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, Seller 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 nonstaple food items include meat (Fedigan, 1990; Surbeck et al., 2009; Watts, 2020) and insects (Bogart & Pruett, 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 & Pruett, 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; Trierweiler-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 "opportunist 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; McIwhee & 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; Mulawa 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 (Mulawa 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:

\[ MFAI = \sum_{i} P_{mi} B_{i} \]
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:

$$dFAI = A_i - \left( \frac{A_i - B_{i+1}}{d} \right) \times D,$$

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
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 found no influence 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 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
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 ± 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 ± 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 ± SD = 9.6 ± 14.3%; Kokoalongo: N = 2128; mean ± SD = 3.5 ± 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 (χ² = 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 (χ² = 16.30, 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. ambiguа* sample that was...
### TABLE 3  
Mineral content (mg/kg dry matter) of *Hysterangium bonobo* and *Palisota ambigu*r 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)

<table>
<thead>
<tr>
<th>Sample</th>
<th>Ape species</th>
<th>Plant part</th>
<th>Ca</th>
<th>Cu</th>
<th>Fe</th>
<th>K</th>
<th>Mg</th>
<th>Mn</th>
<th>Mo</th>
<th>Na</th>
<th>P</th>
<th>S</th>
<th>Zn</th>
</tr>
</thead>
<tbody>
<tr>
<td>H. bonobo(^a)</td>
<td>Bonobo (KP)</td>
<td>-</td>
<td>33.2</td>
<td>76.8</td>
<td>1134</td>
<td>3195</td>
<td>1158</td>
<td>4.0</td>
<td>0.0</td>
<td>14913</td>
<td>4141</td>
<td>2747</td>
<td>23.4</td>
</tr>
<tr>
<td>P. ambigu*a(^a)</td>
<td>Bonobo (KP)</td>
<td>Pith</td>
<td>7297</td>
<td>9.8</td>
<td>1279</td>
<td>24634</td>
<td>5679</td>
<td>718.1</td>
<td>0.0</td>
<td>416.5</td>
<td>1518</td>
<td>1714</td>
<td>38.6</td>
</tr>
<tr>
<td>Haumania liebrechtsiana(^a)</td>
<td>Bonobo</td>
<td>Pith</td>
<td>1540.8</td>
<td>-</td>
<td>62.7</td>
<td>43880.7</td>
<td>2742.4</td>
<td>193.8</td>
<td>-</td>
<td>35.2</td>
<td>-</td>
<td>-</td>
<td>62.4</td>
</tr>
<tr>
<td>Drypetes spp.(^a)</td>
<td>Bonobo</td>
<td>Fruit</td>
<td>694.0</td>
<td>-</td>
<td>19.8</td>
<td>10873.9</td>
<td>1267.7</td>
<td>50.3</td>
<td>-</td>
<td>11.5</td>
<td>-</td>
<td>-</td>
<td>21.5</td>
</tr>
<tr>
<td>Landolphia spp.(^a)</td>
<td>Bonobo</td>
<td>Fruit</td>
<td>807.9</td>
<td>-</td>
<td>49.4</td>
<td>13289.3</td>
<td>782.2</td>
<td>74.6</td>
<td>-</td>
<td>22.8</td>
<td>-</td>
<td>-</td>
<td>68.0</td>
</tr>
<tr>
<td>Parinari excelsia(^a)</td>
<td>Bonobo</td>
<td>Fruit</td>
<td>1023.9</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
</tr>
<tr>
<td>Mammea africana(^a)</td>
<td>Bonobo</td>
<td>Fruit</td>
<td>4070.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Drypetes spp.(^a)</td>
<td>Bonobo</td>
<td>Fruit</td>
<td>975.2</td>
<td>-</td>
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<td>-</td>
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<tr>
<td>Irvingia gabonensis</td>
<td>Bonobo</td>
<td>Fruit</td>
<td>1360.2</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Raphia farinifera</td>
<td>Chimpanzee</td>
<td>Pith</td>
<td>1563.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
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<tr>
<td>Funtumia elastic</td>
<td>Chimpanzee</td>
<td>Bark</td>
<td>1486.5</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Cleistopholis patens</td>
<td>Chimpanzee</td>
<td>Bark</td>
<td>1005.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Astania boonei</td>
<td>Chimpanzee</td>
<td>Bark</td>
<td>4317.5</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Zanha golungensis</td>
<td>Chimpanzee</td>
<td>Leaf</td>
<td>2518.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
</tr>
<tr>
<td>Ficus exasperate</td>
<td>Chimpanzee</td>
<td>Leaf</td>
<td>12449.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>Ficus varifolia</td>
<td>Chimpanzee</td>
<td>Leaf</td>
<td>3130.0</td>
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<tr>
<td>Celtis mildbraedii</td>
<td>Chimpanzee</td>
<td>Leaf</td>
<td>5790.0</td>
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<tr>
<td>Ficus mucuso</td>
<td>Chimpanzee</td>
<td>Fruit</td>
<td>4895.0</td>
<td>-</td>
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<tr>
<td>Ficus exasperate</td>
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<td>Fruit</td>
<td>7563.0</td>
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<tr>
<td>Mangifera indica</td>
<td>Chimpanzee</td>
<td>Fruit</td>
<td>2007.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Broussonetia papyrifera</td>
<td>Chimpanzee</td>
<td>Fruit</td>
<td>10878.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Lantana sp.</td>
<td>Chimpanzee</td>
<td>Fruit</td>
<td>2823.0</td>
<td>-</td>
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<tr>
<td>Bequaertiodendron oblaneolatum</td>
<td>Chimpanzee</td>
<td>Fruit</td>
<td>791.0</td>
<td>-</td>
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Note: All mineral content is expressed in mg/kg.  
Abbreviation: KP, Kokolopori.  
\(^a\)Food species that bonobos in Kokolopori consume.
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).

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 seminundated forest (K. Nara & T. Furuchi, 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 proportionately 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 Cameroonian 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 nonhuman 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.

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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 Kamble: 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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Additional Supporting Information may be found online in the supporting information tab for this article.