Prey preferences of the chimpanzee (*Pan troglodytes*)

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Abstract

Chimpanzees *Pan troglodytes* are the closest extant relative of modern humans, and are often used as a model organism to help understand prehistoric human behavior and ecology. Originally presumed herbivorous, chimpanzees have been observed hunting 24 species of birds, ungulates, rodents, monkeys, and other primates, using an array of techniques from tools to group cooperation. Using the literature on chimpanzee hunting behavior and diet from 13 studies, we aimed to determine the prey preferences of chimpanzees. We extracted data on prey-specific variables such as targeted species, their body weight, and their abundance within the prey community, and hunter-specific variables such as hunting method, and chimpanzee group size and sex ratio. We used these in a generalized linear model to determine what factors drive chimpanzee prey preference. We calculated a Jacobs' Index value for each prey species killed at two sites in Uganda and two sites in Tanzania. Chimpanzees prefer prey with a body weight of 7.6 ± 0.4 kg or less, which corresponds to animals such as juvenile bushbuck *Tragelaphus scriptus* and guereza colobus monkeys *Colobus guereza*. Sex ratio in chimpanzee groups appears to drive chimpanzee prey preference, where chimpanzees increasingly prefer prey when in male-dominated groups. Prey preference information from chimpanzee research can assist conservation management programs by identifying key prey species to manage, as well as contribute to a better understanding of the evolution of human hunting behavior.

Keywords

chimpanzee, hunter-gatherer, prey preference, Jacobs' Index, hunting, optimal foraging theory

Introduction

Modern humans (*Homo sapiens*) share 96% of their genome with chimpanzees (*Pan troglodytes*) (Tomkins, 2016). This shared ancestry means that chimpanzees are often used as a model for understanding early hominid behavioral ecology (Pilbeam & Lieberman, 2017). Originally, chimpanzees were presumed to be herbivorous (Stanford, 1995). It is now known, however, that they actively hunt animals, including primates, small ungulates, birds, reptiles, and invertebrates, which account for up to 4% of the diet (Boesch, 2002; Gilby & Wawrzyniak, 2018; Mitani & Watts, 2001). Prey is highly sought after, sometimes with the use of tools and group hunting parties (Stanford et al., 1994). Chimpanzee hunting behaviors are particularly relevant in determining the role that predation played in hominid evolution, as well as in the evolution of group hunting strategies (Pruetz et al., 2015; Stanford, 1996).

The evolution of chimpanzee prey preferences can be explained by the optimal forage theory, which predicts prey will be selected based on a cost/benefit relationship between the energetic benefits of consuming a prey item compared to the costs of capturing and ingesting it without getting injured (Pyke, 1984). Chimpanzee hunting and the acquisition of preferential prey varies from group to group, forming cultural identities within the species and subspecies. In particular, chimpanzee in home ranges that have heavy seasonal differences, prefer high quality prey and avoid lower quality prey. Under the optimality theory paradigm, we predict that preferential predation is likely to influence chimpanzee prey selection whereby the largest food item that can be safely captured and killed is preferred. Depending on the cultural traditions within the group, transfer of meat or access to carcasses goes to mature members within the group (Hohmann, 2009).

Using the published literature on chimpanzee hunting behavior and diet, we aimed to determine the prey preferences of chimpanzees and the factors that contribute to preferential prey acquisition.

Methods

To assess the prey selection of chimpanzees, we followed the methods of Hayward (2006, 2017). We conducted a primary literature search using JSTOR, Science Direct, Elsevier, and Google Scholar for the following keywords: “chimpanzee” or “Pan troglodytes” AND “prey preference” OR “hunt*” OR “diet” OR “predation” OR “hunting strategies”. Studies that did not have sufficient data were excluded from consideration. Insufficient data included studies that had only one or two prey species listed, or that included only qualitative data. Where only kill or abundance data were provided, the authors were contacted for supplementary information, or we contacted other authors who worked at the same site at about the same time (+/- 5 years). If an author did not respond, we searched for information for the same study area around the same year using Google Scholar.

The crucial information needed for this study from each site included prey species and their population abundance or density (encounter rate or relative), number of kills, hunting method (solitary or group/hunting parties), hunting group size, sex ratio of group, and prey body mass in kilograms (kg). The methods by which chimpanzees hunt prey are typically recorded in each publication, as groups use different methods – whether through solitary hunting, use of human-laid snares (Brand et al., 2014), or hunting parties.

In cases where prey body weight was not reported, we used the low end of adult prey presented in faunal studies from the same area or referred to Kingdon et al. (2013). To account for infant, juvenile, and sub-adult prey, mean adult female body weight was multiplied by 75% (following Jooste et al., 2013). Mean adult male chimpanzee body weight (41.2 kg, n = 43), obtained from Thompson and Wrangham (2013), was used to compare chimpanzee body weight with prey body weight, and the protein requirements of chimpanzees. Note that we use adult male chimpanzee body mass in contrast to other prey preference studies because they do most of the hunting (Gilby et al., 2017).

Jacobs' Selectivity Index (*D*; Jacobs, 1974) was used to determine chimpanzee prey preferences for each prey species at each site. This involved calculating the proportional abundance of each prey species at each site from the total number of prey (p) and the proportion of the kills that species comprised of all chimpanzee kills from the total number of kill records of the particular site (r). These variables were used in the equation: $D = (r - p)/(r + p - 2rp)$. The resulting value *D* is a score ranging from –1 (maximum avoidance) to +1 (maximum preference). Jacobs' Index diminishes the bias of rarer species by actively accounting for species rarity in relation to the total prey population at a given site and considering the heterogeneity of the confidence intervals (Jacobs, 1974). This metric also takes into consideration some of the other techniques, such as the forage ratio and Ivlev's Electivity Index (Ivlev, 1961), addressing the overstated accuracies in results presented, and is preferred in determining the prey preferences of large carnivores and modern human hunter-gatherers (Bugir et al., 2021; Hayward et al., 2017). Where data were normally distributed, we used *t*-tests on the Jacobs' Index (D) values against a mean of 0 to determine if each prey species was significantly avoided or preferred. Where data were not normally distributed, we used a binomial sign test.

We tested for preferred and accessible weight ranges using breakpoint(s) in segmented models. Segmented models identify the ideal and preferred weight range of a predator, as well as which prey species fit within that range. Depending on the number of breakpoints, the change in slope between any two points determines changes of preference (Clements et al., 2014). The Jacobs' Index values of species either side of the breakpoints were tested for significant difference using a *t*-test.

Maximum likelihood statistics through generalized linear models (glm function) were used to identify the factors that affected chimpanzee hunting decisions. To determine which models were strongly supported, we used the Akaike's Information Criterion (Akaike 1973, 1974) and the sum of their weights. The sum of Akaike's weights clarified the relative importance of each variable (i.e., prey body weight, hunt method, chimpanzee group size, sex ratio of chimpanzee group) in driving the Jacobs' Index value for each species. We used R statistical software 1.42.1. (R Core Development Team, 2016) and the *MuMIn* (Barton, 2018), *ggplot2* (Wickham & Chang, 2016), *segmented* (Muggeo, 2015), and *tidyverse* packages (Wickham, 2017).

Results

We found 13 usable studies from two sites in Uganda and two sites in Tanzania (Fig. 1; Table 1). These studies documented chimpanzee hunting from 1984 through 2017. Out of these 13 studies, we estimated Jacobs' Index values for 20 species that were hunted by chimpanzees across 76 different times or places. Eleven of the 20 prey species had a sample size ≥ 3 kills reported. These 11 species were used for further analyses (Table 2).

The most significantly preferred prey of chimpanzees is the ashy red colobus monkey (*Piliocolobus tephrosceles*; Fig. 2). Infant and juvenile bushbuck (*Tragelaphus scriptus*), and western guereza colobus monkey (*Colobus guereza occidentalis*) are taken in accordance with their availability (Table 2; Fig. 2). Significantly avoided species are olive baboon (*Papio anubis*), blue duiker (*Philantomba monticola*), gentle monkey (*Cercopithecus mitis*), and red-tailed monkey (*Cercopithecus ascanius*; Table 2; Fig. 2). The segmented model revealed only one breakpoint or point where the slope changed for preference (at 4.06). This corresponds to about the 7.6 kg threshold---as represented by ashy red colobus (Fig. 3). Species below the 7.6 kg threshold were significantly preferred (t = -7.70, d.f.= 5, p <0.005), while those above were consumed in accordance with their availability in the prey community (t = -0.01, d.f. = 6, p = 0.99). The ratio of ideal prey weight to chimpanzee weight is 1:5.43 (18%) of an adult male chimpanzee's body weight.

The generalized linear model indicated that sex ratio of the entire chimpanzee group was the most important variable (sum of Akaike's weights w = 0.6) in determining prey preference (Fig. 4; Table 3). This is twice as important as chimpanzee group size, prey body weight, or hunting method (Table 3).

Discussion

Like other predators, chimpanzees exhibit preferential predation (Boesch, 1994), but avoid prey that are too large to be worth capturing. The preferred prey of chimpanzees is the ashy red colobus which, at 7.6 kg, is at about the ideal prey weight ratio. Larger prey, such as adult olive baboons or large ungulates, are significantly avoided as they are too large and dangerous to be safely captured by chimpanzees (1:1.75 or 57% the weight of a chimpanzee; Table 1; Harding, 1973). Yet, their offspring are targeted. In comparison, human hunter-gatherers hunt prey weighing up to 276% of the weight of an adult human female (Bugir et al., 2021), yet meat is important food for both species. We conclude that chimpanzees are not apex predators of vertebrates in the way that modern humans, lions (*Panthera leo*), and tigers (*Panthera tigris*) are apex predators (Hayward et al., 2005; 2012).

According to the generalized linear model, the most important variable is the sex ratio of the group studied with hunting more likely to yield larger prey preferences when more males are involved (Fig. 3). Adult males are the primary hunters, much like human hunter-gatherers (Hawkes & Bliege Bird, 2002). Hence, there are similarities here between chimpanzees and humans, with both species possessing the intelligence, innovation with tool use, and skills to hunt and kill a vast array of prey species (Wood, 2019), and that the driver of chimpanzee hunting appear to be more social than dietary.

Human hunter-gatherer prey preferences are, conversely, likely driven by optimal foraging upon terrestrial species that can be captured effectively, minimizing energy expenditure while maximizing energy gain (Milner-Gulland et al., 2003). For traditional human hunter-gatherers, almost any prey within the range 2.5-535 kg (Bugir et al., 2021) is nowadays worth capturing to satisfy the optimal foraging imperatives of dietary protein requirements, because these people tend to persist in ‘empty forests’ (Redford, 1992) where prey populations are persistently over-hunted.

Parallel to human hunter-gatherers hunting and what they can find in 'empty forests', chimpanzees are exploiting red colobus at Ngogo, Kibale Forest, to the point where they may need to switch to new prey species (Watts & Mitani, 2015) or reduce their consumption of meat. Our results indicate that guereza and young bushbuck are taken in accordance with their availability which suggests that they could be replacement prey should red colobus become over-hunted at Ngogo. This suggestion may not necessarily translate to the other sites in this study. Obtaining a baseline of chimpanzee prey preferences has the potential to aid in conservation management of both chimpanzees and their prey species, as well as shed light on the factors driving the evolution of hunting in ancestral hominids.

Conflict of Interest

To the best of our knowledge, there is no conflict of interest.

Data Accessibility Statement

Full dataset for chimpanzee study is available at: https://doi.org/10.5061/dryad.hdr7sqvhc

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Figures and tables

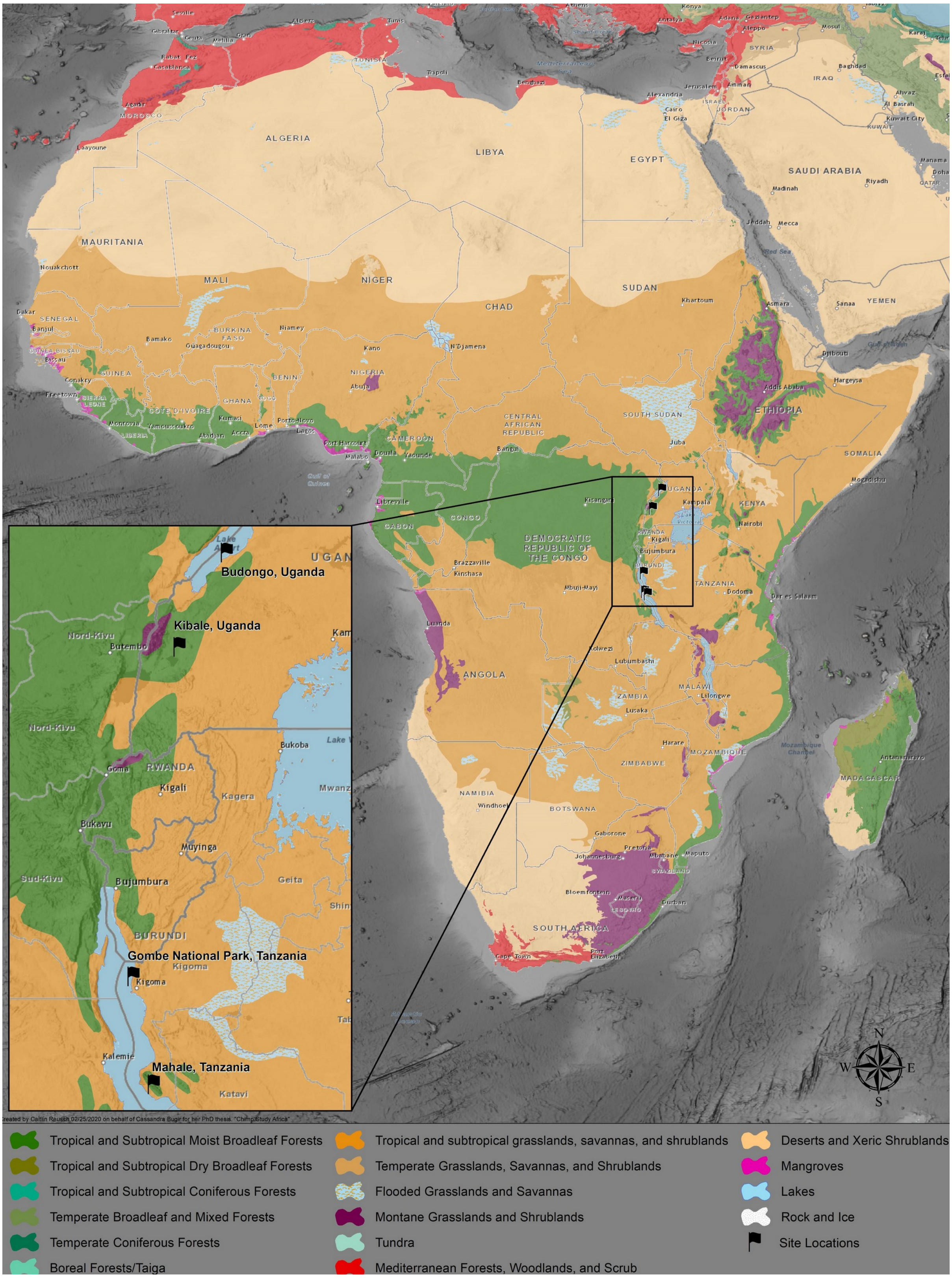

Figure 1. The four sites where data on chimpanzee predation were obtained for this study. (Esri, 2020).

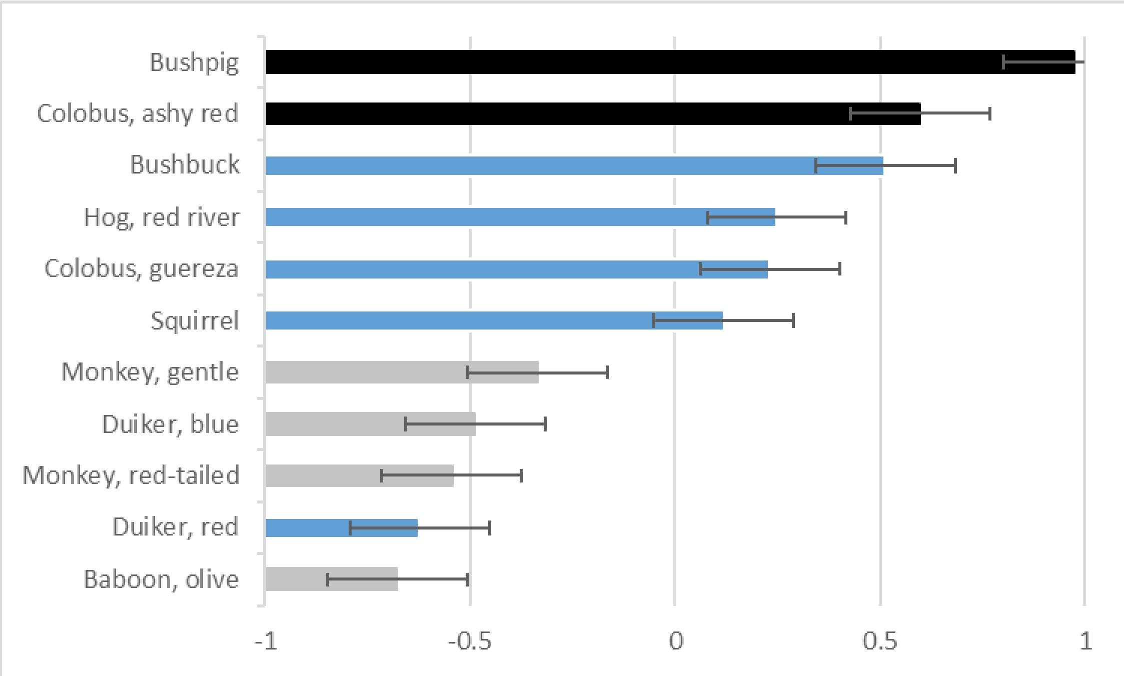

Figure 2. Chimpanzee prey preferences determined by mean Jacobs' Index values ± 1 S.E. calculated from 13 studies at four sites. Significantly preferred prey, taken in excess of their abundance, are delineated by black bars. Grey bars denote significantly avoided prey which are less likely to be pursued irrespective of their abundance. Blue bars are prey that are taken or avoided according to their availability.

Figure 3. Segmented model plot of the cumulative Jacobs' Index (CSJ) against body weight rank (SMR) of the 11 chimpanzee prey species with greater than three kill records (see Table 1). The breakpoint is at 7.6 kg, which corresponds to the body weight of ashy red colobus.

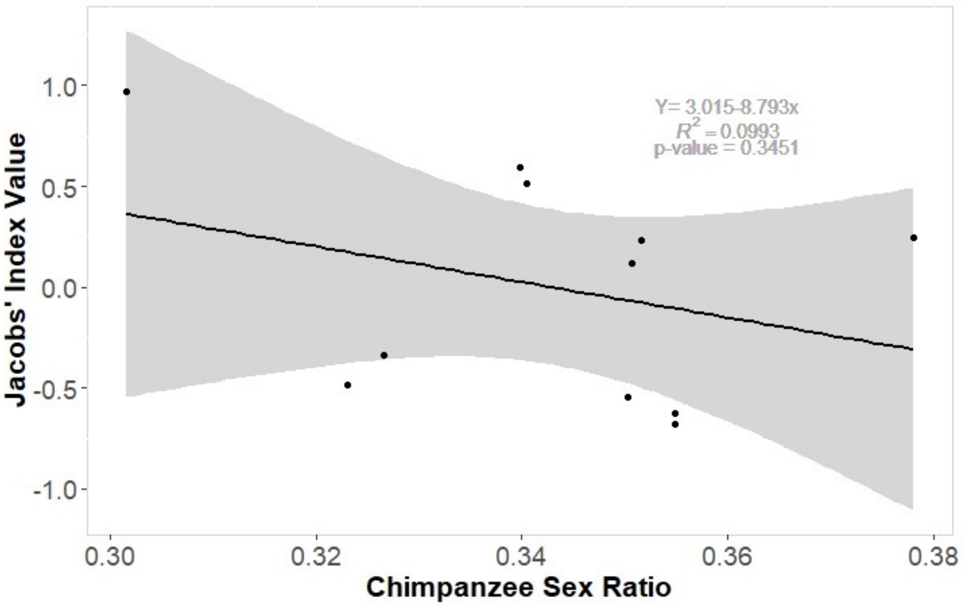

Figure 4. Sex ratio of chimpanzee groups studied, influencing Jacobs' Index for chimpanzee prey preferential selection. This was the most important variable in the AIC models, showing that the groups with sex ratios greater than 0.3 have fewer females to every male. A value of 0.3 implies there are approximately two or more females to every male within one of the groups studied. This regression shows a steady decrease of preference with the more males in a group, however, this regression is not statistically significant.

Table 1. Studies used and species recorded from Tanzania and Uganda.

Species recorded		Tanzania		Uganda	
		Mahale[a]	Gombe[b]	Kibale[c]	Budongo[d]
Baboon, olive	*Papio anubis*	x	x	x	x
Bushbuck (infant, juvenile)	*Tragelaphus sylvaticus*	x	x	x	-
Colobus, ashy red	*Piliocolobus tephrosceles*	x	x	x	-
Colobus, guereza	*Colobus guereza*	-	-	x	x
Duiker, blue	*Philantomba monticola*	x	-	x	x
Duiker, red	*Cephalophus callipygus*	-	-	x	x
Galago, Thomas's dwarf	*Galagoides thomasi*	-	-	x	-
Guineafowl	Numididae spp.	x	-	x	-
Bushpig (infant, juvenile)	*Potamochoerus larvatus*	x	x	x	-
Hog, red river (infant, juvenile)	*Potamochoerus porcus*	x	x	x	-
Mangabey, grey-cheeked	*Lophocebus albigena*	-	-	x	-
Monkey, gentle	*Cercopithecus mitis*	x	-	x	x
Monkey, L'hoest's	*Cercopithecus lhoesti*	-	-	x	-
Monkey, red-tailed	*Cercopithecus ascanius*	x	x	x	x
Monkey, tantalus	*Chlorocebus tantalus*	x	-	-	-
Monkey, vervet	*Chlorocebus pygerythrus*	x	-	-	-
Rat, greater cane	*Thryonomys swinderianus*	x	-	-	-
Shrew, checkered elephant	*Rhynchocyon cirnei*	-	-	-	x
Squirrel	Sciuridae spp.	x	x	-	-
Warthog, common	*Phacochoerus africanus*	x	-	-	-

Sources: [a.] Hosaka et al., 2002; Newton-Fisher et al., 2002; Takahata, 1984; Uehara, 2003; Uehara & Ihobe, 1998. [b.] Gilby et al., 2017; Wrangham & Riss, 1990. [c.] Newton-Fisher et al., 2002; Teelen, 2007. [d.] Hobaiter et al., 2017; Lwanga et al., 2006, 2011; Watts & Mitani, 2012, 2015

Table 2. Preferred and avoided species that chimpanzees hunt. With Jacobs' Index (*D*), negative values indicate 'avoided', whereas positive values indicate 'preferred'. Abundance (*p*) and mean kills (*r*) are proportions, including the standard error (± S.E.). 'n' is the cumulative count of each species recorded from all of the sites.

Common name	**Scientific name**	**Body weight (kg)**	**n**	**Availability (%)**	**Kills (%)**	**D**	**p**	**Binomial (sign)**	***t***
Baboon, olive	*Papio anubis*	24.4	5	0.12 ± 0.06	0.02 ± 0.01	-0.68 ± 0.45	0.02		-3.85
Bushbuck (infant, juvenile)	*Tragelaphus sylvaticus*	10	6	0.06 ± 0.04	0.09 ± 0.03	0.51 ± 0.32	0.09		2.03
Colobus, ashy red	*Piliocolobus tephrosceles*	7.6	4	0.23 ± 0.1	0.77 ± 0.04	0.59 ± 0.03	0.01		3.5
Colobus, guereza	*Colobus guereza*	12.1	5	0.09 ± 0.04	0.22 ± 0.14	0.23 ± 0.31	0.375	0.8	0.75
Duiker, blue	*Philantomba monticola*	8.9	8	0.3 ± 0.06	0.12 ± 0.04	-0.49 ± 0.16	0.02		-2.99
Duiker, red	*Cephalophus callipygus*	11.5	4	0.22 ± 0.03	0.09 ± 0.07	-0.62 ± 0.16	0.07		-2.68
Galago, Thomas's dwarf	*Galagoides thomasi*	0.06	1	0 ± 0	0.001 ± 0	-	1		
Guineafowl	Numididae spp.	0.7	3	0 ± 0	0.01 ± 0.001	-	0.25		
Bushpig (infant, juvenile)	*Potamochoerus larvatus*	18	4	0.001 ± 0.001	0.05 ± 0.02	0.97 ± 0.17	0.63	0.25	
Hog, red river (infant, juvenile)	*Potamochoerus porcus*	11.5	4	0.22 ± 0.03	0.09 ± 0.07	0.25 ± 0.23	1	0.5	
Mangabey, grey-cheeked	*Lophocebus albigena*	5.4	2	0.1 ± 0.09	0.01 ± 0.007	-0.59	0.27		
Monkey, gentle	*Cercopithecus mitis*	5.8	7	0.07 ± 0.03	0.04 ± 0.02	-0.38 ± 0.10	0.01		-3.25
Monkey, L'hoest's	*Cercopithecus lhoesti*	6	1	0.06 ± 0	0.001 ± 0	-0.97	1		
Monkey, red-tailed	*Cercopithecus ascanius*	3.6	8	0.2 ± 0.06	0.04 ± 0.01	-0.55 ± 0.16	0.01		-3.32
Monkey, tantalus	*Chlorocebus tantalus*	3.4	1	0 ± 0	0.04 ± 0	-	0.25		
Monkey, vervet	*Chlorocebus pygerythrus*	5.9	2	0 ± 0	0.007 ± 0	-	0.5		
Rat, greater cane	*Thryonomys swinderianus*	5.1	1	0 ± 0	0.003 ± 0	-	0.25		
Sengi, checkered giant	*Rhynchocyon cirnei*	0.05	1	0 ± 0	0.005 ± 0	0	0.25		
Squirrel	Sciuridae spp.	0.22	3	0.01 ± 0.01	0.01 ± 0.006	-0.15	1	0.33	
Warthog, common	*Phacochoerus africanus*	45	1	0.01 ± 0	0.04 ± 0	0.61	1		

Table 3. Model selection results from the generalized linear model for determining which factors are important in chimpanzee prey selection based on Akaike's Information Criterion corrected for small sample size (AIC_c). 'Weight' refers to the Akaike's weights or the likelihood of each model being the most supported in explaining the data. LogLik (log likelihood) refers to the parameters set within the model. Delta (∆) is the change from the AICc above, reflecting the contribution of additional parameters within the model. 'Importance' (below the model numbers) refers to the sum of the Akaike's weights and is a relative measure of the support for each explanatory variable. Hunting method was the only categorical variable (either solitary or group hunting)

Model	**Intercept**	**Sex Ratio of Chimpanzee**	**Group Size (Chimpanzee)**	**Hunting Method**	**Body Weight (kg)**	**df**	**logLik**	**AICc**	**Δ**	**Weight**
9	-0.845	1.943				3	-57.424	121.269	0	0.2
1	-0.185					2	-58.777	121.761	0.492	0.157
10	-0.898	2.263		+		5	-55.657	122.404	1.135	0.114
13	-0.725	2.143	-0.002			4	-56.871	122.457	1.188	0.111
5	-0.049		-0.001			3	-58.497	123.414	2.145	0.069
11	-0.86	1.951			0.001	4	-57.415	123.544	2.275	0.064
2	-0.142			+		4	-57.538	123.79	2.521	0.057
3	-0.189				0.001	3	-58.776	123.973	2.704	0.052
14	-0.83	2.339	-0.001	+		6	-55.526	124.607	3.337	0.038
15	-0.743	2.155	-0.002		0.002	5	-56.856	124.803	3.534	0.034
12	-0.91	2.269		+	0.001	6	-55.65	124.856	3.587	0.033
7	-0.055		-0.001		0.001	4	-58.495	125.703	4.434	0.022
6	-0.097		-0.0005	+		5	-57.508	126.107	4.838	0.018
4	-0.143			+	<0.001	5	-57.538	126.167	4.898	0.017
16	-0.844	2.349	-0.001	+	0.001	7	-55.516	127.145	5.876	0.011
8	-0.098		-0.0005	+	<0.001	6	-57.508	128.572	7.302	0.005
Null	0.844					4	-0.43	44.23	0	0.25
Importance:		0.6	0.31	0.29	0.24					
N containing models:		8	8	8	8					