

A Test of Foraging Models Using Dietary Diversity Indices for the Lomako Forest Bonobos

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Keywords

Bonobos · Dietary diversity · Functional response model · Optimal diet model

Abstract

Optimal diet and functional response models are used to understand the evolution of primate foraging strategies. The predictions of these models can be tested by examining the geographic and seasonal variation in dietary diversity. Dietary diversity is a useful tool that allows dietary comparisons across differing sampling locations and time periods. Bonobos (*Pan paniscus*) are considered primarily frugivorous and consume fruits, leaves, insects, vertebrates, terrestrial herbaceous vegetation, and flowers. Frugivores, like bonobos, are valuable for examining dietary diversity and testing foraging models because they eat a variety of species and are subject to seasonal shifts in fruit availability. Frugivorous primate species thus allow for tests of how variation in dietary diversity is correlated with variation in ecological factors. We investigated measures of dietary diversity in bonobos at two research camps across field seasons within the same protected area (N'dele and Iyema) in Lomako Forest, Democratic Republic of the Congo. We compared the results

of behavioral observation (1984/1985, 1991, 1995, 2014, and 2017) and fecal washing analysis (2007 and 2009) between seasons and study period using three diversity indices (Shannon's, Simpson's, and SW evenness). The average yearly dietary diversity indices at N'dele were Shannon's $H' = 2.04$, Simpson's $D = 0.82$, and SW evenness = 0.88 while at Iyema, the indices were Shannon's $H' = 2.02$, Simpson's $D = 0.82$, and SW evenness = 0.88. Behavioral observation data sets yielded significantly higher dietary diversity indices than fecal washing data sets. We found that food item (fruit, leaf, and flower) consumption was not associated with seasonal food availability for the 2017 behavioral observation data set. Shannon's index was lower during periods when fewer bonobo dietary items were available to consume and higher when fruit was abundant. Finally, we found that optimal diet models best-explained patterns of seasonal food availability and dietary diversity. Dietary diversity is an essential factor to consider when understanding primate diets and can be a tool in understanding variation in primate diets, particularly among frugivores. Dietary diversity varies across populations of the same species and across time, and it is critical in establishing a complete understanding of how primate diets change over time.

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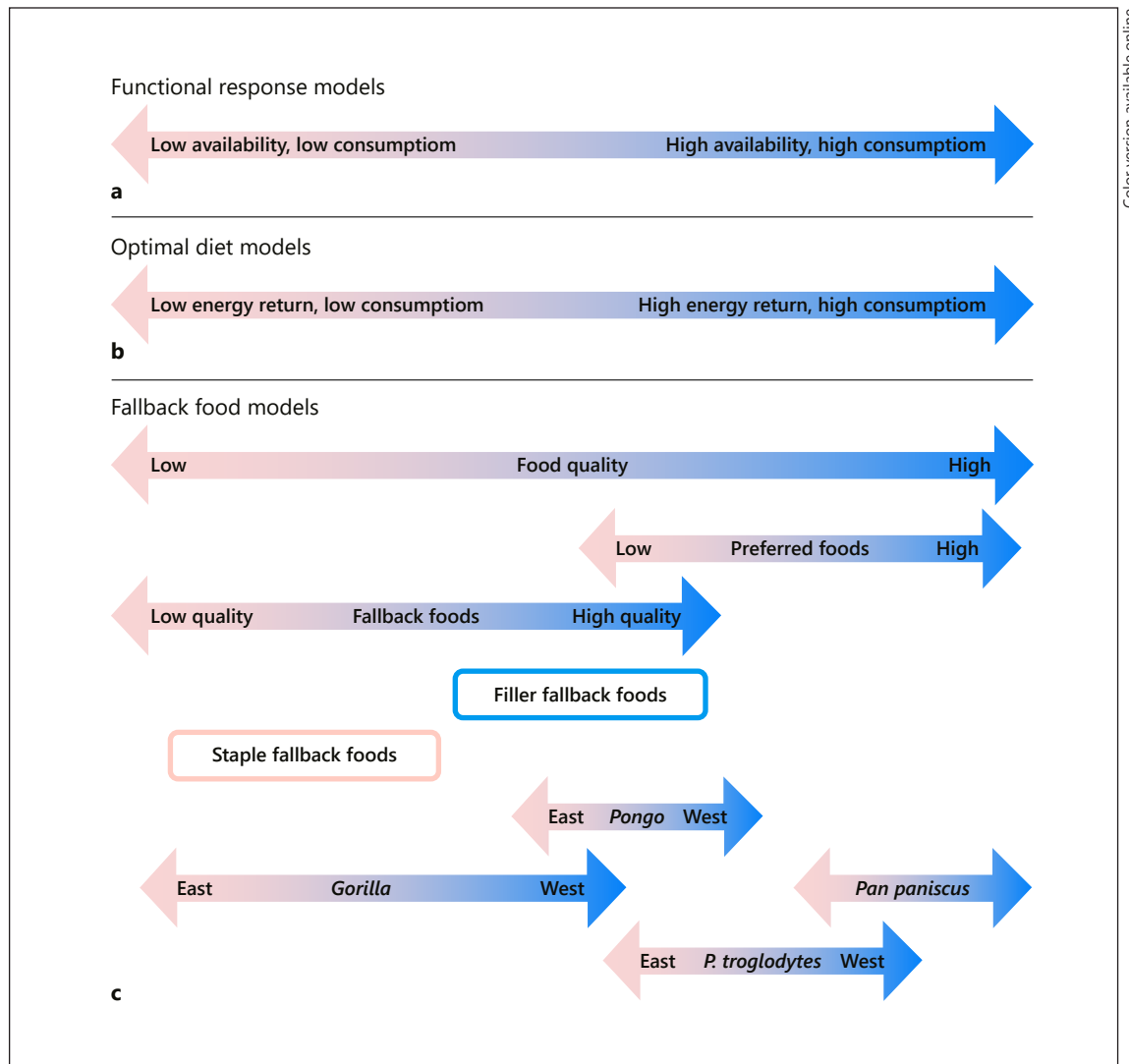
Introduction

The acquisition of food resources is necessary for survival and reproduction and has influenced primate behavior [Clutton-Brock, 1974; Boubli and Dew, 2005; Bray et al., 2018]. Evolutionary models provide a framework for understanding the relative importance of ecological variables in the evolution of primate dietary diversity [Lambert, 1998, 2004; Lambert and Rothman, 2015]. These models help us understand how different ecological variables influence foraging strategies and incorporate dietary breadth, energy return, nutritional quality, mechanical properties, digestibility, food species abundance and distribution, and seasonality [Richard, 1985; Strier, 2015]. Three major model types have been used to understand primate diets: (1) functional response models [Holling, 1959]; (2) optimal foraging or optimal diet models [MacArthur and Pianka, 1966]; and (3) fallback food models [Lambert, 2007; Marshall and Wrangham, 2007]. Each of these model types places emphasis and significance on different ecological factors (Fig. 1). For example, functional response models emphasize food species distribution and abundance [Holling, 1965], whereas optimal diet models focus on aspects of dietary breadth, energy return, and abundance [MacArthur and Pianka, 1966; Charnov, 1976; Pyke et al., 1977], and fallback food models predict how animals will change their diets under conditions when preferred foods are unavailable [Marshall et al., 2009]. These models differ in their usefulness for addressing different hypotheses. For example, functional response and optimal diet models incorporate aspects of dietary breadth that are useful in testing model predictions in highly productive forests where periods of scarcity are rare [Lambert, 2007; Marshall and Wrangham, 2007; Raubenheimer et al., 2009], while fallback food models test predictions under conditions of food scarcity.

Functional response models are often the underlying assumption in most primate feeding ecology studies [Krebs, 1984; Lambert and Rothman, 2015]. The concept that food abundance predicts consumption of those same food items has been documented in Taihangshan macaques (*M. mulatta tcheliensis*), black and white colobus (*Colobus guereza*), masked titi monkeys (*Callicebus personatus melanochir*), orangutans (*Pongo pygmaeus*), and western lowland gorillas (*Gorilla gorilla gorilla*) [Leighton, 1993; Heiduck, 1997; Doran et al., 2002; Cui et al., 2019]. Optimal diet models focus on aspects of dietary breadth, energy return, and abundance but have only sporadically been directly tested in primatology [Altmann and Wagner, 1978; Sayers et al., 2009]. Among

yearly data collected on baboons (*Papio cynocephalus*), tests of optimal diet models found mean energy shortfall was a predictor of female baboon reproductive life span [Altmann, 1991]. In Himalayan langurs (*Semnopithecus entellus*), the energetic currency of food resources generally predicted their consumption [Sayers et al., 2009]. Fallback food models predict how a diet will respond under conditions when preferred foods are unavailable [Lambert, 2007; Marshall and Wrangham, 2007]. Fallback foods are essential in primates, including Japanese macaques (*Macaca fuscata*), sportive lemurs (*Lepilemur ruficaudatus*), chimpanzees (*Pan troglodytes*), and others [Furuichi et al., 2001; Constantino and Wright, 2009; Hanya and Chapman, 2013; Grassi, 2006]. However, to our knowledge, no studies in primates use dietary diversity indices as a tool to test the model predictions of functional response and optimal diet models.

Dietary diversity indices help examine variation in primate diets because they facilitate comparisons across methods, including behavioral observations and fecal washing, and geography [McGrew et al., 1988, 2009; Tutin et al., 1991; Basabose, 2002; Potts et al., 2011; Phillips and McGrew, 2014; Erhart et al., 2018]. The three most commonly used indices are the (1) Shannon-Weaver, also known as Shannon's (H') index, (2) Simpson's index (D), and (3) Shannon-Wiener evenness index (SW evenness), all of which incorporate two main factors: (1) species richness (N) and (2) species evenness [Magurran, 1988]. Dietary species richness describes the number of species eaten, whereas dietary species evenness is concerned with the relative predominance of different species in the diet [Mittelbach and McGill, 2019]. Shannon's index aims to combine evenness and richness into a single metric of diversity and assumes that sampling is from an infinitely large population [Shannon and Weaver, 1949; Magurran, 1988]. In contrast, Simpson's index measures the probability that two randomly sampled items in the diet are the same and is a measure of concentration [Magurran, 1988; Simpson, 1949]. Finally, SW evenness takes the same basic approach as the other indices but detects patterns due to shifts in the overall species availability. When abundant species dominate, the value of the index will be higher [Magurran, 1988; Pielou, 1974]. For example, in examining faunal loss from bushmeat hunting at Bioko Island, Equatorial Guinea, the SW evenness index was higher than Shannon's index in examining temporal variation in the diversity of species taken as bushmeat [Albrechtsen et al., 2007]. Thus, these diversity indices can be used to examine model predictions that deal with changes in richness and evenness.



Color version available online

Fig. 1. Schematic of different dietary models, based on Holling [1959] (a), MacArthur and Pianka [1966] (b), and Marshall et al. [2009] and Lambert [2007] (c). Fallback food models are not the focus of this article.

In community ecology, where many of these indices were developed, the use of these diversity indices to compare across data sets collected at different times and from different locations is the main strength of the diversity indices [Pielou, 1974; Mittelbach and McGill, 2019]. The strength of a diversity index is that it compresses data into a single comparable index [Magurran, 1988; Lehman and Tilman, 2000]. The weakness of these indices is that they do lose resolution when examining the specifics of what species are consumed and at which frequencies, which is why for this paper, we have also provided the frequency of consumption for the different food species across the different data sets (Table 1). In studying the dietary ecol-

ogy for Steller sea lions (*Eumetopias jubatus*) and Holarctic martens (*Martes* spp.), dietary diversity indices were used to investigate changes in diet over space and time using spatially separated field sites over multiple years [Lozano et al., 2006; Zhou et al., 2011]. Thus, borrowing from community ecology, we seek to use dietary diversity indices and how they shift across a year and between data sets to inform our understanding of primate foraging strategies. Shannon's index, Simpson's index, and the SW evenness index have been used in primatology primarily to compress a year's worth of feeding ecology data into a single index [Potts et al., 2011; Erhart et al., 2018; Cui et al., 2019]. Typically, only Shannon's or Simpson's index

Table 1. Percentage of foraging time by species and food type

Species	Plant part	1984 (N'dele)	1991 (N'dele)	1995 (N'dele)	2007 (N'dele)	2009 (N'dele)	2009 (Iyema)	2014 (Iyema)	2017 (Iyema)
<i>Annonidium mannii</i>	Fruit	0.74%					6.45%		
<i>Anothonota fragrans</i>	Seed								2.88%
<i>Anthoclitandra robustior</i>	Fruit							33.33%	
<i>Antiaris toxicana</i>	Fruit/leaves/ Flowers	16.3%							4.32%
<i>Autranella congolensis</i>	Fruit	0.74%	1.47%						
<i>Beilschmiedia corbisieri</i>	Fruit	0.74%							
<i>Blighia welwitschii</i>	Fruit		1.47%						
<i>Carpodinus gentilii</i>	Fruit	4.44%	7.35%						0.72%
<i>Celtis mildbraedii</i>	Fruit	10.37%	0.98%						13.67%
<i>Celtis tessmanii</i>	Fruit/leaves								0.72%
<i>Cephalophus weynsii</i> ¹	Meat								2.16%
<i>Chrysophyllum lacourtianum</i>	Fruit	1.48%							
<i>Cissus dinalagei</i>	Fruit		0.98%	1.52%		2.99%	16.13%		0.72%
<i>Crudia laurentii</i>	Fruit			2.27%					2.16%
<i>Dialium corbisieri</i>	Fruit/leaves/ Flowers								2.88%
<i>Dialium</i> sp.	Fruit/leaves	3.70%			4.76%				
<i>Entandrophragma</i> sp.	Leaves								0.72%
<i>Ficus</i> spp.	Fruit/flowers	20.00%	3.43%		28.57%	22.39%	25.8%	22.22%	1.44%
<i>Funtumia elastica</i>	Fruit		0.98%						
<i>Garcinia cola</i>	Fruit			2.27%					
<i>Garcinia species</i>	Fruit	0.74%							
<i>Gilbertiodendron dewevrei</i>	Leaves/seeds		1.96%					5.56%	
<i>Haumania liebrechtsiana</i>	Pith	11.85%	7.35%	12.88%					2.16%
<i>Irvingia gabonensis</i>	Seed			13.64%					
<i>Irvingia wombulu</i>	Fruit	2.22%							
<i>Klainedoxa gabonensis</i>	Fruit/leaves								1.44%
<i>Macaranga</i> sp.	Leaves								0.72%
<i>Musanga cercropioides</i>	Fruit	0.74%	0.49%					5.56%	
<i>Nauclea diderichii</i>	Leaves	3.70%	8.82%						
<i>Omphalocarpum mortehanii</i>	Leaves								1.44%
<i>Palisita</i> sp.	Leaves/pith								0.72%
<i>Pancovia laurentii</i>	Fruit/seeds	1.48%							
<i>Paramacrolobium coeruleum</i>	Fruit/leaves	0.74%							
<i>Parinaria excelsa</i>	Fruit	0.74%							
<i>Polyalthia suaveolens</i>	Fruit	4.44%	18.14%		4.76%	47.76%	32.25%		15.83%
<i>Pterygota beguaertii</i>	Fruit	2.22%							
<i>Scropholoes zenkeri</i>	Leaves	7.41%	13.24%	32.58%				11.11%	35.97%
<i>Staudtia stipitata</i>	Fruit		0.49%						0.72%
<i>Strombosia glaucescens</i>	Seeds							16.67%	3.6%
<i>Strombosia grandifolia</i>	Leaves								0.72%
<i>Strombosiopsis tetandra</i>	Fruit		6.37%						2.88%
<i>Strombosiopsis zenkeri</i>	Seeds		4.41%		4.76%				
<i>Trachyphylum braunianum</i>	Pith			7.58%					
<i>Treulia africana</i>	Fruit/seeds	1.48%	9.80%	18.18%					0.72%
<i>Uapaca guineensis</i>	Fruit/leaves	0.74%	11.76%						
Unknown sp.	Fruit/leaves/ Flowers	1.48%	0.49%	9.09%	23.81%	26.86%	12.90%	5.56%	0.72%
Unknown sp.	Fruit/leaves/ flowers	0.74%			19.04%		3.22%		
Unknown sp.	Fruit/leaves/ flowers	0.74%			14.28%		3.22%		

Light gray columns represent the fecal washing data sets. The dark gray cells represent the top three food items consumed for the behavioral washing data sets. ¹Several meat-eating events were observed in 2017, see Wakefield et al. [2019].

Table 2. Conditions under which the functional response and optimal diet models will give different results for Shannon's (H'), Simpson's (D) index, and SW evenness

Model	Shannon's index (H')	Simpson's index (D)	SW evenness index ($H'/\ln(N)$)
Index description	Combines evenness and richness into a single metric; assumes that sampling is from an infinitely large population	Measures the probability that two randomly sampled items in the diet are the same, and is a measure of concentration	Detects patterns due to shifts in the overall species availability such that when abundant species dominate, the value of the index will be higher
Functional response	High when fruit is available	Low when fruit is available	H' will parallel changes in N, but will depend weakly, if at all, on N
Optimal diet	Low when preferred fruits are available	Higher when a few food items dominate diets	Inversely related to overall food availability for high-quality items (fruit)

is reported in primatology and is only reported as a single metric in a feeding ecology paper [Potts et al., 2011; Erhart et al., 2018; Cui et al., 2019].

These dietary diversity indices generate different predictions about primate foraging models. Functional response models predict that Shannon's index will correlate positively with food density (Table 2). In contrast, Simpson's index is predicted to be lower when more food items are available for consumption. For SW evenness, functional response models predict that H' will parallel changes in N, but $H'/\ln(N)$ will depend weakly, if at all, on N since individuals are not selective in their choice of dietary items. Optimal diet models predict that Shannon's index will be lower during periods of the year when preferred or highly valued food items are available. In contrast, Simpson's index will be higher during periods of the year when a few highly dominant species are being consumed (Table 2). Meanwhile, $H'/\ln(N)$ should be inversely related to overall food availability, specifically for high-quality items, such as fruit. When high-quality items are abundant, SW evenness will be low. Under optimal diet models, H may increase with N, but the relationship is expected to be weaker than under functional response models and could be inversely related (Table 2).

Optimal diet models suggest that dietary items incorporated in a diet are based on decisions that maximize energy return and economic foraging effort [Altmann and Wagner, 1978; Harrison, 1984; Sayers et al., 2009]. Broadly, there are three significant components to optimal diet models. First, these models predict that every food item has a value equal to the energy content of the food minus the energy it takes to obtain that item (net energy return) [Harrison, 1984; Lambert and Rothman, 2015]. Second, these models rank all food items based on the net energy return [MacArthur and Pianka, 1966; Koenig et al., 1998].

Finally, the optimal diet is determined by starting with the highest-ranked item and consuming items in decreasing order of rank; thus, when high-value resources are available, dietary breadth decreases [Charnov, 1976; Altmann and Wagner, 1978; Richard, 1985]. Optimal diet models are essential when considering what will happen when high-quality foods are abundant, whereas functional response models better explain primate foraging decisions [e.g., Altmann and Wagner, 1978; Harrison, 1984]. Functional response and optimal diet models have been tested in studies of primate diets [Altmann, 1991; Heiduck, 1997; Doran et al., 2002; Chapman et al., 2004a; Sayers et al., 2009; Cui et al., 2019]; however, to our knowledge, none of these studies have used dietary diversity indices to test the predictions of these two models.

Bonobos (*Pan paniscus*) are considered primarily frugivorous and consume fruits, new leaves, insects, vertebrates, terrestrial herbaceous vegetation, and flowers [Kano and Mulavwa, 1984; White, 1986, 1992, 1998; Furuichi, 1989; Hohmann and Fruth, 2003; Serckx et al., 2015; Loudon et al., 2019; Wakefield et al., 2019]. Some populations may use fallback foods (e.g., bonobos living in forest-savannah mosaic habitats at Malebo [Serckx et al., 2015]). However, no direct test of optimal diet models has been undertaken using dietary diversity indices at Lomako Forest, in the Democratic Republic of Congo [White, 1998].

We aim to test the predictions of functional response and optimal diet models in bonobos, using dietary diversity to capture species richness and species evenness when comparing models. We characterize variation in bonobo dietary diversity between seasons, study periods, and two research camps within the same protected contiguous forest. We also consider the efficacy of using fecal washing to capture dietary diversity. We predict that if bonobo forag-

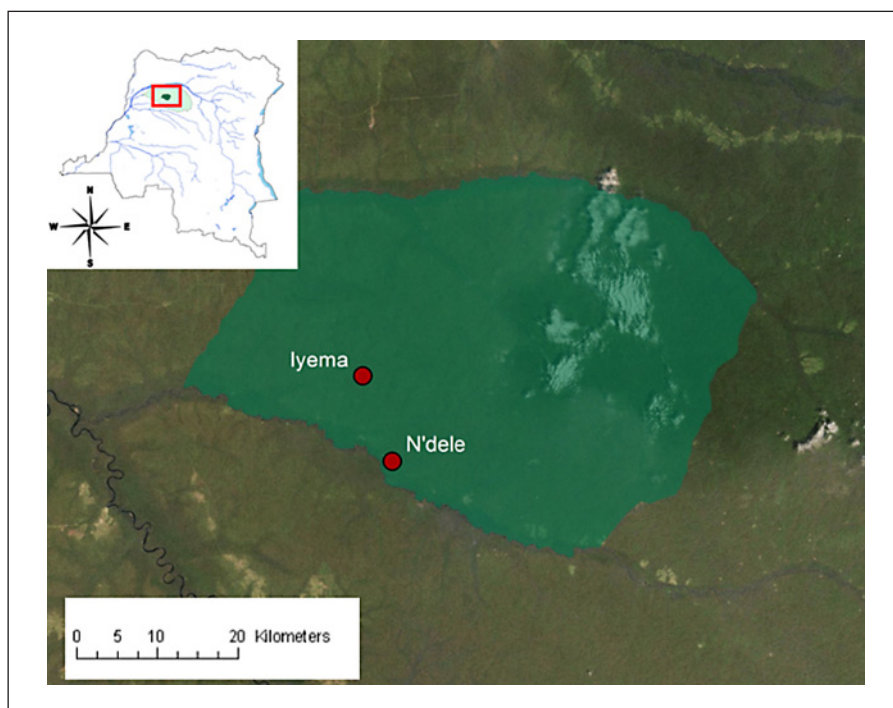


Fig. 2. Map of the Lomako Forest Reserve (dark green). Circles represent the two research camps within the same protected area where data were collected. Iyema and N'dele are approximately 15 km away from each other. The inset map shows the location in the Democratic Republic of the Congo.

ing behavior fits functional response models, then Shannon's index will follow seasonal shifts in measures of food density and abundance. In contrast, Simpson's index will be lower when there is an overall higher abundance of food items in the environment than when there is a lower abundance of food items. Under functional response models, SW evenness will be correlated with changes in species richness (N). If functional response models do not explain bonobo foraging patterns, this index will be weakly linked to species richness. Suppose optimal diet models better explain bonobo foraging strategies. In that case, Shannon's index will be lower during periods of the year when fewer items are available for consumption and high-value items are abundant. Comparatively, we predict SW evenness to be inversely related to food availability. Simpson's index will be higher during periods of the year when a few dominant species and less high-quality food items were consumed. High-value food items, in this case, fruit, are considered high-value food items under the model predictions for optimal diet models.

Materials and Methods

Study Camps

Noninvasive behavioral observations and fecal washings were collected over 7 field seasons (Table 3) between 1984 and 2017 at Iyema and N'dele field camp in Lomako Forest Reserve,

Tshuapa Province (formerly Equateur Province), Democratic Republic of the Congo (Fig. 2). Iyema field camp ($00^{\circ}55'N$, $21^{\circ}06' E$) consists of a trail system encompassing approximately 30 km^2 . Behavioral observations and preliminary genetic analyses suggest 26–66 individual bonobos in the trail system surrounding the Iyema camp, likely in two or more communities [Bertolani, pers. commun.; Sakamaki, pers. commun.; Brand et al., 2016]. The study area consists mostly of undisturbed primary forest with an understory plant community dominated by *Marrantacea* species. Several small streams run through the study area, but swamp forest, seasonally inundated forest, and homogenous *Gilbertiodendron* stands are relatively rare [Cobden, 2014]. N'dele is located about 15 km southeast of Iyema (Fig. 2) and consists of a 40-km^2 trail system. N'dele contains the overlapping ranges of two bonobo communities: Bakumba and Eyengo. Between 1983 and 1985, a group formed around immigrating females and inhabited the region before transitioning into the Bakumba community [White and Wood, 2007]. The study area at N'dele includes a mosaic of forest types, including secondary forest and homogenous *Gilbertiodendron* forest, but is mostly undisturbed primary forest. Several other habitat types at N'dele include streams, swamp forest, swamp grassland, and river habitats [White, 1992].

Data Collection

We collected dietary diversity information using 2 years of fecal washing data and 7 years of behavioral observation using two methods (Table 3). We calculated yearly and monthly Shannon's, Simpson's, and SW evenness diversity indices for each study period (1984/1985, 1991, 1995, 2007, 2009, 2014, and 2017) using the frequency of a particular plant species consumed using the "vegan" package in R version 3.4.3 [R Core Team,

Table 3. Study periods with sample size and methods used in a study of bonobo feeding ecology at N'dele and Iyema, Lomako Forest, Democratic Republic of the Congo

Months of data collection	Site	Method	Hours of observation	Community size	Number of fecal samples collected
Oct. 1984 to July 1985	N'dele	Behavioral observation	248.0	~85	–
June to Sept. 1991	N'dele	Behavioral observation	43.3	~85	–
July to Aug. 1995	N'dele	Behavioral observation	26.8	~85	–
July 2007	N'dele	Fecal washing	–	–	7
July 2009	N'dele	Fecal washing	–	–	52
July 2009	Iyema	Fecal washing	–	–	22
June to July 2014	Iyema	Behavioral observation	9.75	~26–66	–
June to Oct. 2017	Iyema	Behavioral observation	176.5	~26–66	–

2017; Oksanen et al., 2013]. We recorded feeding behavior during focal follows and group scans, identifying which individuals were eating, what they were eating, and the plant part they were eating at each time point [Altmann, 1974]. We also recorded the plant food species and plant parts consumed during both the focal observations and group scans. We followed nesting parties from their night nests or as we contacted them while walking trails. We recorded party composition, social behavior, activity, and GPS location during 15-min scans. We recorded food items introduced to the mouth, plant parts eaten and identified food items down to species level for calculating the different diversity indices.

The fecal washing data sets used 80 noninvasively collected fecal samples from underneath bonobo night nests [White, 1992]. We transported fecal samples to the camp at N'dele. We identified seeds to species level and counted them to obtain approximate amounts of each fruit eaten. We estimated the percentage fiber of each sample to approximate the amount of fiber recently consumed.

We used phenology transects to measure seasonal food abundance using the transect methods in Chapman et al. [1992]. We marked known bonobo food species trees located within 3 m of each transect and scored them monthly for young leaves, fruit, and flowers on a 0–4 scale, where 0 is 0% of a particular resource (fruit, new leaves, or flowers), 1 is 1–24%, 2 is 25–49%, 3 is 50–74%, and 4 is 75–100% of a particular food resource. When fruit was present on the tree, we recorded the percentage of ripe fruit by examining the total area of the tree crown and estimating the percentage (0–4) of that area covered by ripe fruit [Chapman et al., 1992, 1994]. We calculated food availability indices (FAI) following Mitani et al. [2002]. While our measure of fruit abundance is crude, it is the standard established by Chapman et al. [1992] and was used to make our fruit abundance data comparable to chimpanzee sites, like Ngogo [Mitani et al., 2002]. To quantify seasonal shifts in fruit abundance in 2017, we monitored four 1-km phenology transects with 513 marked trees of 27 different species once a month during the entire study period, and in 2007 we monitored two 1-km phenology transects with 53 marked trees of 29 species once a month during the study period. To evaluate prevalent food items for each season, we determined the three most dominant species in the diet for that year for only the behavioral observation data sets (Table 1).

Data Analysis

To test if each dietary diversity index depended on the month or year it was collected, we created a dissimilarity matrix for each diversity index to see if diversity indices were comparable given the long-time spans between data sets. We ran Mantel tests on each diversity index's dissimilarity matrix and the time dissimilarity matrix to determine whether they correlated. To test the conditions under which the functional response and optimal diet models will give different results, we ran Kruskal-Wallis tests separately on each index (Shannon's, Simpson's, and SW evenness), comparing between methods and then within methods but across two research camps within the same protected area. During the behavioral observation data collection, food items were identified when bonobos entered a feeding patch. The tree or food type was identified, and then the plant part was identified as the feeding bout began. We calculated the Shannon index as $H' = \sum [p_i \log p_i]$, where p_i is the proportion of species i in the sample area [Pielou, 1974]. We calculated Simpson's index as $D = \sum (n_i^2)$, where n_i represents the probability that two randomly selected individuals in the community belong to the same category [Simpson, 1949]. We report indices based on fecal washing and behavioral observations separately. We used Kruskal-Wallis tests in R to test differences in dietary diversity indices using behavioral observations and fecal washing. Correlating the seeds to plant species was done by trained local guides for the fecal washing data sets. Percent fiber was estimated by taking the weight before washing and after washing to estimate the approximate weight of the fiber in the fecal sample. We used a Kruskal-Wallis test to test for differences in dietary diversity across two research camps within the same protected area (Iyema vs. N'dele) and between study periods for each method. Sampling was unequal between study periods, but dietary indices weight the values according to richness and evenness, accounting for differences in sample size, and allow comparisons across different sample sizes and across time and space [Lehman and Tilman, 2000; Mittelbach and McGill, 2019]. We compared the FAI calculated from our available monthly phenology data to two diversity indices calculated per month for 2017. We used linear regression to test whether food availability was related to dietary diversity as measured using the three diversity indices under the predictions of functional response models, using FAI to measure food quantity. We used “ggplot2” to visualize our data [Wickham, 2009].

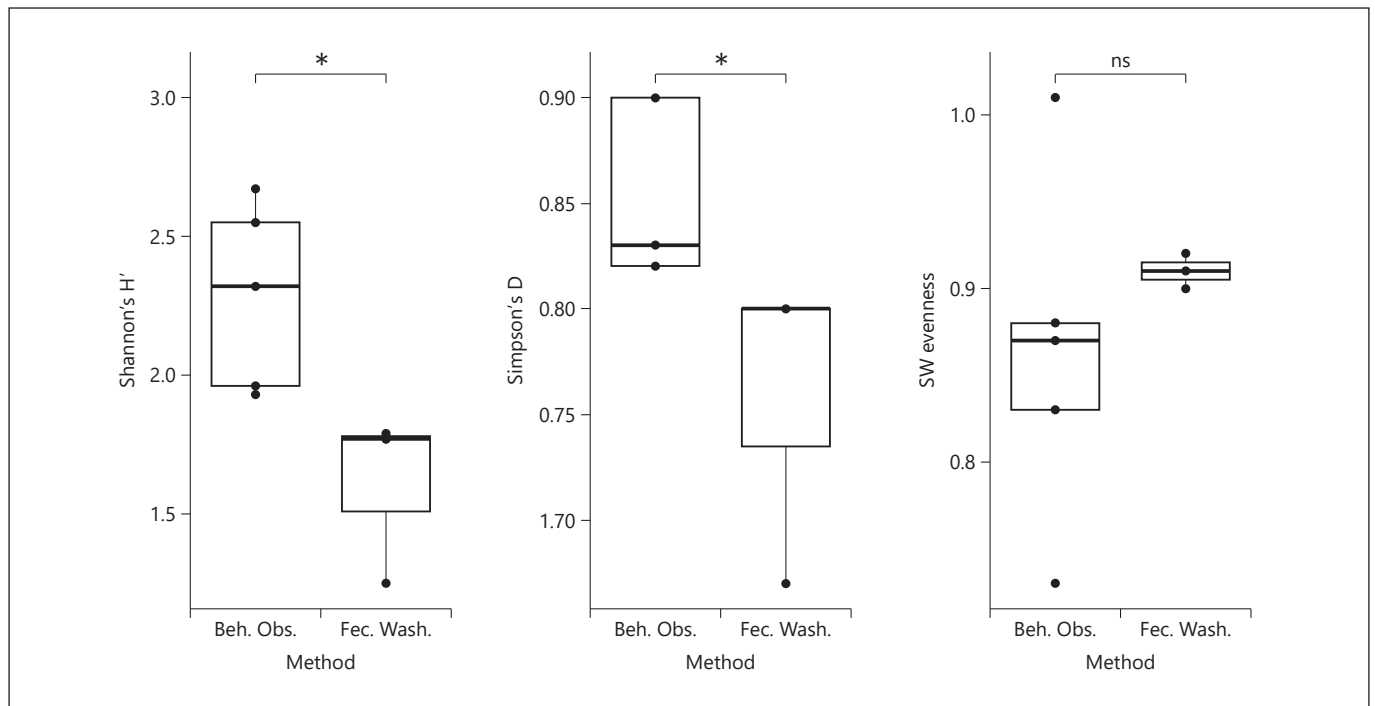


Fig. 3. The method comparison (behavioral observation vs. fecal washing) for the three indices (Shannon's, Simpson's, and SW evenness). Asterisks indicate significant differences ($p < 0.05$). Shannon's and Simpson's indices showed significant differences.

Results

Percentage of Foraging by Species and Food Type

Highly consumed items varied by study period and included *Anthoclitandra robustior* (20149), *Antiaris toxicaria* (1984), *Celtis mildbraedii* (1984, 2017), *Ficus* spp. (1984, 2014), *Irvingia gabonensis* (1995), *Polyalthia suaveolens* (1991, 2017), *Scropholoes zenkeri* (1991, 1995, 2017), *Strombosia glaucescens* (2014), *Treculia africana* (1995), and *Uapaca guineensis* (1991) (Table 1). Species richness (N) of food items varied between study periods: bonobos at N'dele consumed 25 (1984–1985), 19 (1991), 9 (1995), 7 (2007), and 4 (2009) species, while those at Iyema consumed 7 (2009, 2014) and 24 (2017) species (Table 1). Most of the top three food items across years are fruit, but *Scropholoes zenkeri*, a top food item consumed for 1991, 1995, and 2017, is notable because only the leaves of this tree are consumed (Table 1).

Dietary Diversity Variation by Method, Camp, and Study Period

The results of the Mantel tests for the time matrix compared to Shannon's diversity index (H') ($R = -0.048$; $p = 0.238$), Simpson's diversity index (D) ($R = 0.041$;

$p = 0.483$), and SW evenness ($R = 0.047$; $p = 0.416$) were all not significantly different across time indicating that the variation in diversity index was not a consequence of the time between sampling periods. Overall, Shannon's diversity index (H') ranged from 1.25 to 2.67, Simpson's diversity index (D) ranged from 0.10 to 0.33, and SW evenness ranged from 0.73 to 1.01. The mean dietary diversity indices for all study periods for N'dele were $H' = 2.04 \pm 0.58$, $D = 0.18 \pm 0.09$, and SW evenness = 0.88 ± 0.03 while for Iyema they were $H' = 2.02 \pm 0.28$, $D = 0.18 \pm 0.02$, and SW evenness = 0.88 ± 0.14 (Table 4).

Behavioral observation had a significantly higher Shannon's (H') index than fecal washing data with a mean difference of 0.51 (Kruskal-Wallis: $H = 5$, $df = 1$, $p = 0.03$). Simpson's (D) index for behavioral observation was significantly lower than for fecal washing data with a mean difference of 0.10 (Kruskal-Wallis: $H = 5$, $df = 1$, $p = 0.03$). The SW evenness index did not differ significantly between different methods (Fig. 3). We found no significant differences between two research camps within the same protected area (Iyema and N'dele) for Shannon's H' , Simpson's D , and the SW evenness index (Fig. 4) for behavioral observation data sets. There were no significant

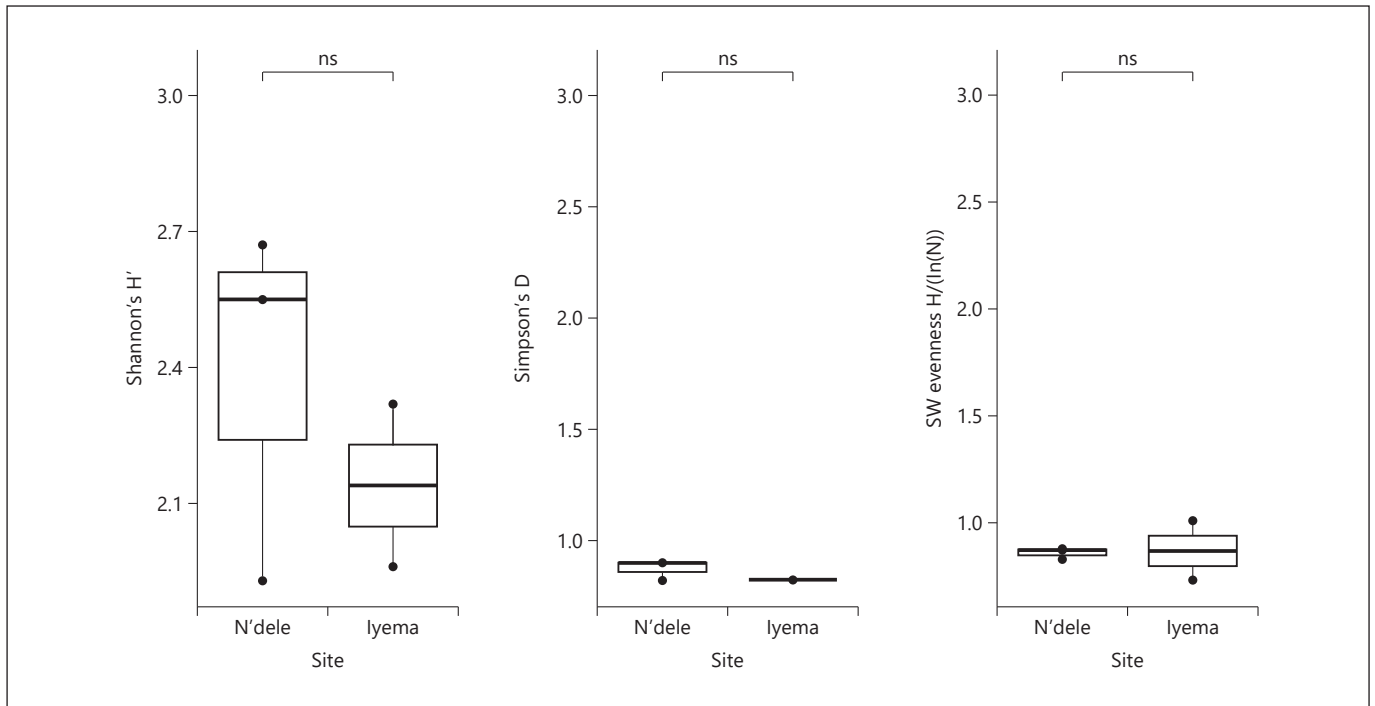


Fig. 4. Two research camps within the same protected area (N'dele vs. Iyema) for the three indices (Shannon's, Simpson's, and SW evenness). Asterisks indicate significant differences ($p < 0.05$). No significant differences were found between the two research camps within the same protected area.

Table 4. Yearly diversity indices for bonobos at two sites in Lomako Forest, Democratic Republic of the Congo

Year	Months of data collection	Shannon's H'		Simpson's D		SW evenness	
		N'dele	Iyema	N'dele	Iyema	N'dele	Iyema
1984/1985	10	2.67	–	0.10	–	0.83	–
1991	4	2.55	–	0.10	–	0.87	–
1995	2	1.93	–	0.18	–	0.88	–
2007	1	1.79	–	0.20	–	0.92	–
2009	1	1.25	–	0.67	–	0.90	–
2009	1	–	1.77	–	0.80	–	0.91
2014	2	–	1.96	–	0.17	–	1.01
2017	6	–	2.32	–	0.18	–	0.73
Mean		2.04	2.02	0.18	0.18	0.88	0.88

Shaded cells indicate data from fecal washing. Other cells indicate data from behavioral observation.

differences in all three diversity indices between study periods (Kruskal-Wallis: $H = 7$, $df = 7$, $p = 0.43$).

Dietary Diversity and FAI

There is a large range of variation in monthly dietary diversity indices (Table 5). Comparing the fruit, new leaf,

and flower availability data for Iyema in 2017, we found that August had the highest fruit availability (Fig. 5). We regressed Shannon's (H') index against ripe fruit availability ($F = 0.013$, $df = 1, 3$, $p = 0.91$, $R^2_{adj} = -0.32$), flower availability ($F = 5.4$, $df = 1, 3$, $p = 0.65$, $R^2_{adj} = -0.23$), and new leaf availability ($F = 0.24$, $df = 1, 3$, $p = 0.10$, R^2_{adj}

Table 5. Monthly dietary diversity indices for Shannon's H' , Simpson's D, and Shannon-Weiner evenness

Year	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1984/1985	1.58; 0.26; 0.88	2.10; 0.17; 0.85	0.89; 0.46; 0.81	0.84; 0.58; 0.60	1.31; 0.29; 0.94	2.17; 0.14; 0.90	0.95; 0.44; 0.86			0.87; 0.50; 0.79	1.59; 0.24; 0.89	1.50; 0.24; 0.93
1991						1.64; 0.22; 0.92	2.10; 0.16; 0.82	1.36; 0.26; 0.98	1.45; 0.33; 0.75			
1995							1.34; 0.67; 0.83	1.67; 0.20; 0.93				
2007							1.79; 0.80; 0.92					
2009							1.25; 0.67; 0.90					
2009							1.77; 0.80; 0.91					
2014							1.63; 0.08; 0.91					
2017						1.60; 0.29; 0.77	1.43; 0.39; 0.69	1.61; 0.28; 0.73	1.77; 0.23; 0.81	0.87; 0.50; 0.79		

Shaded rows represent data from Iyema, Lomako Forest, Democratic Republic of the Congo. Unshaded rows are data from N'dele, Lomako Forest, Democratic Republic of the Congo. Indices are presented in the following order: Shannon's H' ; Simpson's D; SW evenness.

= 0.52). Fruit availability for July 2017 and July 2007 was similar (online suppl. Tables 1 and 2; for all online suppl. material, see www.karger.com/doi/10.1159/000519722). However, Iyema appears to have more species of fruit available while N'dele has fewer fruit species but more fruit available on those trees in July (online suppl. Tables 1 and 2).

Shannon's diversity ranged from 0.86 to 1.77 for this period, whereas Simpson's diversity index ranged from 0.34 to 0.5. In 2017, the decrease in dietary diversity during October occurred when food availability was highest. Comparatively, September had relatively low fruit availability (Fig. 5). Three species, *Scropholoes zenkeri* (35.97%), *Polyalthia suaveolens* (15.89%), and *Celtis mildbraedii* (13.67%), were highly dominant in the diet (Table 1). All three species had relatively high numbers of available fruit, new leaves, and flowers during September, the month with the highest Simpson's index. The percent of trees with fruit, new leaves, and flowers during September were *Scropholoes zenkeri* (fruit: 0%, new leaves:

54.55%, flowers: 0%), *Polyalthia suaveolens* (fruit: 10.20%, new leaves: 93.88%, flowers: 24.49%), and *Celtis mildbraedii* (fruit: 0%, new leaves: 0%, flowers: 50.00%) (online suppl. Table 1).

Discussion/Conclusion

Anthoclitandra robustior (2014), *Antiaris toxicana* (1984), *Celtis mildbraedii* (1984, 2017), *Ficus* spp. (1984, 2014), *Irvingia gabonensis* (1995), *Polyalthia suaveolens* (1991, 2017), *Scropholoes zenkeri* (1991, 1995, 2017), *Strombosia glaucescens* (2014), *Treculia africana* (1995), and *Uapaca guineensis* (1991) were our top consumed food items. *Scropholoes zenkeri* is the only food item whose leaves are primarily consumed. As for *Strombosia glaucescens* and *Irvingia gabonensis*, bonobos primarily consume the seeds of the fruit. All of the other top food items per year are fruit, which for frugivorous bonobos is a preferred high-quality food item. Additionally, for those

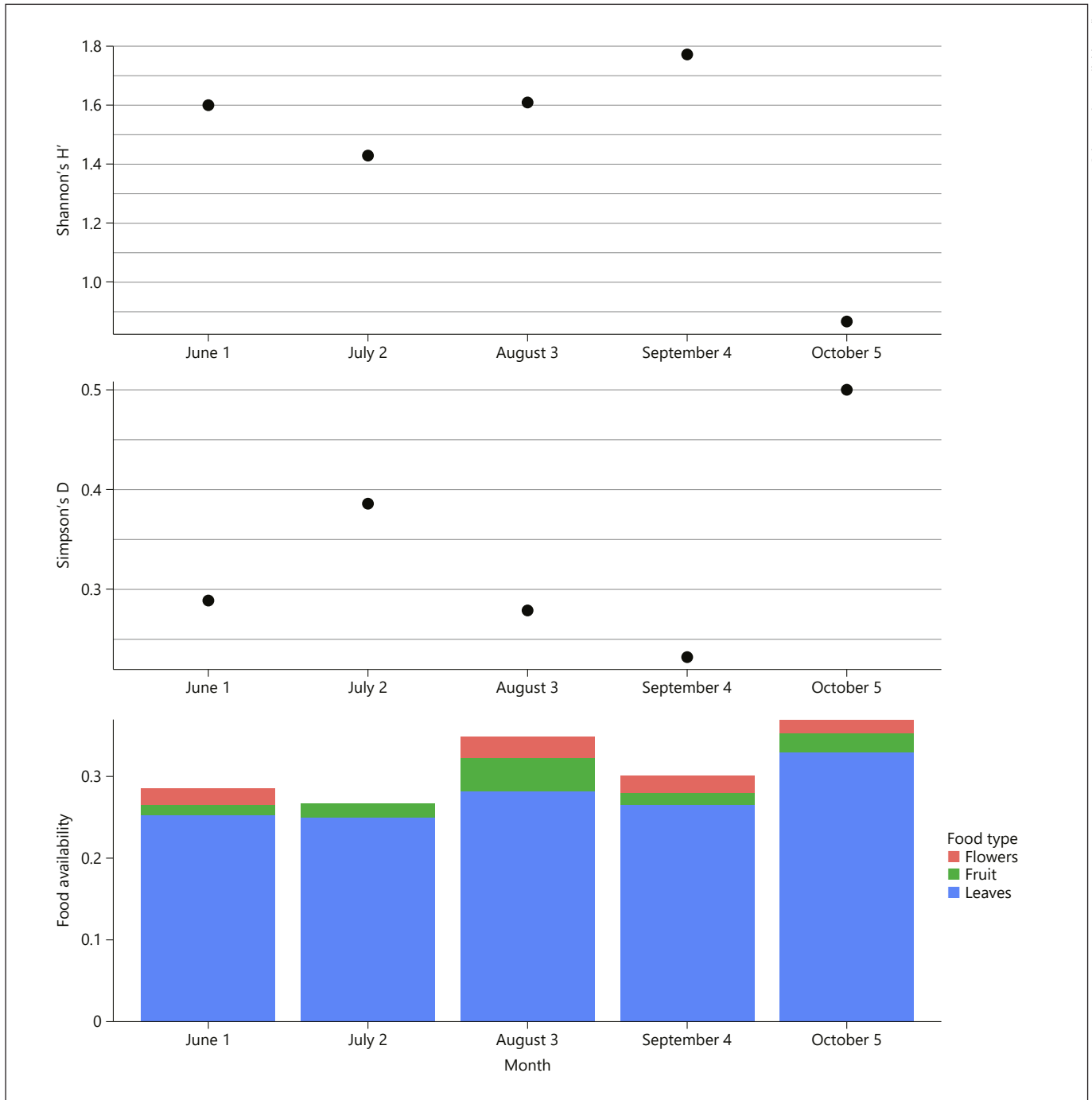


Fig. 5. Monthly comparison of FAI, Shannon's H' , Simpson's D , and SW evenness for bonobos at Iyema, Lo-mako, Democratic Republic of the Congo, from June to October 2017.

years with the highest Shannon's and lowest Simpson's index the most frequently consumed food item is the high-quality fruits like *Antiaris toxicana*, *Celtis mildbraedii*, and *Ficus* spp. (Tables 1 and 2). For the monthly di-

etary diversity indices, again those months with high Shannon's index and low Simpson's tend to be the months where high-quality fruit items are available and consumed at higher rates; e.g., in October of 2017, *Ficus* spp.

were the primary food items consumed (Fig. 5). These patterns are consistent with the predictions of optimal diet models.

We found that Shannon's indices, which assess dietary evenness and richness, were lower when fewer items were available for consumption. Simpson's index was higher during periods of the year, where a few highly dominant species and less high-value food items were consumed. SW evenness indices had a weak inverse relationship with food availability, supporting the predictions of optimal diet models (Fig. 5). Based on the results of the linear regressions, abundance was not significantly related to dietary diversity indices, possibly indicating that bonobos do not select food under the functional response model for the periods where we collected data. Shannon's indices were lower when fewer items were available for consumption and higher when high-value items were abundant, fitting with the predictions of optimal diet models.

These results demonstrate that measures of bonobo dietary diversity are dependent on the method. Fecal washing data yielded significantly lower Shannon's diversity index and Simpson's diversity index than behavioral observation. This result is not surprising due to the loss of information that occurs with fecal washing [Rothman et al., 2012; Edwards and Ullrey, 1999]. Behavioral observation data collection confirms what is consumed by the individual and can consider the amount of time spent feeding on a particular dietary item. Thus, it is logical to assume that this method would be more accurate in measuring the diversity of food items consumed in the bonobo diet.

Bonobo diets are understood to be primarily frugivorous with new leaves, insects, vertebrates, terrestrial herbaceous vegetation, and flowers consumed at different rates at different field sites [Kano and Mulavwa, 1984; White, 1986, 1992, 1998; Furuichi, 1989; Hohmann and Fruth, 2003; Serckx et al., 2015; Loudon et al., 2019; Wakefield et al., 2019]. The extent to which forest ecology has shaped bonobo feeding ecology and bonobo foraging behavior is still debated today [Kano and Mulavwa, 1984; White and Wrangham, 1988; Kano, 1989; White and Wood, 2007; Cobden, 2014; Fruth and Hohmann, 2018; Loudon et al., 2019]. What is needed is long-term data on bonobo field sites, and our study provides that, along with much-needed measures of food availability [White, 1996; Gruber and Clay, 2016]. Bonobo foraging behavior exhibits variation depending on the environment [Kano and Mulavwa, 1984; Surbeck and Hohmann, 2008; Oelze et al., 2011; Fruth and Hohmann, 2018]. In a savannah-mosaic environment, fallback foods are important in the diet of bonobos in more secondary mosaic environments

[Serckx et al., 2015]. The tropical forests bonobos inhabit are characterized by a high abundance of dense food patches and ubiquitous terrestrial herbaceous vegetation, yet long-term measures of consumption paired with food availability are important for understanding what foraging models structure feeding behavior [White and Wrangham, 1988; White, 1996; Gruber and Clay, 2016]. Our study suggests that in productive, intact, primary forests, bonobo foraging strategies may fit with the predictions of optimal diet models rather than fallback food models as found at other more mosaic habitats [Serckx et al., 2015; Oelze et al., 2016; Loudon et al., 2017]. Our approach using dietary diversity indices to examine these models is just a piece of the puzzle in understanding the variation in bonobo foraging strategies across bonobo field sites.

One of the strengths of our approach is that diversity indices make data from different field data collection periods easily comparable and allow for a direct comparison across different field sites. Additionally, they shift in predictable ways that make them a good tool for testing foraging models, especially when using multiple diversity indices, as we did in this study. The weakness of using a diversity index is that it does compress data losing resolutions. Thus, we recommend including the frequencies of food item consumption along with the different dietary diversity indices (e.g., Tables 1, 4 and 5). Additionally, we must be careful because our comparisons between different periods/sites have unequal sampling. Another weakness is our sample sizes are small for some study periods. However, it might be expected that the length of the study period used to calculate the diversity index matters. We tested for similarity in adjacent months to the same month in different years, and date of collection did not drive the pattern in the three diversity indices.

We recommend using all of Shannon's, Simpson's, and SW evenness indexes on behavioral observations in the future, as each index has its strengths and weaknesses. Most primatology papers only report one of the indices, and using all three gives a more complete picture. Fecal washing data sets are helpful in certain circumstances and may be used to gain a rough picture of the diet when other data are challenging to obtain. Our results need to be taken as a first attempt to understand the foraging behavior of the Lomako Forest bonobos and need to be evaluated in light of the limitations of using previously collected data sets. These sample sizes are small, and ideally, there would be even sampling across study periods, but as the logistics of studying primates are complicated, especially in light of the COVID-19 pandemic, utilizing diversity indices to answer questions about primate foraging

Table 6. Comparisons of dietary diversity indices across hominoids

	Bonobo, <i>Pan paniscus</i>		Eastern chimpanzee, <i>Pan troglodytes schweinfurthii</i>			Mountain gorilla, <i>Gorilla gorilla beringei</i>	Müller and agile gibbon, <i>Hylobates muelleri</i> × <i>agilis</i>
	N'dele ¹	Iyema ¹	Ngogo ²	Kanyawara ²	Budongo ³	Karisoke ⁴	Barito Ulu ⁵
Months of data collection	18	9	19	19	16	17	12
Mean Shannon's index	2.04	2.02	1.55	1.78	1.78	1.55	2.67
Range of Shannon's index	1.25–2.67	1.77–2.32	–	–	1.37–2.29	0.12–2.17	1.80–3.60

¹ This study. ² Potts et al. [2011]. ³ Newton-Fisher [1999]. ⁴ Watts [1985]. ⁵ McConkey et al. [2003].

behavior is necessary. Additionally, the strength of these dietary indices lies in that they weigh the values according to richness and evenness, accounting for differences in sample size from previously collected data sets [Lehman and Tilman, 2000; Mittelbach and McGill, 2019].

Our results appear to support the predictions of the optimal diet model and not the functional response model. Abundance did not relate to consumption using dietary diversity indices, indicating that bonobos are not selecting food under the functional response model. This interpretation is, however, preliminary given the limited sample size. Thus, when understanding dietary diversity and its relationship to bonobo diets, optimal diet models and optimizing energy return may be the main factor in structuring bonobo foraging strategies. Bonobos as optimal foragers seem to suggest that we need to incorporate aspects of optimality into future models of great ape foraging research.

Dietary Diversity Comparisons across Apes

Among apes, the dietary diversity in the Lomako Forest bonobos is relatively high, particularly compared to chimpanzees from multiple sites (Table 6). However, our results need to be considered with the caveat of our small sample size. Our data are limited in the hours of observation and months of observation when compared to other species. Interestingly, gibbons and bonobos exhibit similarly high levels of dietary diversity, which may be due to behavioral or ecological similarities [Newton-Fisher, 1999; McConkey et al., 2003; Kim et al., 2012; Tutin and Fernandez, 1993]. Investigations into the plastic and flexible nature of dietary diversity of several species have documented intraspecific variation including, e.g.: gorillas, *Gorilla gorilla beringei* [Watts, 1984]; red colobus, *Procolobus tephrosceles* [Chapman and Chapman, 1999]; black and white colobus, *Colobus guereza* [Harris and

Chapman, 2007]; *Cercopithecus* spp. [Chapman et al., 2004b]; chimpanzees, *Pan troglodytes* [Potts et al., 2011]; Strepsirrhines [Kappeler et al., 2017].

We see the potential for future investigations to elucidate some of the remaining challenges to understanding bonobo diets. Examining the extent of diversity captured by fecal washing by focusing on seed dispersal and fiber breakdown through comparisons between behavioral observation, fecal washing, and genetic barcoding methods would be interesting as an avenue of future research. Future research projects will determine if a correction factor could be applied to fecal washing data to estimate dietary diversity indices. Additionally, bonobos appear to be optimal foragers and understanding how fruit quality and fruit size affect foraging decisions would be an ideal avenue for future research.

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Statement of Ethics

This research was completed with the approval of the University of Oregon's Institutional Animal Care and Use Committee (AUP-17-10). Research abided by the International Primatological Society's Code of Best Practices for Field Primatology and the American Society of Primatologist's Principles for the Ethical Treatment of Human Primates and followed the legal requirements laid out by the Democratic Republic of the Congo government.

Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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References

- Albrechtsen L, Macdonald DW, Johnson PJ, Castelo R, Fa JE (2007). Faunal loss from bushmeat hunting: empirical evidence and policy implications in Bioko Island. *Environmental Science and Policy* 10: 654–667.
- Altmann J (1974). Observational study of behavior: sampling methods. *Behaviour* 49: 227–266.
- Altmann SA (1991). Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. *Proceedings of the National Academy of Sciences* 88: 420–423.
- Altmann SA, Wagner SS (1978). A general model of optimal diet. *Recent Advances in Primatology* 1: 407–414.
- Basabose AK (2002). Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. *American Journal of Primatology* 58: 1–21.
- Boubli JP, Dew JL (2005). *Tropical Fruits and Frugivores: The Search for Strong Interactors*. Berlin, Springer.
- Brand CM, White FJ, Wakefield ML, Waller MT, Ruiz-López MJ, Ting N (2016). Initiation of genetic demographic monitoring of bonobos (*Pan paniscus*) at Iyema, Lomako Forest, DRC. *Primate Conservation* 30: 103–111.
- Bray J, Emery Thompson M, Muller MN, Wrangham RW, Machanda ZP (2018). The development of feeding behavior in wild chimpanzees (*Pan troglodytes schweinfurthii*). *American Journal of Physical Anthropology* 165: 34–46.
- Chapman CA, Chapman LJ (1999). Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates* 40: 215.
- Chapman CA, Chapman LJ, Cords M, Gathua JM, Gautier-Hion A, Lambert JE, Rode K, Tutin CE, White LJ (2004b). Variation in the diets of *Cercopithecus* species: differences within forests, among forests, and across species. In *The Guenons: Diversity and Adaptation in African Monkeys* (Glenn ME, Cords M, eds.), pp 325–350. Boston, Springer.
- Chapman CA, Chapman LJ, Naughton-Treves L, Lawes MJ, McDowell LR (2004a). Predicting folivorous primate abundance: validation of a nutritional model. *American Journal of Primatology* 62: 55–69.
- Chapman CA, Chapman LJ, Wrangham R, Hunt K, Gebo D, Gardner L (1992). Estimators of fruit abundance of tropical trees. *Biotropica* 24: 527–531.
- Chapman CA, Wrangham R, Chapman LJ (1994). Indices of habitat-wide fruit abundance in tropical forest. *Biotropica* 26: 160–171.
- Charnov EL (1976). *Optimal foraging, the marginal value theorem*. *Theoretical Population Biology* 9: 129–136.
- Clutton-Brock TH (1974). Primate social organization and ecology. *Nature* 250(5467): 539–542.
- Cobden AK (2014). *Party Animals: Food, Sociality and Stress in Wild Bonobos (Pan paniscus) of Iyema, Lomako Forest, Democratic Republic of Congo*. PhD thesis, Emory University.
- Constantino PJ, Wright BW (2009). The importance of fallback foods in primate ecology and evolution. *American Journal of Physical Anthropology* 140: 599–602.
- Cui Z, Shao Q, Grueter CC, Wang Z, Lu J, Raubenhimer D (2019). Dietary diversity of an ecological and macronutritional generalist primate in a harsh high-altitude habitat, the Taihangshan macaque (*Macaca mulatta tcheliensis*). *American Journal of Primatology* 81: e22965.
- Doran DM, McNeillage A, Greer D, Bocian C, Mehlman P, Shah N (2002). Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling methods. *American Journal of Primatology* 58: 91–116.
- Edwards MS, Ullrey DE (1999). Effect of dietary fiber concentration on apparent digestibility and digesta passage in non-human primates. II. Hindgut- and foregut-fermenting folivores. *Zoo Biology: Published in Affiliation with the American Zoo and Aquarium Association* 18: 537–549.
- Erhart EM, Tecot SR, Grassi C (2018). Interannual variation in diet, dietary diversity, and dietary overlap in three sympatric strepsirrhine species in southeastern Madagascar. *International Journal of Primatology* 39: 289–311.
- Fruth B, Hohmann G (2018). Food sharing across borders: first observation of intercommunity meat sharing by bonobos at LuiKotale, DRC. *Human Nature* 29: 91–103.
- Furuichi T (1989). Social interactions and the life history of female *Pan paniscus* in Wamba, Zaire. *International Journal of Primatology* 10: 173–197.
- Furuichi T, Hashimoto C, Tashiro Y (2001). Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: examination of fallback foods. *International Journal of Primatology* 22: 929–945.
- Grassi C (2006). Variability in habitat, diet, and social structure of *Haplemur griseus* in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology* 131: 50–63.
- Gruber T, Clay Z (2016). A comparison between bonobos and chimpanzees: a review and update. *Evolutionary Anthropology: Issues, News, and Reviews* 25: 239–252.
- Hanya G, Chapman CA (2013). Linking feeding ecology and population abundance: a review of food resource limitation on primates. *Ecological Research* 28: 183–190.
- Harris TR, Chapman CA (2007). Variation in diet and ranging of black and white colobus monkeys in Kibale National Park, Uganda. *Primates* 48: 208–221.

- Harrison MJ (1984). Optimal foraging strategies in the diet of the green monkey, *Cercopithecus sabaeus*, at Mt. Assirik, Senegal. *International Journal of Primatology* 5: 435.
- Heiduck S (1997). Food choice in masked titi monkeys (*Callicebus personatus melanochir*): selectivity or opportunism? *International Journal of Primatology* 18: 487–502.
- Hohmann G, Fruth B (2003). Lui Kotal – a new site for field research on bonobos in the Salonga National Park. *Pan Africa News* 10: 25–27.
- Holling CS (1959). Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91: 385–398.
- Holling CS (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *The Memoirs of the Entomological Society of Canada* 97(suppl 45): 5–60.
- Kano T (1989). The sexual behavior of pygmy chimpanzees. In *Understanding Chimpanzees* (Heltne PG, Marquardt LA, eds.), pp 176–183. Cambridge, Harvard University Press.
- Kano T, Mulavwa M (1984). Feeding ecology of the pygmy chimpanzees (*Pan paniscus*) of Wamba. In *The Pygmy Chimpanzee* (Susman RL, ed.), pp 233–274. New York, Springer US.
- Kappeler PM, Cuzzo FP, Fichtel C, Ganzhorn JU, Gursky-Doyen S, Irwin MT, Ichino S, Lawler R, Nekaris KA-I, Ramanamanjato J-B, Radespiel U, Sauter ML, Wright PC, Zimmermann E (2017). Long-term field studies of lemurs, lorises, and tarsiers. *Journal of Mammalogy* 98: 661–669.
- Kim S, Lappan S, Choe JC (2012). Responses of Javan gibbon (*Hylobates moloch*) groups in submontane forest to monthly variation in food availability: evidence for variation on a fine spatial scale. *American Journal of Primatology* 74: 1154–1167.
- Koenig A, Beise J, Chalise MK, Ganzhorn JU (1998). When females should contest for food – testing hypotheses about resource density, distribution, size, and quality with hanuman langurs (*Presbytis entellus*). *Behavioral Ecology and Sociobiology* 42: 225–237.
- Krebs J (1984). Optimization in behavioural ecology. In *Behavioural Ecology: An Evolutionary Approach* (Krebs JR, Davies NB, eds.), pp 91–121. Oxford, Blackwell.
- Lambert J (2007). Seasonality, fallback strategies, and natural selection: a chimpanzee and cercopithecoid model for interpreting the evolution of hominin diet. In *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable* (Ungar PS, ed.), pp 324–343. Oxford, Oxford University Press.
- Lambert JE (1998). Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evolutionary Anthropology: Issues, News, and Reviews* 7: 8–20.
- Lambert JE, Rothman JM (2015). Fallback foods, optimal diets, and nutritional targets: primate responses to varying food availability and quality. *Annual Review of Anthropology* 44: 493–512.
- Lehman CL, Tilman D (2000). Biodiversity, stability, and productivity in competitive communities. *The American Naturalist* 156: 534–552.
- Leighton M (1993). Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. *International Journal of Primatology* 14: 257–313.
- Loudon JE, Kimel HM, Waller MT, Wakefield ML, Hickmott A, White FJ, Sponheimer M (2017). Pairing feeding observations with stable isotope data from bonobo (*Pan paniscus*) fecal samples from the Lomako Nature Reserve, Democratic Republic of the Congo. *American Journal of Physical Anthropology* 162: 267.
- Loudon JE, Wakefield ML, Kimel HM, Waller MT, Hickmott AJ, White FJ, Sponheimer M (2019). Stable isotope data from bonobo (*Pan paniscus*) faecal samples from the Lomako Forest Reserve, Democratic Republic of the Congo. *African Journal of Ecology* 57: 437–442.
- Lozano J, Moleón M, Virgós E (2006). Biogeographical patterns in the diet of the wildcat, *Felis silvestris* Schreber, in Eurasia: factors affecting the trophic diversity. *Journal of Biogeography* 33: 1076–1085.
- MacArthur RH, Pianka ER (1966). On optimal use of a patchy environment. *The American Naturalist* 100: 603–609.
- Magurran AE (1988). *Ecological Diversity and Its Measurement*. Princeton, Princeton University Press.
- Marshall AJ, Boyko CM, Feilen KL, Boyko RH, Leighton M (2009). Defining fallback foods and assessing their importance in primate ecology and evolution. *American Journal of Physical Anthropology* 140: 603–614.
- Marshall AJ, Wrangham RW (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology* 28: 1219–1235.
- McConkey KR, Ario A, Aldy F, Chivers DJ (2003). Influence of forest seasonality on gibbon food choice in the rain forests of Barito Ulu, Central Kalimantan. *International Journal of Primatology* 24: 19–32.
- McGrew WC, Baldwin PJ, Tutin CEG (1988). Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Assirik, Senegal. I. Composition. *American Journal of Primatology* 16: 213–226.
- McGrew WC, Marchant LF, Phillips CA (2009). Standardised protocol for primate faecal analysis. *Primates* 50: 363–366.
- Mitani JC, Watts DP, Lwanga JS (2002). Ecological and social correlates of chimpanzee party size and composition. In *Behavioural Diversity in Chimpanzees and Bonobos* (Boesch C, Hohmann G, Marchant LF, eds.), pp 102–111. Cambridge, Cambridge University Press.
- Mittelbach GG, McGill BJ (2019). *Community Ecology*. Oxford, Oxford University Press.
- Newton-Fisher N (1999). The diet of chimpanzees in the Budongo Forest Reserve, Uganda. *African Journal of Ecology* 37: 344–354.
- Oelze VM, Fuller BT, Richards MP, Fruth B, Surbeck M, Hublin J-J, Hohmann G (2011). Exploring the contribution and significance of animal protein in the diet of bonobos by stable isotope ratio analysis of hair. *Proceedings of the National Academy of Sciences* 108: 9792–9797.
- Oelze VM, Fahy G, Hohmann G, Robbins MM, Leinert V, Lee K, Eshuis H, Seiler N, Wessling EG, Head J, Boesch C, Kühl HS (2016). Comparative isotope ecology of African great apes. *Journal of Human Evolution* 101: 1–16.
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solyomos P, Stevens MHH, Wagner H (2013). Package “vegan.” *Community Ecology Package, Version 2(9)*: 1–295.
- Phillips CA, McGrew WC (2014). Macroscopic inspection of ape feces: what's in a quantification method? *American Journal of Primatology* 76: 539–550.
- Pielou EC (1974). *Population and Community Ecology: Principles and Methods*. Boca Raton, CRC Press.
- Potts KB, Watts DP, Wrangham RW (2011). Comparative feeding ecology of two communities of chimpanzees (*Pan troglodytes*) in Kibale National Park, Uganda. *International Journal of Primatology* 32: 669–690.
- Pyke GH, Pulliam HR, Charnov EL (1977). Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology* 52: 137–154.
- Raubenheimer D, Simpson SJ, Mayntz D (2009). Nutrition, ecology and nutritional ecology: toward an integrated framework. *Functional Ecology* 23: 4–16.
- R Core Team (2017). R: a language and environment for statistical computing.
- Richard AF (1985). *Primates in Nature*. Vol 4. New York, Freeman.
- Rothman JM, Chapman CA, Van Soest PJ (2012). Methods in primate nutritional ecology: a user's guide. *International Journal of Primatology* 33: 542–566.
- Sayers K, Norconk MA, Conklin-Brittain NL (2009). Optimal foraging on the roof of the world: Himalayan langurs and the classical prey model. *American Journal of Physical Anthropology* 141: 337–357.
- Serckx A, Kühl HS, Beudels-Jamar RC, Poncin P, Bastin J-F, Huynen M-C (2015). Feeding ecology of bonobos living in forest-savannah mosaics: diet seasonal variation and importance of fallback foods: bonobo diet in forest-savannah mosaics. *American Journal of Primatology* 77: 948–962.
- Shannon CE, Weaver W (1949). *A Mathematical Model of Communication*. Vol 11. Urbana, University of Illinois Press.
- Simpson EH (1949). Measurement of diversity. *Nature* 163: 688.
- Strier KB (2015). *Primate Behavioral Ecology*. Abingdon, Routledge.
- Surbeck M, Hohmann G (2008). Primate hunting by bonobos at LuiKotale, Salonga National Park. *Current Biology* 18: R906–R907.

- Tutin CEG, Fernandez M (1993). Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. *American Journal of Primatology* 30: 195–211.
- Tutin CEG, Fernandez M, Rogers ME, Williamson EA, McGrew WC (1991). Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. *Philosophical Transactions of the Royal Society of London Series B* 334: 179–186.
- Wakefield ML, Hickmott AJ, Brand CM, Takaoka IY, Meador LM, Waller MT, White FJ (2019). New observations of meat eating and sharing in wild bonobos (*Pan paniscus*) at Iyema, Lomako Forest Reserve, Democratic Republic of the Congo. *Folia Primatologica* 90: 179–189.
- Watts D (1984). Composition and variability of mountain gorilla diets in the Central Virungas. *American Journal of Primatology* 7: 323–356.
- White F (1986). Census and preliminary observations on the ecology of the black-faced black spider monkey (*Ateles paniscus chamek*) in Manu National Park, Peru. *American Journal of Primatology* 11: 125–132.
- White FJ (1992). Pygmy chimpanzee social organization: variation with party size and between study sites. *American Journal of Primatology* 26: 203–214.
- White FJ (1996). Comparative socio-ecology of *Pan paniscus*. In *Great Ape Societies* (McGrew WC, Marchant LF, Nishida T, eds.), pp 29–41. Cambridge, Cambridge University Press.
- White FJ (1998). Seasonality and socioecology: the importance of variation in fruit abundance to bonobo sociality. *International Journal of Primatology* 19: 1013–1027.
- White FJ, Wood KD (2007). Female feeding priority in bonobos, *Pan paniscus*, and the question of female dominance. *American Journal of Primatology* 69: 837–850.
- White FJ, Wrangham RW (1988). Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour* 105: 148–164.
- Wickham H (2009). Ggplot: using the grammar of graphics with R.
- Zhou Y-B, Newman C, Xu W-T, Buesching CD, Zaleski A, Kaneko Y, Macdonald DW, Xie Z-Q (2011). Biogeographical variation in the diet of Holarctic martens (genus *Martes*, Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists. *Journal of Biogeography* 38: 137–147.