RESEARCH ARTICLE

Importance of subterranean fungi in the diet of bonobos in Kokolopori

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Abstract

Nonstaple food is a food resource which sole consumption does not allow the maintenance of regular physiological functions, thus constituting a minor portion of an individual's diet. Many primates consume nonstaple food such as meat, insects, and fungi. Hypotheses on the dietary importance of nonstaple food include its role as fallback food and as source of specific nutrients. We tested these two hypotheses by investigating mycophagy (i.e., the consumption of fungi) in a population of wild bonobos in the Kokolopori Bonobo Reserve, DRC. Specifically, we examined the relationship between fungus consumption and various factors relevant to bonobo feeding ecology (i.e., fruit abundance and the consumption of other food types). Additionally, we measured the deviation from linear travel when bonobos searched for fungi to evaluate the nature of fungus consumption (e.g., opportunistic or targeted). Lastly, we examined the nutritional content of the major fungus species consumed (*Hysterangium bonobo*) to test whether this food item was potentially consumed as source of specific nutrients. We found that bonobos spent a higher proportion of their time feeding on fungi when fruit abundance was higher, indicating that fungi were not consumed as a fallback food. Moreover, bonobos deviated from linear travel when visiting fungus patches more than observed when visiting fruit patches, suggesting that they actively sought out fungi. Lastly, initial analyses suggest that *H. bonobo* samples contained high concentration of sodium. Collectively, these results suggest that subterranean fungi appear to be attractive food source to Kokolopori bonobos, and that mycophagy may serve to supplement nutrients, like sodium, in bonobo diet.

KEYWORDS
apes, fallback food, nutritional content, *Pan paniscus*, sodium, staple food

1 | INTRODUCTION

Food is a key resource influencing the life of animals. For instance, the availability of food strongly affects the distribution and density of animal taxa (e.g. Choquenot, 1998, Johnson & Sherry, 2001, Seiler et al., 2017, Wheelock, 1980), and the mechanical and biochemical properties of food are important factors in shaping individuals' anatomical traits (e.g. Lambert et al., 2004, Robinson & Wilson, 1998). Food resources are defined staple when their sole consumption is sufficient for individuals to maintain regular physiological functions (Marshall & Wrangham, 2007). Staple resources can thus seasonally constitute the major food source for a species. In contrast, nonstaple food does not allow individuals to survive in the absence of other food resources, thus only constituting a minor portion of the diet of a species (Marshall & Wrangham, 2007). Examples of non-staple food items include meat (Fedigan, 1990; Surbeck et al., 2009; Watts, 2020) and insects (Bogart & Pruetz, 2011; McGrew, 2014; Webster et al., 2014) for primates, salty rocks and soil for elephants and ungulates (Holdø et al., 2002; Lundquist & Varnedoe, 2006), as well as fungi and seeds for some rodents (Markova et al., 2020). A nonstaple food item may function at times as fallback food, that is, food consumed in periods when the preferred food is scarce (Marshall & Wrangham, 2007; Watts et al., 2012), or as a source of particular nutrients needed to meet specific dietary requirements (Hohmann et al., 2019; Lundquist & Varnedoe, 2006).

Feeding behaviors on nonstaple food items can be particularly informative for behavioral ecologists, because the availability of these food items can influence individuals' health (e.g. Bergstrom et al., 2019, Koops et al., 2019), and movement patterns (e.g. Grueter et al., 2018, McNaughton, 1988, Potts et al., 2015). In particular, it has been proposed that the availability of fallback food plays an important role in influencing the geographic and temporal distribution of many primate species (Grueter et al., 2009; Marshall et al., 2009), and the need to acquire specific nutrients can have important influence on their ranging and feeding behavior (e.g. Bogart & Pruetz, 2011, Grueter et al., 2018, Hanson et al., 2003, Hohmann et al., 2019, Matsubayashi et al., 2011, Reynolds et al., 2009).

Mycophagy, that is, the eating of fungi, is a feeding behavior which is widespread across animal taxa, including mammals (Claridge & Cork, 1994; Hanson et al., 2006; Trierveiler-Pereira, 2016), birds (Elliott & Vernes, 2019; Tanney & Hutchison, 2011), reptiles (Cooper & Vernes, 2011; Elliott, 2019), and arthropods (Bultman & Mathews, 1996; Hammond & Lawrence, 1989). Ecologically, mycophagy can play a crucial role in contributing to the overall health of forest ecosystems. In fact, most terrestrial plant species form a symbiotic relationship with mycorrhizal fungi to facilitate the uptake of nutrients (Maser et al., 2008), which generally enhances plant productivity and influences plant biodiversity and community structure (Kiers et al., 2000; Klironomos et al., 2000). By assisting with the dispersal of fungal spores, particularly of truffle-like hypogeous fungi which lack the ability to forcibly discharge their spores (Trappe, 2009), mycophagous animals are critical contributors to ecosystem health in ecosystems dependent on these fungi (Beenken et al., 2016;

Caldwell et al., 2005; Colgan & Claridge, 2002). Most mycophagous mammals can be classified as "opportunistic mycophagists," that is, they consume fungi occasionally when available or encountered and not as a staple food resource (Claridge & Trappe, 2005). In fact, in order for fungi to constitute an energetically viable food source, animals need specialized digestive systems able to break down the carbohydrates through fermentation by gut microorganisms, which is characteristic of only a small number of mammals mainly belonging to the marsupial taxon (Claridge & Cork, 1994; Claridge & Trappe, 2005; Claridge, 2002; Mcilwee & Johnson, 1998).

The majority of primates lack digestive systems with extensive fermentation capabilities necessary for the efficient extraction of macronutrients from fungi; thus fungi are commonly considered a relatively low-quality food resource for them (Claridge & Trappe, 2005; Hanson et al., 2006). Why a primate may engage in mycophagy is hypothesized to be a fallback food strategy adopted in periods when a preferred food source is scarce, and/or as a way to acquire particular nutrients otherwise lacking in the diet (Hanson et al., 2003).

Bonobos (*Pan paniscus*) are primarily frugivorous, although terrestrial herbaceous vegetation (THV) is consumed in significant proportions year round (Hohmann et al., 2006; Inogwabini & Matungila, 2009). Bonobo social groups, hereafter "communities," regularly fission into smaller parties that vary in size and composition (Furuichi et al., 2008; Mulavwa et al., 2008; Surbeck et al., 2015). Bonobos have been reported to consume various foods such as meat (Hohmann & Fruth, 2008), insects and honey (McGrew et al., 2007), aquatic plants (Hohmann et al., 2019) and fungi (Bermejo et al., 1994; Elliott et al., 2020; Kano, 1983). Due to their sporadic and often opportunistic consumption, these food items can be categorized as nonstaple food for this ape species. In the Kokolopori Bonobo Reserve, Democratic Republic of the Congo (DRC), we have observed bonobos consuming the sporocarps of at least two species of subterranean truffle-like mycorrhizal fungi, called Simbokilo (Kimura et al., 2015) and Iyango (S. Lucchesi, L. Cheng, E. G. Wessling, & M. Surbeck, unpublished data) in the local Bantu language of Longando. Simbokilo has been described by Elliott et al. (2020) as a new species *Hysterangium bonobo*, and is the predominant fungus consumed by this bonobo population (E. G. Wessling, personal communication). Local human inhabitants of the area use this fungus as bait for catching small game (Kimura et al., 2015), an indication of its palatability to various animals of the forest.

We examined the dietary role of mycophagy in the bonobo population of Kokolopori, to test whether fungi were consumed opportunistically, as a fallback food resource, or as potential source of particular nutrients. First, we investigated the relative importance of fungi in relation to other food types (i.e., fruits and THV) and tested whether fungi were consumed as a fallback food resource by examining the relationship between fungus-feeding behavior and food availability. If fungi were indeed a fallback food, we should expect the bonobos to feed on them in periods when the preferred food source (i.e., fruits) was scarce. Moreover, if fungi were a sought-after food item, we would expect bonobos to travel with the purpose of reaching locations where fungi could be found (Elliott et al., 2020; S. Lucchesi, personal observation). We therefore

measured the deviation from linearity in sections of daily foraging routes and evaluated if bonobos targeted fungi by traveling to them specifically, or if they consumed them along travel routes between food sources, which was largely dominated by fruits. Finally, we conducted preliminary nutritional analyses on one of the key fungus species that were consumed by the bonobos in Kokolopori, *H. bonobo*, to better understand whether the consumption of this fungus species was related to specific mineral composition.

2 | METHODS

2.1 | Ethic statement

All methods applied were strictly noninvasive. Permits to conduct research at the Kokolopori Bonobo Reserve, DRC, were granted by the Ministry of Research of the Democratic Republic of the Congo. This study complied with the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates (https://www.asp.org/society/resolutions/EthicalTreatmentOfNonHumanPrimates.cfm), as well as ethical guidelines on the use of animals from the former Department of Primatology in Max-Planck Institute for Evolutionary Anthropology (https://www.eva.mpg.de/primat/ethical-guidelines.html).

2.2 | Study site and population

We collected data on the feeding ecology of two neighboring bonobo communities, Ekalakala and Kokoalongo, in the Kokolopori Bonobo Reserve (Surbeck et al., 2017), central DRC, from October 2016 to February 2018. At the time of the study, Ekalakala consisted of 13 individuals including three adult males (≥15 years), five parous adult females (≥15 years), one nulliparous subadult female (10–15 years), and four immatures (i.e., infants/juveniles; <10 years). Kokoalongo comprised 44 individuals including eight adult males, 13 parous and two nulliparous adult females, two subadult males, two subadult females, and 17 immatures at the time. Annual rainfall at Kokolopori was 2336 mm (averaged across 3 years from March 2016 until February 2019; monthly average = 195 mm; range = 16–352 mm). Generally, there are two relatively dry periods (June to September, and January to February) and two relatively wet periods (March to May, and October to December) at this site (L. Cheng, personal observation). Three predominant habitat types are present in the research area: (1) mixed mature forest on terra firma, (2) disturbed forest, and (3) seasonally inundated, riparian swamp forest occurring predominantly along the two major rivers crossing the study area. While the ecology of the fungus identified locally as Iyango and other potential fungus species consumed by bonobos need further exploration, the fungus most often consumed by bonobos in Kokolopori, *H. bonobo*, grows in both monodominant forests of *Gilbertiodendron dewevrei* that straddle streams and mature forests of *Brachystegia laurentii* (all authors, personal communication).

2.3 | Ranging and feeding observation

Teams comprising trained international students and local field assistants followed parties of each of the two communities daily from morning nests to night nests. All community members were habituated to researchers' presence before the onset of the study and were individually recognized. We recorded the identities of all individuals present in the party over 30-min intervals to measure a cumulative party composition (Mulavwa et al., 2008), and we calculated the daily *party size* as the daily average number of individuals present in the 30-min party compositions. During daily party follows we recorded the geographic location of all fruit (i.e., trees and lianas) and fungus patches (altogether referred to as feeding patches) on which the bonobos fed using a handheld GPS device (Garmin GPS 62). Bonobo parties were observed feeding on underground fungi in multiple locations of their home range, however they most frequently consumed them in dry forest stands dominated by *G. dewevrei* adjacent to the two main rivers crossing the research site (Figure 1). Once arriving to these areas, bonobos extracted the sporocarps of the subterranean fungi by digging into the ground. Typically, the vast majority of the individuals engaged in fungus-digging whenever this activity occurred in the party. To quantify feeding behaviors, we recorded the activity of all individuals in view using a group scan sampling method at 10-min intervals (Altmann, 1974). If at least one bonobo in the party was feeding, we recorded the food type (fruit, THV, fungi) and the species eaten; if party members were feeding on different food items, we recorded the food eaten by the majority of the individuals (Gilby et al., 2010). From these data, we calculated the proportion of fungus-, fruit-, and THV-feeding scans (out of all party scans) per community per day, as the number of party scans in which the majority of party members were feeding on the given food type on a given day, corrected by daily observation effort (i.e., the total number of party scans on that day). Bonobos of the same party fed on different food types on a given scan in only 0.6% of all group feeding scans ($N = 4200$). We did not have phenological data of fungus species consumed by the bonobos and therefore our data reflect solely bonobo fungus consumption (via group scan data), rather than objective measures of abundance. As a proxy for the availability of fruits in a given month, we calculated (separately for each community) a *Fruit Abundance Index* (FAI), which was previously extrapolated for this population (Lucchesi et al., 2021) based on the monthly fruit availability measure of Anderson et al. (2005). We first calculated the monthly FAI (*MFAI*) based on monthly phenological data of bonobo feeding trees and lianas along selected transects, as well as data on tree and liana size and abundance from floristic plots distributed evenly over the home ranges of each community (see Lucchesi et al. 2021). The calculation is as follows:
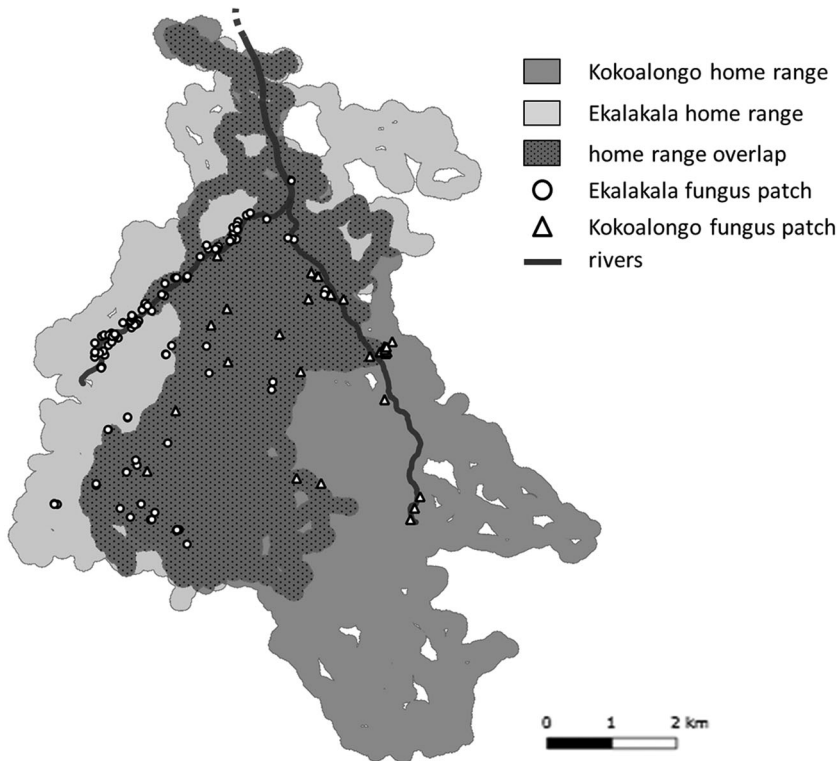
$$MFAI = \sum_i^S P_{im}B_i,$$

FIGURE 1 The home ranges of Ekalakala and Kokoalongo with the locations of fungus-feeding events on *Hysterangium bonobo*. The circles indicate fungus-feeding locations of Ekalakala, the triangles those of Kokoalongo

where P_{im} is the proportion of trees of species i in the phenology trail bearing ripe fruits in month m, B_i is the basal area of species i (i.e., the total cross-sectional area of tree trunks measured at 1.3 m above ground derived from floristic plot data; see above), and S is the total number of species. To obtain a more precise measure of the changes in fruit availability from one month to another, we then extrapolated this monthly index to create a daily FAI (*dFAI*) as below:

$$dFAI = A_i - \frac{(A_i - B_{i+1})}{d_i} * D,$$

where A is the *MFAI* value of a given month i, B is the *MFAI* value of the following month, d is the number of days in month i, and D is the day of the month for which the *dFAI* value is calculated.

2.4 | Statistical analyses

To evaluate whether variation in fungi consumption was associated with the consumption of fruits and THV, as well as overall fruit abundance, we used a generalized linear mixed model with a Poisson error structure (Baayen et al., 2008), with the *number of scans the majority of the party members fed on fungi* on a given day as the response variable. We included the *number of daily scans the majority of the party members fed on THV* and *fruits*, and daily *fruit abundance (dFAI)* as test predictors, and we controlled for the potential effects of *party size*, *community identity* and *daily rainfall* (which may affect fungus phenology; Johnson, 1994) on the response. Additionally, we included an autocorrelation term calculated as in Lucchesi et al.

(2021) to control for the likelihood that fungus-feeding scans were similar on days in close temporal proximity, and included the total number of scans on a day (log-transformed) as an offset term to account for variation in observation time. Finally, we included the random effect of date to account for uneven sampling over the study period.

To evaluate whether bonobos specifically sought out fungi and did not simply consume them opportunistically along their daily travel route between fruit patches, we tested whether the degree of deviation from straight-line travel between fruit patches was dependent on the food type (i.e., fungus or fruit) of the middle patch. Specifically, we measured the straight-line distance between three consecutive feeding patches, when the first and third patch were both fruit patches and the second patch was either a fruit patch or a fungus patch. We then calculated a *deviation from linearity index* by dividing the sum of the distances between the first and second patch and the distance between the second and third patch with the distance between the first and third patch (see Figure 2; Jang et al., 2019). A higher value of this index would indicate a larger deviation from linearity, which in turn implies less opportunistic discovery of the second feeding patch along travel routes and more goal-directed traveling specifically towards the location of that second patch. We ensured that at least one individual was consistently present in the party across the three locations to ensure that this index represents movement of individual group members and not a byproduct of the fission-fusion patterns of bonobo communities over the day. We used a linear mixed model with Gaussian error structure (Baayen et al., 2008) including the *deviation from linearity index* as

FIGURE 2 Schematic representation of the calculation of the *deviation from linearity index*. The index is calculated as (F1F2 + F2F3)/F1F3, where F1F2 is the straight distance between the first and second food patch, F2F3 is the straight distance between the second and third food patch, and F1F3 is the straight distance between the first and third food patch. (a) is the condition in which the second food patch is a *fruit patch*; (b) is the condition in which the second food patch is a *fungus patch*
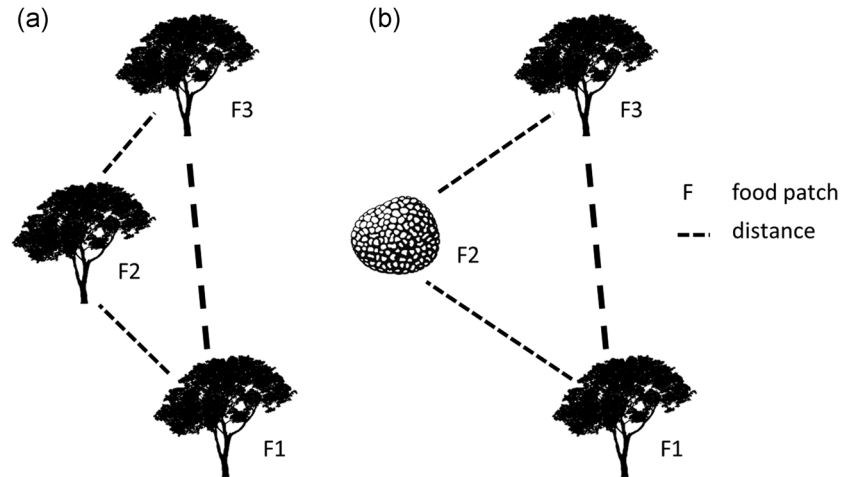
the response variable, and we included *whether the second feeding patch was a fruit patch or a fungus patch* as test predictor, while controlling for the influence of *dFAI* and *community identity* on the response. Finally, we included the random effect of date to account for uneven sampling across days.

All models were implemented in R (version 3.5.0; R Core Team 2018) using the function *lmer* and *glmer* of the R package "lme4" (version 1.1-17; Bates et al., 2014) with the optimizer *bobyqa*. Before fitting the models, we normalized all predictors by rescaling them to a mean of zero and a SD of one to facilitate the interpretability of the resulting estimates (Schielzeth, 2010). For the Gaussian model measuring the deviation from linear travel, to verify the assumptions of normally distributed and homoscedastic residuals, we visually inspected q-q plots and the distribution of the residuals plotted against the fitted values, and did not find any violation of these assumptions. For our Poisson model investigating potential factors influencing the occurrence of mycophagy, we verified that the model did not suffer from overdispersion (Cameron & Trivedi, 1990). We assessed model stability by omitting each level of random effects one at a time and comparing the derived model estimates with those of the full model; we found no influential cases. To exclude potential issues with collinearity amongst predictors, we evaluated Variance Inflation Factors (VIF, Field, 2005) with the function *vif* of the R package "car" (Fox & Weisberg, 2011) for standard linear models excluding the random effects, and found no issues (largest VIF = 1.91). As an initial test of significance, we compared the full models including all predictors with their respective null models including only the random effects and the control predictors (Forstmeier & Schielzeth, 2011), using a likelihood ratio test (R function *anova* with argument test set to "Chisq"; Dobson, 2002). If the full model was significant against the null model, we proceeded to examine the effect of individual fixed effect by excluding each fixed effect one at a time and comparing this reduced model to the respective full model with a likelihood ratio test (Barr et al., 2013). Confidence intervals were derived using the function *bootMer* of the package "lme4," using 1000
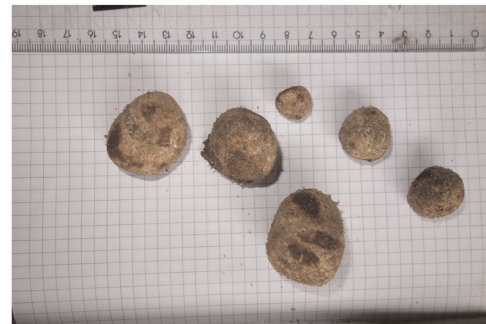

FIGURE 3 Analyzed samples of *Hysterangium bonobo*

parametric bootstraps and bootstrapping also over the random effects.

2.5 | Nutritional analyses

We opportunistically collected samples of *H. bonobo* (see Figure 3) in a dry forest area near the river to identify if there were specific nutritional properties of this fungus species that may elucidate its consumption by the bonobos. For nutrient content analyses, we collected 20 g (wet mass) of *H. bonobo* into sample tubes frozen in liquid nitrogen within 2 h of collection. Often we also observed bonobos commonly consuming a specific THV plant, *Palisota ambigua*, concurrently while feeding on *H. bonobo* (see Video S1). To have an additional value of mineral content in plants grown at the locations of *H. bonobo*, we collected 20 g (wet mass) of *P. ambigua* from the same location as the *H. bonobo* sample. All samples were stored in liquid nitrogen in the field and then at minus 20°C in Kinshasa, before they were shipped on dry ice to the Leibniz Institute for Zoo and Wildlife Research, Germany. Before the analyses, all dried samples were grounded with an IKA A 11 Basic mill (79219 Staufen; IKA-Werke GmbH & Co. KG) to a particle size of about 1 mm. Dry
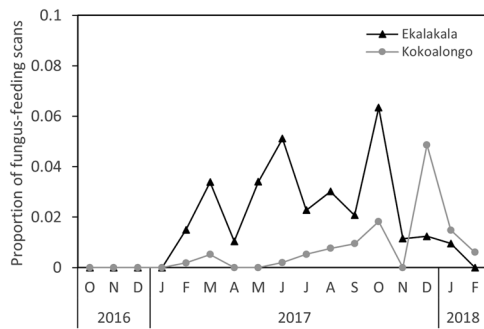
FIGURE 4 Variation in the proportion of fungus-feeding scans (out of the total number of party scans per month per community) across the 17-month study period

matter content was obtained by drying part of the sample at 105°C overnight. Mineral content (Cu, Fe, K, Mg, Mn, Mo, Na, P, S, Zn) was assessed after microwave digesting the samples, and analyzing them by inductively coupled plasma optical emission spectrometry.

3 | RESULTS

During the study period, we recorded the behavior of the bonobos on 342 days (monthly average: 20.1 ± 4.2 (SD) days; range 12–28 days), resulting in a total of 7214 10-min party scans in Ekalakala and 7824 party scans in Kokoalongo. Altogether, both groups of bonobos were recorded feeding on fungi on 75 days in 13 out of the 17 months of observations, with a mean of 4.4 ± 3.4 (SD) days per month (range: 0–11 days), or a mean of $21.9 \pm 0.4\%$ (SD) of monthly observation days (range: 0%–39.3%). These fungi comprised a minor portion of the apes' diet in terms of their contribution to feeding observations: bonobos spent an average of $6.5 \pm 0.2\%$ (SD) (range: 0%–23%) of their daily feeding time (measured as 10-min group-level scans) extracting and consuming them over the 17 months of observation. Broadly, the smaller community Ekalakala consumed fungi to a greater degree than Kokoalongo, as indicated by the proportion of fungus-feeding scans out of all feeding scans (Ekalakala: $N = 2072$; mean $\pm$ SD = $9.6 \pm 14.3\%$; Kokoalongo: $N = 2128$; mean $\pm$ SD = $3.5 \pm 6.4\%$). Overall, we observed fluctuations in fungus consumption across the 17-month study period, especially in Ekalakala (Figure 4).

The full model investigating the effects of fruit abundance and other feeding behavior on the number of party scans bonobos fed on fungi was significant relative to the null model ($\chi^2 = 17.24$, df = 4, $p = .002$). We observed that bonobos fed on fungi more frequently when fruit abundance was high, but fungus consumption was not related to the consumption of fruits or THV after we accounted for the effect of fruit abundance (Table 1).

The full model investigating travel linearity during foraging activities dependent upon whether the second feeding patch among three consecutive feeding patches was a fungus patch or a fruit patch significantly differed from the null model ($\chi^2 = 16.30$,

TABLE 1 Summary of the results of the model investigating the relation between the proportion of fungus-feeding scans, fruit abundance, and other feeding behavior

	Estimate	SE	p
Intercept	−2.014	0.706	-
Fruit abundance	**0.714**	**0.217**	**0.001**
Number of THV-feeding scans	0.118	0.171	0.489
Number of fruit-feeding scans	−0.233	0.196	0.236
Party size	0.195	0.207	-
Community (Kokoalongo)[a]	−1.543	0.379	**-**
Rainfall	0.011	0.182	-
Autocorrelation term	0.747	3.857	-

Note: Significant test predictors ($p \le 0.05$) are indicated in bold, p values for control predictors are not reported.
[a]The reference value for *community* (Kokoalongo/Ekalakala) is "Ekalakala."

TABLE 2 Summary of the results of the model investigating travel linearity during foraging activities, depending on whether the second food patch among three consecutive food patches (where the first and third patch were both fruit patches) was a fungus patch or a fruit patch

	Estimate	SE	p
Intercept	−0.394	0.120	-
Second feeding patch (fungus patch)[a]	**0.658**	**0.159**	**<0.001**
FAI	−0.092	0.082	-
Community (Kokoalongo)[b]	0.402	0.166	-

Note: Significant test predictors ($p \le 0.05$) are indicated in bold, p values for control predictors are not reported.
[a]The reference level for *second feeding patch* (fruit patch/fungus patch) is "fruit patch."
[b]The reference value for *community* (Kokoalongo/Ekalakala) is "Ekalakala."

df = 1, $p < 0.001$). The *deviation from linearity index* was significantly larger when the second feeding patch was a fungus patch as opposed to a fruit patch (Table 2).

3.1 | *H. bonobo* nutritional content

To contextualize the nutritional value, in particular sodium concentration, of *H. bonobo* relative to other plant species that were consumed by bonobos (including the *P. ambigua* sample that was collected together with the *H. bonobo* sample in Kokolopori) and other apes, we have compiled nutritional data of plant food sources that constituted a major part of ape diet, including but not exclusively bonobo food items, from existing literature in LuiKotale, Budongo and Rwanda (Table 3).

TABLE 3 Mineral content (mg/kg dry matter) of *Hysterangium bonobo* and *Palisota ambigua* in KP, in relation to plant food species that are frequently consumed in other ape populations (data extracted from Grueter et al., 2018; Hohmann et al., 2019; Reynolds et al., 2009)

Sample	Ape species	Plant part	Ca	Cu	Fe	K	Mg	Mn	Mo	Na	P	S	Zn
H. bonobo[a]	Bonobo (KP)	-	33.2	76.8	1134	3195	1158	4.0	0.0	14913	4141	2747	23.4
P. ambigua[a]	Bonobo (KP)	Pith	7297	9.8	1279	24634	5679	718.1	0.0	416.5	1518	1714	38.6
Haumania liebrechtsiana[a]	Bonobo	Pith	1540.8	-	62.7	43880.7	2742.4	193.8	-	35.2	-	-	62.4
Drypetes spp.[a]	Bonobo	Fruit	694.0	-	19.8	10873.9	1267.7	50.3	-	11.5	-	-	21.5
Landolphia spp.[a]	Bonobo	Fruit	807.9	-	49.4	13289.3	782.2	74.6	-	22.8	-	-	68.0
Parinari excelsia[a]	Bonobo	Fruit	1023.9	-	24.5	12986.9	865.4	4.7	-	29.3	-	-	5.8
Mammea africana[a]	Bonobo	Fruit	4070.6	-	61.2	10334.6	3155.3	115.9	-	19.3	-	-	14.4
Dialium gossweiler[a]	Bonobo	Fruit	975.2	-	33.1	8919.7	1673.1	74.8	-	8.3	-	-	18.1
Gambeya lacourtiana	Bonobo	Fruit	339.9	-	19.6	8595.8	366.0	17.1	-	15.4	-	-	12.4
Irvingia gabonensis	Bonobo	Fruit	1360.2	-	26.2	15259.0	1333.0	84.4	-	25.1	-	-	22.3
Raphia farinifera	Chimpanzee	Pith	1563.1	-	128.3	6650.3	2430.1	425.1	-	5037.9	-	-	176.7
Funtumia elastic	Chimpanzee	Bark	1486.5	-	13.0	2909.0	302.5	24.0	-	70.5	-	-	12.0
Cleistopholis patens	Chimpanzee	Bark	1005.0	-	301.0	2261.0	443.0	11.0	-	800.0	-	-	−2.0
Astonia boonei	Chimpanzee	Bark	4317.5	-	33.0	835.0	388.0	19.5	-	1277.5	-	-	39.5
Zanha golungensis	Chimpanzee	Leaf	2518.0	-	117.0	-	2740.0	16.0	-	289.0	-	-	243.0
Ficus exasperate	Chimpanzee	Leaf	12449.0	-	118.0	24993.0	4114.0	81.0	-	408.0	-	-	69.0
Ficus varifolia	Chimpanzee	Leaf	3130.0	-	16.0	7479.0	1112.0	23.0	-	156.0	-	-	34.0
Celtis mildbraedii	Chimpanzee	Leaf	5790.0	-	86.0	-	3738.0	253.0	-	436.0	-	-	68.0
Ficus mucuso	Chimpanzee	Fruit	4895.0	-	49.0	-	1751.0	20.0	-	135.0	-	-	74.0
Ficus exasperate	Chimpanzee	Fruit	7563.0	-	72.0	-	2889.0	41.0	-	192.0	-	-	143.0
Mangifera indica	Chimpanzee	Fruit	2007.0	-	21.0	-	1132.0	44.0	-	321.0	-	-	32.0
Broussonettia papyrifera	Chimpanzee	Fruit	10878.0	-	63.0	-	3634.0	23.0	-	546.0	-	-	94.0
Lantana sp.	Chimpanzee	Fruit	2823.0	-	34.0	10073.0	767.0	20.0	-	164.0	-	-	39.0
Beoquartiodendron oblanceolatum	Chimpanzee	Fruit	791.0	-	30.0	-	1305.0	43.0	-	55.0	-	-	59.0
Carduus nyassanus	Gorilla	Stem	-	-	-	-	-	-	-	67	-	-	-
Peucedanum linderi	Gorilla	Stem	-	-	-	-	-	-	-	40	-	-	-
Rubus runssorensis	Gorilla	Leaf	-	-	-	-	-	-	-	204	-	-	-
Laportea alatipes	Gorilla	Leaf	-	-	-	-	-	-	-	35	-	-	-
Carduus nyassanus	Gorilla	Leaf	-	-	-	-	-	-	-	34	-	-	-
Galium sp.	Gorilla	All	-	-	-	-	-	-	-	31	-	-	-
Yushania alpina	Gorilla	Shoot	-	-	-	-	-	-	-	23	-	-	-

Note: All mineral content is expressed in mg/kg.

Abbreviation: KP, Kokolopori.

[a]Food species that bonobos in Kokolopori consume.

4 | DISCUSSION

We investigated the feeding ecology and potential dietary importance of subterranean fungi in wild bonobos. We tested whether mycophagy could be considered a fallback food strategy or as a means to acquire specific nutrients. We found that bonobos spent proportionately more time feeding on fungi when fruit abundance was relatively high, suggesting that fungi were not consumed as fallback food. The role of fungi as a nonfallback food item is also supported by their presence in the diet throughout the majority of

the study period. Moreover, bonobos deviated to a greater degree from linear traveling routes when visiting fungus patches than fruit patches, suggesting that they actively sought out these fungi. Lastly, nutritional analyses on one of the fungus species consumed, *H. bonobo*, revealed a remarkably high concentration of sodium in relation to other plant foods comprising ape diets (Table 3). Additionally, we found that the content of other nutrients found in *H. bonobo* was within the range of values in other plant foods. Collectively, our results suggest that subterranean fungi are an attractive food source to bonobos in Kokolopori and mycophagy may potentially serve to supplement specific nutrients, such as sodium, in bonobo diet.

Mycophagy has been documented in other bonobo populations (Bermejo et al., 1994; Kano, 1983). In Wamba, a nearby bonobo population, bonobos feed on *Elaphomyces labyrinthinus*, a species of fungus that grows in semiinundated forest (K. Nara & T. Furuichi, personal communication). While *E. labyrinthinus* is the most frequently consumed fungi by the bonobos in Wamba (ibid.), bonobos in Kokolopori mainly feed on *H. bonobo* in dry forest areas near rivers. This population difference in the fungus species consumed may be attributed to differences in habitat types or home range utilization between the two study sites. In Kokolopori, bonobos consumed fungi on a regular basis (21.9% of all observation days), with an average daily feeding time (6.5%) slightly higher than the average time (i.e., <5%) primates spend feeding on fungi (Hanson et al., 2003). It therefore appears that subterranean fungi are an important component of the bonobos' diet despite their role as nonstaple food. While we did not set out the present study to investigate this, we observed differences in fungus consumption rates between our two study communities, with the smaller community, Ekalakala, feeding on fungi more frequently than Kokoalongo. This dietary difference mirrors observed differences in the species of meat hunted by each group, supporting a potentially social component to dietary preference, even by two groups whose home ranges overlap (Samuni et al., 2020). However, without detailed information on fungus phenology, we cannot conclude whether the observed group difference in fungus consumption can be attributed to potential differences in fungus distribution across the two home ranges, or other socioecological and/or cultural factors (e.g., differences in feeding habits, food preferences, the usage of home range, or even intercommunity dynamics).

Fungi such as *H. bonobo* are presumably challenging to find due to their subterranean nature. Bonobos appear to rely on olfactory cues when searching for these fungi and frequently exhibit excitement when a piece of fungus is discovered (see Video S1). The effort and time bonobos appear to invest in searching for fungi is unexpected because fungal sporocarps are generally regarded as a poor source of nutrients to primates without a foregut fermentation digestive system to extract the majority of the protein or energy available (Hanson et al., 2003). Generally, most primates spend <5% of their feeding time consuming fungi (Hanson et al., 2003), and only a few primate species are known to utilize fungi as a staple food resource (Hanson et al., 2003; Hilário & Ferrari, 2011) or to consume

them as conspicuous portion of their diet (Correa, 1995; Kirkpatrick et al., 2001). One hypothesis on the substantial role of fungi in the diet of some primates is that these fungi serve as fallback foods in periods of fruit scarcity. Such is argued to be the case with Goeldi's monkeys, who spend a substantial proportion of their feeding time (29%) on fungi and consume high amounts of sporocarps relative to other foods when fruit availability is low (Porter, 2001). Similarly, the consumption of fungi is associated with fruit scarcity in Japanese macaques (Hanya et al., 2003). However, fungi are unlikely a fallback food resource for the bonobos in Kokolopori as we observed bonobos spending proportionally more time feeding on fungi (up to as much as 29.4%) when fruit abundance was high.

Unfortunately, we cannot exclude the possibility that the abundance of fungi followed a pattern similar to that of fruits in Kokolopori, and that its consumption was higher when both fruits and fungi were most abundant. The effect of seasonal variation on fungus distribution and abundance in tropical forest habitat remains elusive. A study conducted on fungus diversity and phenology in Côte d'Ivoire revealed that fructification of the five *Termitomyces* species present in tropical forests occurs in both rainy and dry seasons, with some species occurring during the beginning of rainy season and others towards the end of rainy season/beginning of dry season (Koné et al., 2018). Although an increase in humidity within dry-seasonal forest habitat has been shown to favor the growth of various soft-bodied sporocarps including *Hysterangium* sp. (Johnson, 1994), the effect of rainfall on sporocarp production may be less marked in tropical rainforests. While we cannot identify a clear seasonal pattern in fungus consumption by bonobos in Kokolopori from our preliminary data (see Figure 4), comprehensive identification of fungus species consumed by bonobos and regular monitoring of local fungus phenology are needed to elucidate potential effect of spatiotemporal variation in fungus production on overall fungus consumption, as well as to better understand the contribution of different fungus species to the diet of bonobos.

Subterranean fungi appear to be an attractive food source to bonobos in Kokolopori, given that they actively sought these fungi. What makes these fungi an attractive food source to bonobos? As the proportion of time bonobos spent feeding on fungi did not correlate with the proportion of time they spent feeding on fruits and THV, it is unlikely that fungi are consumed to meet energetic needs or to supplement macronutrients like protein or fiber that are readily accessible from THV, given its widespread availability (Malenky, 1990; Rafert & Vineberg, 1997). Collectively, in concert with an aforementioned lack of specialized digestive system for fungal consumption, it is unlikely that bonobos could acquire considerable amount of energy and macronutrients from fungi (Claridge & Trappe, 2005).

Alternatively, fungi may be consumed as a source of particular micronutrients and minerals. In particular, we found notably high sodium concentration in our *H. bonobo* samples relative to other plant foods that constitute major part of ape diet (Grueter et al., 2018; Hohmann et al., 2019; Reynolds et al., 2009; see Table 3). It is therefore plausible that bonobos

consume fungi such as *H. bonobo* to supplement their diet with sodium. However, mineral content of plants and soil can vary across sites and habitats (Claridge & Trappe, 2005). Without detailed nutritional data on the major food items that are regularly consumed by the Kokolopori bonobos, we cannot discount the possibility that the food items consumed by bonobos in Kokolopori may be generally richer in sodium than those in LuiKotale. Indeed, the sodium content of our *P. ambigua* samples is higher than that of fruits and THV found in LuiKotale (Hohmann et al., 2019), but it is comparable to plants consumed by chimpanzees in Uganda (Reynolds et al., 2009) and by mountain gorillas in Rwanda (Grueter et al., 2018; Table 3). Potential ecological or dietary differences across study populations and species notwithstanding, sodium concentration of *H. bonobo* in Kokolopori is substantially higher than that of *P. ambigua* (collected in the same location as the fungus samples), thereby suggesting that Kokolopori bonobos may select and consume fungi to meet sodium requirements.

The consumption of nonstaple food items to meet micronutritional or mineral dietary requirements is common across primate species. For example, Luikotale bonobos consume aquatic plants from swamps to presumably supplement their diet with iodine (Hohmann et al., 2019). In Cameroon, chimpanzees consume termites likely as a source of protein and nutrients such as manganese, and gorillas appear to consume them as source of iron (Deblauwe & Janssens, 2008). In Guinea, chimpanzees have been observed feeding on fresh-water crabs as a source of fatty acid and minerals such as sodium and calcium (Koops et al., 2019). Minerals, such as sodium, are essential to the physiology of mammals, particularly lactating females, because sodium deficiency can result in poor growth and high infant mortality (Morris et al., 2008). Many non-human primates living in tropical environments are particularly susceptible to sodium deficiency due to the scarcity of this mineral in their typical fruit- or plant-based diet (Rode et al., 2003; Rothman et al., 2006; Silver et al., 2000). However, some primates have adapted their feeding behavior to increase their sodium intake. For instance, gorillas in the Republic of Congo congregate in swampy forest clearings, called Bais, to consume sodium-rich plants (Magliocca & Gautier-Hion, 2002). Mountain gorillas in Eastern Central Africa have also been observed to feed on decaying wood (Rothman et al., 2006), Eucalyptus bark (Grueter et al., 2018), and soil (Mahaney et al., 1990) to likely supplement their diet with sodium. Similarly, orangutans in Borneo visit mineral-rich natural-licks to acquire sodium (Matsubayashi et al., 2011). To combat sodium deficiency, black-and-white colobus and red colobus monkeys in Uganda consume Eucalyptus leaves and bark, as well as aquatic plants (Rode et al., 2003).

In conclusion, bonobos in Kokolopori appear to target fungi in their daily foraging activities, and one of the key fungus species that they consume potentially serves to supplement a presumably rare mineral in their diet. While mycophagy and spore dispersal are crucial for the survival of host plants which depend on the symbiotic relationship (Colgan & Claridge, 2002; Klironomos et al., 2000), mycophagy may also have great impact on the physiology and ranging behavior of the mycophagous

animal. The widespread occurrence of mycophagy across nearly 60 primate species (Sawada, 2014) and many other taxa (Claridge & May, 1994; Claridge & Trappe, 2005) raises questions of its importance as a feeding strategy in humans and nonhuman animals. This study thus provides a promising avenue for future research on the role of mycophagy in the diet and health of primates.

AUTHOR CONTRIBUTIONS

Leveda Cheng: data curation (equal); formal analysis (supporting); investigation (equal); writing original draft (supporting); writing review & editing (lead). **Erin G. Wessling**: formal analysis (supporting); methodology (equal); writing original draft (supporting); writing review & editing (supporting). **Bienfait Kambale**: data curation (supporting); investigation (supporting); writing original draft (supporting); writing review & editing (supporting). **Albert Lokasola**: writing original draft (supporting); writing review & editing (supporting). **Sylvia Ortmann**: formal analysis (supporting); writing original draft (supporting); writing review & editing (supporting). **Martin Surbeck**: conceptualization (lead); resources (lead); supervision (lead); writing original draft (supporting); writing review & editing (supporting).

DATA AVAILABILITY STATEMENT

The datasets generated and analyzed during the current study are available in the Figshare repository at https://doi.org/10.6084/m9.figshare.13385426.

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REFERENCES

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49(3), 227–266. https://doi.org/10.1163/156853974X00534

Anderson, D. P., Nordheim, E. V., Moermond, T. C., Bi, Z. B. G., & Boesch, C. (2005). Factors influencing tree phenology in Taï National Park, Côte d'Ivoire. *Biotropica*, 37(4), 631–640. https://doi.org/10.1111/j.1744-7429.2005.00080.x

Baayen, R., Davidson, D., & Bates, D. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, 59(4), 390–412. https://doi.org/10.1016/j.jml.2007.12.005

Barr, D., Levy, R., Scheepers, C., & Tily, H. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, 68(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. http://arxiv.org/abs/1406.5823

Beenken, L., Sainge, M. N., & Kocyan, A. (2016). *Lactarius megalopterus*, a new angiocarpous species from a tropical rainforest in Central Africa, shows adaptations to endozoochorous spore dispersal. *Mycological Progress*, 15(6), 58. https://doi.org/10.1007/s11557-016-1198-4

Bergstrom, M. L., Hogan, J. D., Melin, A. D., & Fedigan, L. M. (2019). The nutritional importance of invertebrates to female *Cebus capucinus* imitator in a highly seasonal tropical dry forest. *American Journal of Physical Anthropology*, 170(2), 207–216. https://doi.org/10.1002/ajpa.23913

Bermejo, M., Illera, G., & Pí, J. S. (1994). Animals and mushrooms consumed by bonobos (*Pan paniscus*): New records from lilungu (Ikela), Zaire. *International Journal of Primatology*, 15(6), 879–898. https://doi.org/10.1007/BF02736074

Bogart, S. L., & Pruetz, J. D. (2011). Insectivory of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. *American Journal of Physical Anthropology*, 145(1), 11–20. https://doi.org/10.1002/ajpa.21452

Bultman, T. L., & Mathews, P. L. (1996). Mycophagy by a millipede and its possible impact on an insect-fungus mutualism. *Oikos*, 75(1), 67–74. https://doi.org/10.2307/3546322

Caldwell, I. R., Vernes, K., & Bärlocher, F. (2005). The northern flying squirrel (*Glaucomys sabrinus*) as a vector for inoculation of red spruce (*Picea rubens*) seedlings with ectomycorrhizal fungi. *Sydowia*, 57(2), 166–178.

Cameron, A. C., & Trivedi, P. K. (1990). Regression-based tests for overdispersion in the Poisson model. *Journal of Econometrics*, 46(3), 347–364. https://doi.org/10.1016/0304-4076(90)90014-K

Choquenot, D. (1998). Testing the relative influence of instrinsic and extrinsic variation in food availability on feral pig populations in Australia's rangelands. *Journal of Animal Ecology*, 67(6), 887–907. https://doi.org/10.1046/j.1365-2656.1998.6760887.x

Claridge, A., & Trappe, J. (2005). Sporocarp mycophagy: Nutritional, behavioral, evolutionary, and physiological aspects. In J. Dighton, J. White, & P. Oudemans (Eds.), *The fungal community* (Vol. 20050554, pp. 599–611). CRC Press. https://doi.org/10.1201/9781420027891.ch29

Claridge, A. W. (2002). Ecological role of hypogeous ectomycorrhizal fungi in Australian forests and woodlands. In S. E. Smith & F. A. Smith (Eds.), *Diversity and Integration in Mycorrhizas: Proceedings of the 3rd International Conference on Mycorrhizas (ICOM3) Adelaide, Australia, 8–13 July 2001* (pp. 291–305). Springer. https://doi.org/10.1007/978-94-017-1284-2_29

Claridge, A. W., & Cork, S. J. (1994). Nutritional-value of hypogeal fungal sporocarps for the long-nosed potoroo (*Potorous-Tridactylus*), a forest-dwelling mycophagous marsupial. *Australian Journal of Zoology*, 42(6), 701–710. https://doi.org/10.1071/zo9940701

Claridge, A. W., & May, T. W. (1994). Mycophagy among Australian mammals. *Australian Journal of Ecology*, 19(3), 251–275. https://doi.org/10.1111/j.1442-9993.1994.tb00489.x

Colgan, W., & Claridge, A. W. (2002). Mycorrhizal effectiveness of Rhizopogon spores recovered from faecal pellets of small forest-dwelling mammals. *Mycological Research*, 106(3), 314–320. https://doi.org/10.1017/S0953756202005634

Cooper, T., & Vernes, K. (2011). Mycophagy in the larger bodied skinks of the genera Tiliqua and Egernia: Are there implications for ecosystem health? *Australian Zoologist*, 35(3), 681–684. https://doi.org/10.7882/AZ.2011.020

Correa, H. K. M. (1995). Ecologia e Comportamento Alimentar de um Grupo de Saguis-da-Serra-Escuros (Callithrix aurita E. Geoffroy 1812) no Parque Estadual da Serra do Mar, Nucleo Cunha, Sao Paulo. *Master's Thesis, Univ. Federal of Minas Gerais*. https://ci.nii.ac.jp/naid/10015028767/

Deblauwe, I., & Janssens, G. P. J. (2008). New insights in insect prey choice by chimpanzees and gorillas in Southeast Cameroon: The role of nutritional value. *American Journal of Physical Anthropology*, 135(1), 42–55. https://doi.org/10.1002/ajpa.20703

Dobson, A. (2002). *An introduction to generalized linear models*. Chapman & Hall/CRC. https://doi.org/10.1201/9781420057683

Elliott, T. F. (2019). Reptilian mycophagy: A global review of mutually beneficial associations between reptiles and macrofungi. *Mycosphere*, 10(1), 776–797. https://doi.org/10.5943/mycosphere/10/1/18

Elliott, T. F., Georgiev, A. V., Lokasola, A. L., & Smith, M. E. (2020). *Hysterangium bonobo*: A newly described truffle species that is eaten by bonobos in the Democratic Republic of Congo. *Mycologia*, 1–9. https://doi.org/10.1080/00275514.2020.1790234

Elliott, T. F., & Vernes, K. (2019). Superb Lyrebird *Menura novaehollandiae* mycophagy, truffles and soil disturbance. *Ibis*, 161(1), 198–204. https://doi.org/10.1111/ibi.12644

Fedigan, L. M. (1990). Vertebrate predation in *Cebus capucinus*: Meat eating in a neotropical monkey. *Folia Primatologica*, 54(3–4), 196–205. https://doi.org/10.1159/000156444

Field, A. (2005). *Discovering statistics using SPSS*. Sage Publications.

Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, 65(1), 47–55. https://doi.org/10.1007/s00265-010-1038-5

Fox, J., & Weisberg, S. (2011). *An R companion to applied regression* (2nd edition). Sage. https://onlinelibrary.wiley.com/doi/abs/10.1002/ece3.2073

Furuichi, T., Mulavwa, M., Yangozene, K., Yamba-Yamba, M., Motema-Salo, B., Idani, G., Ihobe, H., Hashimoto, C., Tashiro, Y., & Mwanza, N. (2008). Relationships among fruit abundance, ranging rate, and party size and composition of bonobos at Wamba. In T. Furuichi, & J. Thompson (Eds.), *The bonobos* (pp. 135–149). Springer. https://doi.org/10.1007/978-0-387-74787-3_8

Gilby, I. C., Pokempner, A. A., & Wrangham, R. W. (2010). A direct comparison of scan and focal sampling methods for measuring wild chimpanzee feeding behaviour. *Folia Primatologica*, 81(5), 254–264. https://doi.org/10.1159/000322354

Grueter, C. C., Li, D., Ren, B., Wei, F., Xiang, Z., & van Schaik, C.P. (2009). Fallback foods of temperate-living primates: A case study on snub-nosed monkeys. *American Journal of Physical Anthropology*, 140(4), 700–715. https://doi.org/10.1002/ajpa.21024

Grueter, C. C., Wright, E., Abavandimwe, D., Ortmann, S., Mudakikwa, A., Musana, A., Uwingeli, P., Ndagijimana, F., Vecellio, V., Stoinski, T. S., & Robbins, M. M. (2018). Going to extremes for sodium acquisition: Use of community land and high-altitude areas by mountain gorillas *Gorilla beringei* in Rwanda. *Biotropica*, 50(5), 826–834. https://doi.org/10.1111/btp.12598

Hammond, P., & Lawrence, J. (1989). Mycophagy in insects: A summary. In N. Wilding, N. M. Collins, P. M. Hammond, & J. F. Webber (Eds.), *Insect–fungus interactions* (pp. 275–324). Academic Press.

Hanson, A. M., Hall, M. B., Porter, L. M., & Lintzenich, B. (2006). Composition and nutritional characteristics of fungi consumed by *Callimico goeldii* in Pando, Bolivia. *International Journal of Primatology*, 27(1), 323–346. https://doi.org/10.1007/s10764-005-9014-z

Hanson, A. M., Hodge, K. T., & Porter, L. M. (2003). Mycophagy among primates. *Mycologist*, 17(1), 6–10. https://doi.org/10.1017/S0269915X0300106X

Hanya, G., Noma, N., & Agetsuma, N. (2003). Altitudinal and seasonal variations in the diet of Japanese macaques in Yakushima. *Primates*, 44(1), 51–59. https://doi.org/10.1007/s10329-002-0007-7

Hilário, R. R., & Ferrari, S. F. (2011). Why feed on fungi? The nutritional content of sporocarps consumed by buffy-headed marmosets,

Callithrix flaviceps (Primates: *Callitrichidae*), in Southeastern Brazil. *Journal of Chemical Ecology*, 37(2), 145–149. https://doi.org/10.1007/s10886-011-9911-x

Hohmann, G., & Fruth, B. (2008). New records on prey capture and meat eating by bonobos at Lui Kotale, Salonga National Park, Democratic Republic of Congo. *Folia Primatologica*, 79(2), 103–110. https://doi.org/10.1159/000110679

Hohmann, G., Ortmann, S., Remer, T., & Fruth, B. (2019). Fishing for iodine: What aquatic foraging by bonobos tells us about human evolution. *BMC Zoology*, 4(1), 5. https://doi.org/10.1186/s40850-019-0043-z

Hohmann, G., Robbins, M. M., & Boesch, C. (2006). Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: The influence of abundance and nutritional quality of fruit. In G. Hohmann (Ed.), *Feeding ecology in Apes and other Primates* (pp. 123–159). Cambridge University Press.

Holdø, R. M., Dudley, J. P., & McDowell, L. R. (2002). Geophagy in the African elephant in relation to availability of dietary sodium. *Journal of Mammalogy*, 83(3), 652–664. https://doi.org/10.1644/1545-1542(2002)083%3C0652:GITAEI%3E2.0.CO;2

Inogwabini, B.-I., & Matungila, B. (2009). Bonobo food items, food availability and bonobo distribution in the Lake Tumba Swampy Forests, Democratic Republic of Congo. *The Open Conservation Biology Journal*, 3(1), 14–23. https://doi.org/10.2174/1874839200903010014

Jang, H., Boesch, C., Mundry, R., Ban, S. D., & Janmaat, K. R. L. (2019). Travel linearity and speed of human foragers and chimpanzees during their daily search for food in tropical rainforests. *Scientific Reports*, 9(1), 11066. https://doi.org/10.1038/s41598-019-47247-9

Johnson, C. (1994). Fruiting of hypogeous fungi in dry sclerophyll forest in Tasmania, Australia: Seasonal variation and annual production. *Mycological Research*, 98(10), 1173–1182. https://doi.org/10.1016/S0953-7562(09)80201-3

Johnson, M. D., & Sherry, T. W. (2001). Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. *Journal of Animal Ecology*, 70(4), 546–560.

Kano, T. (1983). An ecological study of the pygmy chimpanzees (*Pan paniscus*) of Yalosidi, Republic of Zaire. *International Journal of Primatology*, 4(1), 1–31. https://doi.org/10.1007/BF02739358

Kiers, E. T., Lovelock, C. E., Krueger, E. L., & Herre, E. A. (2000). Differential effects of tropical arbuscular mycorrhizal fungal inocula on root colonization and tree seedling growth: Implications for tropical forest diversity. *Ecology Letters*, 3(2), 106–113. https://doi.org/10.1046/j.1461-0248.2000.00126.x

Kimura, D., Lingomo-Bongoli, Masuda, H., & Yamaguchi, R. (2015). Change in land use among the Bongando in the Democratic Republic of the Congo. *African Study Monographs. Supplementary Issue*, 51, 5–35. https://doi.org/10.14989/197208

Kirkpatrick, R. C., Zou, R. J., Dierenfeld, E. S., & Zhou, H. W. (2001). Digestion of selected foods by Yunnan snub-nosed monkey *Rhinopithecus bieti* (*Colobinae*). *American Journal of Physical Anthropology*, 114(2), 156–162. https://doi.org/10.1002/1096-8644(200102)114:2%3C156::AID-AJPA1015%3E3.0.CO;2-A

Klironomos, J. N., McCune, J., Hart, M., & Neville, J. (2000). The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity. *Ecology Letters*, 3(2), 137–141. https://doi.org/10.1046/j.1461-0248.2000.00131.x

Koné, N. A., Soro, B., Vanié-Léabo, L. P. L., Konaté, S., Bakayoko, A., & Koné, D. (2018). Diversity, phenology and distribution of *Termitomyces* species in Côte d'Ivoire. *Mycology*, 9(4), 307–315. https://doi.org/10.1080/21501203.2018.1500498

Koops, K., Wrangham, R. W., Cumberlidge, N., Fitzgerald, M. A., van Leeuwen, K. L., Rothman, J. M., & Matsuzawa, T. (2019). Crab-fishing by chimpanzees in the Nimba Mountains, Guinea. *Journal of Human Evolution*, 133, 230–241. https://doi.org/10.1016/j.jhevol.2019.05.002

Lambert, J. E., Chapman, C. A., Wrangham, R. W., & Conklin-Brittain, N. L. (2004). Hardness of cercopithecine foods: Implications for the critical function of enamel thickness in exploiting fallback foods. *American Journal of Physical Anthropology*, 125(4), 363–368. https://doi.org/10.1002/ajpa.10403

Lucchesi, S., Cheng, L., Deschner, T., Mundry, R., Wessling, E. G., & Surbeck, M. (2021). Better together? How intergroup encounters affect energy balance and feeding behavior in wild bonobos. *Behavioral Ecology and Sociobiology*, 75, 2. https://doi.org/10.1007/s00265-020-02943-9

Lundquist, C., & Varnedoe, W. (2006). Salt ingestion caves. *International Journal of Speleology*, 35(1), 13–18. https://doi.org/10.5038/1827-806X.35.1.2

Magliocca, F., & Gautier-Hion, A. (2002). Mineral content as a basis for food selection by western lowland gorillas in a forest clearing. *American Journal of Primatology*, 57(2), 67–77. https://doi.org/10.1002/ajp.10034

Mahaney, W. C., Watts, D. P., & Hancock, R. G. V. (1990). Geophagia by mountain gorillas (*Gorilla gorilla beringei*) in the Virunga Mountains, Rwanda. *Primates*, 31(1), 113–120. https://doi.org/10.1007/BF02381034

Malenky, R. (1990). *Ecological factors affecting food choice and social organization in Pan paniscus* (Doctoral Dissertation), SUNY at Stony Brook. https://www.ci.nii.ac.jp/naid/10014820700/

Markova, E. A., Trofimova, S. S., Sibiryakov, P. A., & Yalkovskaya, L. E. (2020). Secondary types of food in the diet of a small-sized mammalian herbivore: From species ecology to habitat inferences. *Mammal Research*, 65(2), 289–300. https://doi.org/10.1007/s13364-019-00472-z

Marshall, A. J., Boyko, C. M., Feilen, K. L., Boyko, R. H., & Leighton, M. (2009). Defining fallback foods and assessing their importance in primate ecology and evolution. *American Journal of Physical Anthropology*, 140(4), 603–614. https://doi.org/10.1002/ajpa.21082

Marshall, A. J., & Wrangham, R. W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology*, 28(6), 1219–1235. https://doi.org/10.1007/s10764-007-9218-5

Maser, C., Claridge, A. W., & Trappe, J. M. (2008). *Trees, truffles, and beasts: How forests function*. Rutgers University Press.

Matsubayashi, H., Ahmad, A. H., Wakamatsu, N., Nakazono, E., Takyu, M., Majalap, N., Lagan, P., & Jum Rafiah, A. S. (2011). Natural-licks used by orangutans and conservation of their habitats in bornean tropical production forest. *Raffles Bulletin of Zoology*, 59(1), 109–115.

McGrew, W. C., Marchant, L. F., Beuerlein, M. M., Vrancken, D., Fruth, B., & Hohmann, G. (2007). Prospects for bonobo insectivory: Lui Kotal, Democratic Republic of Congo. *International Journal of Primatology*, 28(6), 1237–1252. https://doi.org/10.1007/s10764-007-9215-8

McGrew, W. C. (2014). The "other faunivory" revisited: Insectivory in human and non-human primates and the evolution of human diet. *Journal of Human Evolution*, 71, 4–11. https://doi.org/10.1016/j.jhevol.2013.07.016

Mcilwee, A. P., & Johnson, C. N. (1998). The contribution of fungus to the diets of three mycophagous marsupials in Eucalyptus forests, revealed by stable isotope analysis. *Functional Ecology*, 12(2), 223–231. https://doi.org/10.1046/j.1365-2435.1998.00181.x

McNaughton, S. J. (1988). Mineral nutrition and spatial concentrations of African ungulates. *Nature*, 334(6180), 343–345. https://doi.org/10.1038/334343a0

Morris, M. J., Na, E. S., & Johnson, A. K. (2008). Salt craving: The psychobiology of pathogenic sodium intake. *Physiology & Behavior*, 94(5), 709–721. https://doi.org/10.1016/j.physbeh.2008.04.008

Mulavwa, M., Furuichi, T., Yangozene, K., Yamba-Yamba, M., Motema-Salo, B., Idani, G., Ihobe, H., Hashimoto, C., Tashiro, Y., & Mwanza, N. (2008). Seasonal changes in fruit production and party size of bonobos at Wamba. In T. Furuichi, & J. Thompson (Eds.), *The bonobos* (pp. 121–134). Springer. https://doi.org/10.1007/978-0-387-74787-3_7

Porter, L. M. (2001). Dietary differences among sympatric *Callitrichinae* in Northern Bolivia: *Callimico goeldii, Saguinus fuscicollis* and *S. labiatus. International Journal of Primatology, 22*(6), 961–992. https://doi.org/10.1023/A:1012013621258

Potts, K. B., Baken, E., Ortmann, S., Watts, D. P., & Wrangham, R. W. (2015). Variability in population density is paralleled by large differences in foraging efficiency in chimpanzees (*Pan troglodytes*). *International Journal of Primatology, 36*(6), 1101–1119. https://doi.org/10.1007/s10764-015-9880-y

Rafert, J., & Vineberg, E. O. (1997). Bonobo nutrition-relation of captive diet to wild diet. *Bonobo Husbandry Manual.* 3-1

Reynolds, V., Lloyd, A. W., Babweteera, F., & English, C. J. (2009). Decaying *Raphia farinifera* palm trees provide a source of sodium for wild chimpanzees in the Budongo Forest, Uganda. *PLOS One, 4*(7), e6194. https://doi.org/10.1371/journal.pone.0006194

Robinson, B. W., & Wilson, D. S. (1998). Optimal foraging, specialization, and a solution to Liem's Paradox. *The American Naturalist, 151*(3), 223–235. https://doi.org/10.1086/286113

Rode, K. D., Chapman, C. A., Chapman, L. J., & McDowell, L. R. (2003). Mineral resource availability and consumption by colobus in Kibale National Park, Uganda. *International Journal of Primatology, 24*(3), 541–573. https://doi.org/10.1023/A:1023788330155

Rothman, J. M., Van Soest, P. J., & Pell, A. N. (2006). Decaying wood is a sodium source for mountain gorillas. *Biology Letters, 2*(3), 321–324. https://doi.org/10.1098/rsbl.2006.0480

Samuni, L., Wegdell, F., & Surbeck, M. (2020). Behavioural diversity of bonobo prey preference as a potential cultural trait. *eLife, 9,* e59191. https://doi.org/10.7554/eLife.59191

Sawada, A. (2014). Mycophagy among primates—What has been done and what can be done. *Primate Research, 30,* 5–21. https://doi.org/10.2354/psj.30.010

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients: Interpretation of regression coefficients. *Methods in Ecology and Evolution, 1*(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Seiler, N., Boesch, C., Mundry, R., Stephens, C., & Robbins, M. M. (2017). Space partitioning in wild, non-territorial mountain gorillas: The impact of food and neighbours. *Royal Society Open Science, 4*(11), 170720. https://doi.org/10.1098/rsos.170720

Silver, S. C., Ostro, L. E. T., Yeager, C. P., & Dierenfeld, E. S. (2000). Phytochemical and mineral components of foods consumed by black howler monkeys (*Alouatta pigra*) at two sites in Belize. *Zoo Biology, 19*(2), 95–109. https://doi.org/10.1002/1098-2361(2000)19:2%3C95::AID-ZOO1%3E3.0.CO;2-D

Surbeck, M., Coxe, S., & Lokasola, A. L. (2017). Lonoa: The establishment of a permanent field site for behavioural research on bonobos in the Kokolopori Bonobo Reserve. *Pan Africa News, 24*(2), 13–15.

Surbeck, M., Deschner, T., Behringer, V., & Hohmann, G. (2015). Urinary C-peptide levels in male bonobos (*Pan paniscus*) are related to party size and rank but not to mate competition. *Hormones and Behavior, 71,* 22–30. https://doi.org/10.1016/j.yhbeh.2015.03.007

Surbeck, M., Fowler, A., Deimel, C., & Hohmann, G. (2009). Evidence for the consumption of arboreal, diurnal primates by bonobos (*Pan paniscus*). *American Journal of Primatology, 71*(2), 171–174. https://doi.org/10.1002/ajp.20634

Tanney, J. B., & Hutchison, L. J. (2011). A brief survey of mycophagy in ruffed grouse, *Bonasa umbellus,* from Northwestern Ontario. *The Canadian Field-Naturalist, 125*(1), 72–73. https://doi.org/10.22621/cfn.v125i1.1132

Trappe, J. (2009). *Diversity, ecology, and conservation of truffle fungi in forests of the Pacific Northwest.* U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station

Trierveiler-Pereira, L. (2016). Mycophagy by small mammals: New and interesting observations from Brazil. *Mycosphere, 7*(3), 297–304. https://doi.org/10.5943/mycosphere/7/3/5

Watts, D. P. (2020). Meat eating by nonhuman primates: A review and synthesis. *Journal of Human Evolution, 149,* 102882. https://doi.org/10.1016/j.jhevol.2020.102882

Watts, D. P., Potts, K. B., Lwanga, J. S., & Mitani, J. C. (2012). Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 2. Temporal variation and fallback foods. *American Journal of Primatology, 74*(2), 130–144. https://doi.org/10.1002/ajp.21015

Webster, T. H., McGrew, W. C., Marchant, L. F., Payne, C. L. R., & Hunt, K. D. (2014). Selective insectivory at Toro-Semliki, Uganda: Comparative analyses suggest no "savanna" chimpanzee pattern. *Journal of Human Evolution, 71,* 20–27. https://doi.org/10.1016/j.jhevol.2014.02.005

Wheelock, N. (1980). Environmental sodium as a factor in the behavior and distribution of African elephants. *Elephant, 1*(4), 169–177. https://doi.org/10.22237/elephant/1521731760

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