sharing is likely where prey tend to be small, such as squirrels or galagos (cf. Pruetz and Bertolani, 2007). By this logic, the frequency of hunting at Mt. Assirik might in fact be greater than at Gombe or Mahale (multiplying, rather than dividing, Mt. Assirik's prevalence by 8 = 14.3%). Only observational data can address the frequency of hunting.

Intersite variation

McGrew (1983) reviewed possible ecological explanations for intersite variation in chimpanzee vertebrate consumption rates. Firstly, of course, the absence of suitable prey taxa might explain low rates. Newton-Fisher (2015) listed 32 mammalian taxa reported to have been consumed by chimpanzees (excluding chimpanzees, i.e., cannibalism); pooling allopatric variants (e.g., lumping yellow and olive baboons as 'baboons') reduces this to 27. Twenty of the 27 are reported to be present at savanna sites; Ugalla alone has 16, including favorite chimpanzee prey, red colobus (*Procolobus badius tephrosceles*), blue duiker, bushbuck (*Tragelaphus scriptus*), and bushpig (*Potamochoerus porcus*). In fact, the Issa study area at Ugalla has the largest number (40) of medium/large mammal genera (this excludes rodents, bats, and elephant shrews) reported for any chimpanzee study site (Johnson, 2014; cf. 37 for Kibale: Russak and McGrew, 2008). Secondly, McGrew (1983) suggested that abundant predators might inhibit chimpanzee hunting by cropping sick or injured prey, as well as making hunting on the ground more dangerous for chimpanzees. Ugalla has a full complement of mammalian predators, which do interact with chimpanzees (e.g., McLester et al., 2016): lion (*Panthera leo*), leopard (*Panthera* *pardus*), spotted hyena (*Crocuta crocuta*), and wild dog (*Lycaon pictus*), as well as smaller carnivores. The possible impact of predator competition/threat on Ugalla chimpanzee vertebrate consumption is hard to evaluate, but high rates of hunting at sites with healthy predator populations (e.g., leopard at Taï and leopard, lion, hyena, and wild dog at Mahale) suggest that competition with carnivores is unlikely to explain low meat consumption at Ugalla.

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

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

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

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

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

Seasonality

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

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

For comparison with non-savanna sites, at Gombe about 39% of all predations occurred during the peak three months of July-September (dry season, calculated from Stanford et al. [1994]), and at Mahale, about 45% in August-October (late dry season, calculated from Hosaka et al. [2001]). At Taï, the three peak months for successful predations are non-consecutive: June and September-October, with no data available for July. Thirty-three percent of prey captures occurred during September-October and 44% in August-October (calculated from Boesch and Boesch-Achermann, 2000:Fig. 8.1). These are the three rainiest months (Boesch and Boesch-Achermann, 2000:Fig. 1.3). Based on the available evidence, vertebrate consumption appears more strongly seasonal at savanna sites.

Pickering and Domínguez-Rodrigo (2010, 2012) have argued that chimpanzee hunting is motivated at least in part by seasonal nutritional shortfalls (but not energetic ones; Mitani and Watts, 2001; Tennie et al., 2014), and thus that vertebrate consumption should be more sharply seasonal at savanna sites, which are more seasonal than forested sites (Moore, 1992). This prediction seems to be upheld. However, the peak vertebrate consumption months correspond with annual increases in average party size at Fongoli (Pruetz and Bertolani, 2009) and Ugalla (Ugalla Primate Project [UPP], unpublished data), consistent with social hypotheses for chimpanzee hunting (e.g., Stanford et al., 1994; Mitani and Watts, 2001). Existing data are not adequate to distinguish between these nutritional shortfall and social facilitation hypotheses, but we note that most of the prey at Fongoli, Mt. Assirik, and Ugalla are small, hole-dwelling prosimians and squirrels (McGrew 1983; Pruetz et al., 2015). Isaac and Crader (1981:101) argued that while the pursuit of large mobile prey is clearly hunting, "as the quarry becomes smaller and less mobile, the pursuit becomes less and less like hunting"—and they excluded from "hunting" the capture of nestling birds and "the digging up of small burrowing animals." While this conflates size and mobility, it does get at an important feature of 'hunting' that is central to hypotheses that chimpanzees hunt for social reasons: although capture of galagos and squirrels may carry some risk (Pickering and Domínguez-Rodrigo, 2012; Pruetz et al., 2015), it is unlikely to be a venue for display (Bliege Bird and Bird, 2005) or acquiring meat to use as a social currency (Moore, 1984; Nishida et al., 1992; Mitani and Watts, 2001) because the risk is slight and there is little to share. This conclusion is supported by behavioral observations at Fongoli, which show that about half of galago captures are by females and immatures, and sharing of these vertebrate prey is limited (Pruetz and Bertolani, 2007; Bogart et al., 2008; Pruetz and Marshack, 2009; Pruetz et al., 2015). Although seasonal peaks in meat-eating and party size are correlated at Fongoli and Ugalla, the association is not likely related to male social strategies.

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

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

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

Conclusions

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

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

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

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

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

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

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

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

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

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

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Figure legends

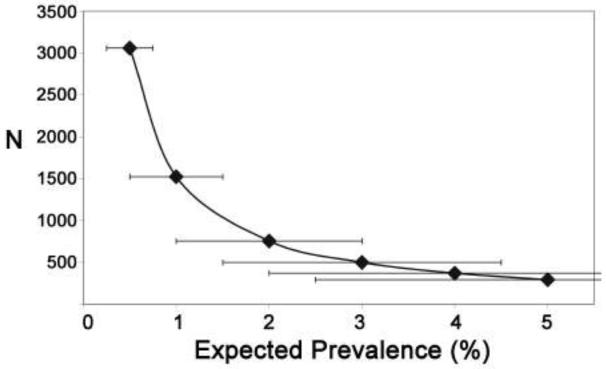
Figure 1. Recommended sample sizes to detect vertebrate remains (i.e., to exclude 0 from the 95% confidence interval) given expected prevalence under 5%.

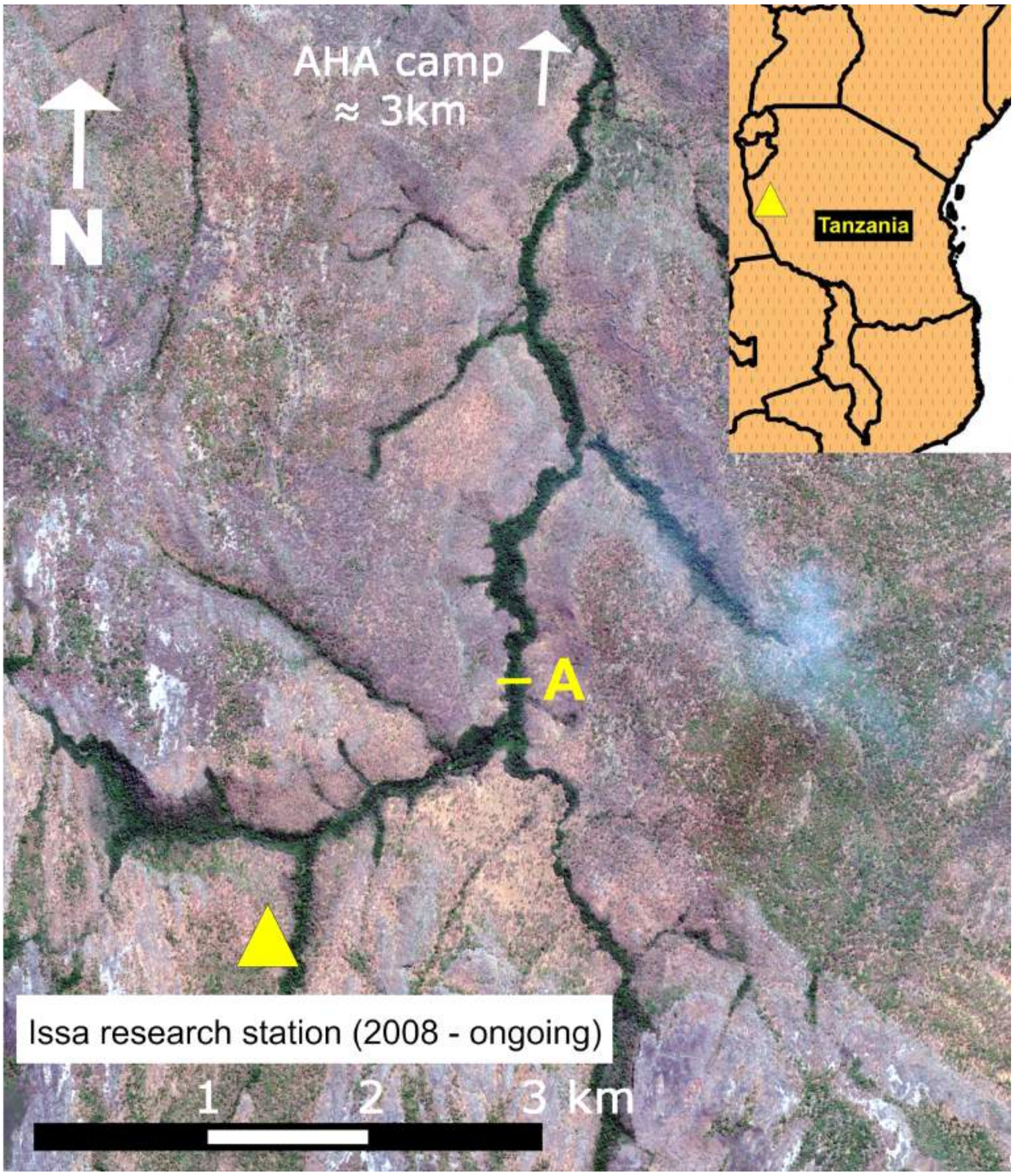
Figure 2. Central portion of Issa study area, Ugalla. The area shown is approximately 42 km^2 (cf. Gombe National Park ≈36 km^2); it is about half the area currently monitored on a regular basis. Width of the riverine evergreen forest strip at 'A' is ≈120 m.

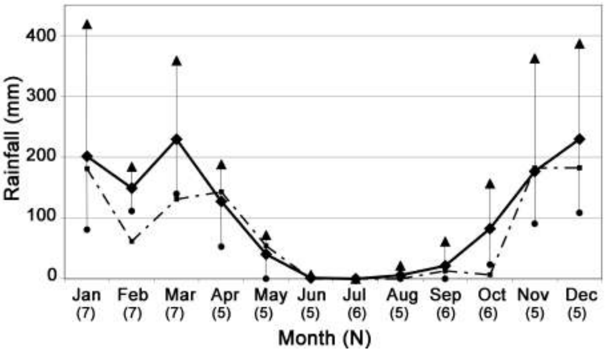
Figure 3. Monthly rainfall at Issa. Solid line = mean, minimum, and maximum monthly rainfall at permanent camp, 2009–2015. Intermittent failures of HOBO Data Logging Rain Gauge resulted in lost data; number of months used indicated in parentheses. Dashed line = mean monthly rainfall at RAHA's camp, March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

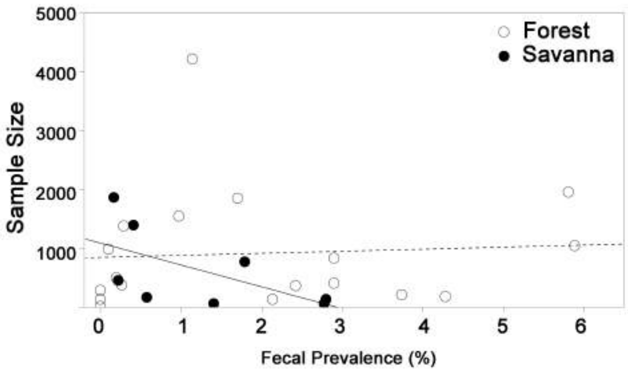
Figure 4. Prevalence of vertebrate remains in feces as a function of sample size, all studies. The three chimpanzee studies with prevalence >10% appear to be outliers. Bonobos included for comparison only (note negative slope suggesting publication bias).

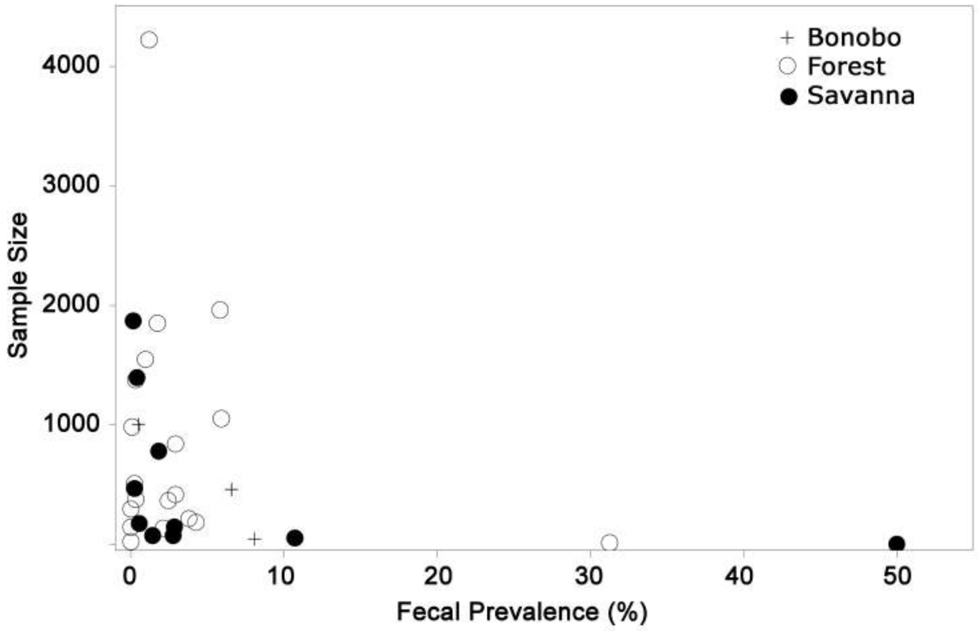
Figure 5. Funnel plot of prevalence of vertebrate remains in chimpanzee feces, outliers excluded. Dashed line = forest populations, solid line = Savanna populations.


3500
3000
2500
2000
1500
1000
500
N
0
1
2
3
4
5
Expected Prevalence (%)


AHA camp
≈ 3km
N
Tanzania
A
Issa research station (2008 - ongoing)
1
2
3 km


Rainfall (mm)
400
300
200
100
0
Jan (7)
Feb (7)
Mar (7)
Apr (5)
May (5)
Jun (5)
Jul (6)
Aug (5)
Sep (6)
Oct (6)
Nov (5)
Dec (5)
Month (N)


Forest
Savanna
Sample Size
5000
4000
3000
2000
1000
0
1
2
3
4
5
6
Fecal Prevalence (%)


Bonobo
Forest
Savanna
Sample Size
4000
3000
2000
1000
0
10
20
30
40
50
Fecal Prevalence (%)