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# Seasonal and individual predictors of diet in a free-ranging population of mandrills

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## Abstract

Deciphering the dietary habits of a species is central to understanding its ecology, resource requirements, and the evolution of its life history traits. Detailed information on how primates use their environment to address their nutritional needs is available for many primate species. Such basic, but necessary data are, however, fragmented for secretive primates, especially regarding direct behavioral observations of individuals. In this study, we evaluated the impact of seasonality and demographic characteristics on diet and feeding habits in the only free-ranging population of habituated mandrills (*Mandrillus sphinx*), a forest-dwelling species inhabiting the dense humid forests of Central Africa. We collected fine-grained quantitative data on feeding behavior of 57 individually-recognized animals of both sexes and different age classes during a 17-month period. We identified most consumed plant species and determined their abundance in the habitat of the studied mandrills. We showed that diet in this species was extremely diverse and included approximately 150 different plant species, but also mushrooms, invertebrates, and vertebrates. This omnivorous and highly diverse diet presented, however, a clear frugivorous tendency. While we identified three food items largely consumed throughout the year, we also found a strong seasonal signature on diet that was partly, but not only, related to food availability. Age and sex also influenced feeding habits with some feeding specializations according to the individual categories considered and their associated nutritional needs. Our quantitative data provide a basis for future studies examining the nutritional and mineral content of food items, which will further elucidate important aspects of the ecology of this little studied forest primate.

KEYWORDS
feeding ecology, *Mandrillus sphinx*, omnivorous species, seasonality

## 1 | INTRODUCTION

Temporal and spatial variations of food availability affect animal populations in a variety of ways, including their local densities (Chapman, Chapman, Bjorndal, & Onderdonk, 2002; Ganzhorn, 1992), individual spacing patterns (Ganzhorn, 2002), and seasonal migrations (Gates, Caithamer, Moritz, & Tacha, 2001; Moore, Lawler, Wallis, Beale, & Foley, 2010; Overdorff, 1993), as well as individual body conditions, growth rates (Ganzhorn, 2002; Koenig, Borries, Chalise, & Winkler, 1997; Post, Langvatn, Forchhamer, & Stenseth, 1999; Randrianambinina, Rakotondravony, Radespiel, & Zimmerman, 2003), and mortality patterns (Gogarten et al., 2012). Dietary ecology studies often constitute a first step toward the understanding of global ecological characteristics of an animal species. As such, studies on the various determinants of feeding selectivity and the impact of environmental factors, such as seasonality, on diet composition are numerous (Hemingway & Bynum, 2005; Marsh & Chapman, 2013; Stevenson, 2001). By contrast, for some species, often the secretive or cryptic ones, basic knowledge on diet composition may be fragmented. This is the case for wild mandrills (*Mandrillus sphinx*), an Old World primate living in the dense humid forests of Central Africa.

Mandrill is a semi-terrestrial primate living in large multimale–multifemale social groups, sometimes comprising several hundreds of individuals (Abernethy, White, & Wickings, 2002; Rogers et al., 1996). Its conservation status is "vulnerable" (A2cd; IUCN red list; Oates & Butynski, 2008), but the absence of long-term demographic data on this species probably led to underestimated population size. Relatively few individually-based studies have been conducted on wild populations because of an itinerant lifestyle and the dense forests where mandrills live (Abernethy et al., 2002). Basic ecological data on this species are therefore still fragmented and mainly concern early reports of short observation periods and/or based on indirect estimations relying on stomach content and fecal material (Lahm, 1985, 1986; Rogers et al., 1996). Detailed quantitative data on mandrills' feeding behavior based on direct observations are, for example, lacking because wild mandrills' groups have never been habituated to human presence. An early observational, individually-based study on a provisioned semi-free-ranging population living in large enclosures showed, however, that mandrills mainly foraged on the ground (for 76% of the consumed food items) and that males and females displayed different feeding preferences (Norris, 1988). In natural conditions, indirect evidence based on the examination of fecal material showed that mandrills consumed 63 different plant species (representing 27 families) with fruits constituting the principal food source, representing more than 80% in dry weight of fecal remains (Hoshino, 1985). Fruiting species were also over-represented in the mandrill's diet during the rainy season (Hoshino, 1985). Indirect analyses based on non-invasive fecal samples further showed that 88% of consumed food items belonged to more than one hundred plant species (Gautier-Hion, Colyn, & Gautier, 1999). Finally, mandrills also regularly consumed several animal species including invertebrates and vertebrates (Gautier-Hion et al., 1999).

In this study and during a 17-month period, we followed individually-recognized animals from the only free-ranging population of habituated mandrills worldwide, within the framework of a long-term field project (Mandrillus Project; Brockmeyer et al., 2015). The studied social group is constituted of ~130 habituated individuals with approximately one hundred individually-known animals that are daily followed. In this study, and using focal-sampling methods (Altmann, 1974), we evaluated the foraging behavior and feeding preferences of 57 individuals of both sexes and different age classes. In particular, we provided qualitative and quantitative data on plant consumption, including their abundance in the surrounding environment. We further tested for environmental and demographic effects on food choice and selectivity. Given the marked seasonality in Gabon and the diversity of the mandrill's diet (Gautier-Hion et al., 1999), we predicted a pronounced seasonal variation in overall diet (Hoshino, 1985) as well as some feeding specializations according to the age and sex of the studied animals (Norris, 1988).

## 2 | MATERIAL AND METHODS

### 2.1 | Study site

This study was conducted in the Lékédi Park located 7 km northwest away from the village of Bakoumba in Southern Gabon from May 2013 to Dec. 2014. This 14,000-ha park is composed of a mosaic of savannas, grassland, and evergreen forests. Forested blocks are mainly composed of primary and secondary Marantaceae forests with patches of humid open savannas. The study area covers approx. 1,000 ha, roughly corresponding to the home range of the studied population of mandrills (Brockmeyer et al., 2015). The park hosts several primate species typically found in Southern Gabon including central chimpanzees (*Pan troglodytes troglodytes*) and western lowland gorillas (*Gorilla gorilla gorilla*) and also large groups of wild mandrills. While intergroup encounters were never recorded between the study group and other wild groups, solitary male mandrills were regularly observed in the vicinity of the study group in which they may immigrate.

Gabonese habitats are characterized by four different seasons: a long rainy season (Feb.–May; during the study period: $\bar{x} \pm SD$ temperatures: 23.8 ± 3.2°C; total amount of rainfalls: 1,256.8 mm), a long dry season (Jun.–Sep.; 22.1 ± 2.6°C; 142.2 mm), a short rainy season (Oct.–Nov.; 23.3 ± 3.0°C; 535.2 mm), and a short dry season (Dec.–Jan.; 23.4 ± 2.9°C; 312 mm).

### 2.2 | Study population

We studied a free-ranging population of approx. 130 habituated individuals living in the Lékédi Park and its vicinity (Brockmeyer et al., 2015). The population originated from 65 captive individuals initially housed at the CIRMF (Centre International de Recherche Médical de Franceville, Gabon) and released into the park on two occasions (2002 and 2006; see for details on the first release: Peignot et al., 2008). Daily behavioral monitoring combined with genetic analyses of the individuals from this population indicated that more than 85% of the study individuals were wild-born animals. Mandrills foraged freely in the park and its vicinity but from 2002 to 2012, they were weekly supplemented with bananas and monkey chow. Supplementation, however, never provided their full caloric requirements to boost their foraging behavior. At the very beginning, food was provided three to four times a week, but the pace decreased rapidly to occasional supplementations (on average once or twice a week). Food supplementation completely stopped in Apr. 2012, 14 months before the beginning of this study. Mandrills occupied a home range of 866 ha including areas both inside and outside the park boundaries (Brockmeyer et al., 2015).

### 2.3 | Behavioral data collection

We used two observational data sets in the analyses below. Mandrills were followed every day from 6:00 a.m. to 6:00 p.m. by trained field assistants who recorded detailed behavioral data (Poirotte et al., 2017), including time budgets, using 5-min focal observation periods (Altmann, 1974). We retrieved the time spent foraging from all focals performed during 17 months (from May 2013 to Oct. 2014) on 57 individually recognized animals (33 females aged 2–21 years and 24 males aged 3–19 years) of the study group. For each studied individual and across all four seasons, we divided the total time spent foraging by the total time of focal observation (in hours) to obtained the first data set ("percentages of time spent foraging"). We restricted our analyses to these animals that were observed for more than an hour a given season (*N* = 131 individual.seasons representing 48 animals).

In addition, detailed data on feeding behavior were collected on these 57 individually recognized animals of the study group during the same period, again using 5-min focal observation periods. During these sampling periods, a trained observer (GNA) recorded all food items consumed by a focal individual and, whenever possible, the number of bites performed on each consumed food item. If an item was consumed more than once during a same 5-min focal period, we considered this as a single event to avoid pseudo-replication. During the entire study period, we collected a total of 6,350 focal observations representing approximately 517 hr of focal data on the feeding behavior of 57 mandrills ($\bar{x} \pm SD$ of focal time per individual in hours: 8.9 ± 7.3). For the analyses below, this second data set was also restricted to the individuals that were observed for more than an hour a given season (*N* = 121 individual.seasons representing 45 animals).

## 2.4 | Plant collection and identification

We collected all the plant species and plant parts consumed by the studied mandrills and then pressed and identified them at the National Herbarium of the Institute of Tropical Medicine and Pharmacopoeia (IPHAMETRA, Libreville, Gabon) after a first identification using relevant standard literature including various regional and local field guides (Letouzey, 1982a, 1982b; Walker & Sillans, 1961; White & Abernethy, 1996; Wilks & Issembé, 2000). Only seven species remained unidentified (Table 1). We deposited specimens in the herbarium of the University of Sciences and Techniques of Masuku in Franceville, Gabon.

## 2.5 | Frequencies of consumed plants in the environment

We determined the frequencies in the environment of the plant species consumed by the studied mandrills using the species rarity index (*Ri*; as defined per: Géhu & Géhu, 1980). In Nov.–Dec. 2014, we positioned 115 quadrates (25 m × 25 m) in an area covering about 7 ha of the total home range of the study population and representing typical mandrills' habitats (large forested blocks, gallery, and riverine forests, e.g., Abernethy et al., 2002; White et al., 2010). We divided each quadrat into 25 smaller squares (5 m × 5 m) to minimize risks of leaving out cryptic herbaceous species. We recorded all plant species consumed by the studied mandrills found in each square; however, if the same species was found in several squares of the same quadrat, we counted it as a single occurrence. We then calculated the *Ri* of each consumed plant species as follows:

$$Ri = \left(1 - \frac{ni}{N}\right) \times 100$$

where *ni* represented the number of quadrats where the plant species *i* was recorded and *N*, the total number of quadrats. When $Ri < 80$, the plant species was considered frequent in the study area; when $80 < Ri < 100$, the species was rare in the area; and finally when $Ri = 100$, the species was considered as extremely rare or absent in the area.

## 2.6 | Statistical analyses

### 2.6.1 | Foraging time

We first studied the impact of the season (class variable, four modalities) and individual's age (class variable, three modalities) and sex (class variable, two modalities) on the percentages of time spent foraging across all four seasons (131 individual.seasons, 48 individuals), using General Linear Mixed Model (LMM, proc GLIMMIX, SAS V4). We considered three classes of individual's age. Juveniles were animals aged between 1.5 years (the youngest animal in our data set) and 4 years (*N* = 12; 8 males and 4 females). Because of a strong sexual dimorphism in this species, the pace of sexual maturity is different between sexes (Setchell, Lee, Wickings, & Dixson, 2001). We therefore considered as adolescent, females aged 4–5 years (*N* = 2) and males aged 4–9 years (*i* = 6). Finally, adult females were older than 5 years (*N* = 20) and adult males were older than 9 years (*N* = 5). Birth dates of captive-born individuals were exactly known while the age of wild-born animals was either known or estimated using general body condition (a combination of size, stature, and signs of senescence) and for some of the animals, patterns of tooth eruption, and wear (Galbany et al., 2014).

In this model, we considered individual's identity as a random effect as well as all first-order interactions. We kept the full model excluding only non-significant interactions. When a significant effect was found, we further tested for pairwise differences in least square means using the lsmeans function (proc GLIMMIX, SAS V4). We visually checked that data were not over-dispersed.

### 2.6.2 | Descriptive analyses of diet

We performed descriptive analyses of the mandrill's diet by calculating both the "rate" of consumption of each item (number of times an item was consumed divided by the total number of occurrences of all consumed items, across all 57 individuals) and its "frequency" (number of times an item was consumed per hour, across all 57 individuals, either during all four seasons or during each of the four seasons; as per: Table 1). On average, mandrills consumed a high number of plant species in low quantities. For clarity sake, we therefore defined two categories of plant species: those that were frequently consumed

**TABLE 1** Plant species consumed by the 57 studied mandrills of the Lékédi Park and their botanical family

| Botanical family | Species | Plant parts | *Ri* (%) | All seasons | LD | SR | SD | LR | Note |
|---|---|---|---|---|---|---|---|---|---|
| Anacardiaceae | *Antrocaryon klaineanum* | *FR* | 99.3 | 0.041 | 0.052 | 0.206 | 0 | 0 | ND |
| Anacardiaceae | *Lannea welwitschii* | *L, F, FR* | 100 | 0.006 | 0.003 | 0 | 0.04 | 0 | ND |
| Anacardiaceae | *Manguifera indica* | *FR* | 99.3 | 0.015 | 0 | 0.034 | 0.138 | 0 | ND |
| Anacardiaceae | *Pseudospondias longifolia* | *U* | 97.3 | 0.06 | 0.101 | 0 | 0.02 | 0.007 | ND |
| Annonaceae | *Neostenanthera myristicifolia* | *ST* | 57.3 | 0.002 | 0.003 | 0 | 0 | 0 | ND |
| Annonaceae | *Uvaria klaineana* | *FR* | 98 | 0.012 | 0.01 | 0 | 0 | 0.02 | ND |
| Annonaceae | *Uvaria scrabida* | *FR* | 60 | 0.002 | 0.003 | 0 | 0 | 0 | ND |
| Annonaceae | *Xylopia aethiopica* | *FR, S* | 58 | 0.675 | 0.184 b | 5.556 a,b,d | 1.363 a | 0.434 d | SR |
| Annonaceae | *Xylopia staudtii* | *FR, S* | 52 | 0.044 | 0.056 | 0 | 0 | 0.047 | ND |
| Apocynaceae | *Landolphia breviloba* | *B, L, FR, S, RO, ST* | 90 | 0.153 | 0.164 | 0.034 | 0.099 | 0.174 | ND |
| Apocynaceae | *Landolphia dewevrei* | *FR* | 86.67 | 0.064 | 0 | 0 | 0.613 | 0.013 | ND |
| Apocynaceae | *Landolphia glabra* | *FR* | 94.67 | 0.056 | 0 b | 0.72 a,b,d | 0.158 a | 0 d | SR |
| Apocynaceae | *Landolphia hirsuta* | *FR, S, RO* | 92 | 0.043 | 0.077 | 0 | 0 | 0 | ND |
| Apocynaceae | *Landolphia incerta* | *B, L, FR, S, RO* | 92 | 0.162 | 0.003 b,c | 0.652 b | 0.988 c,f | 0.094 f | |
| Apocynaceae | *Landolphia mannii* | *FR, S* | 98 | 0.05 | 0.042 | 0 | 0 | 0.094 | ND |
| Apocynaceae | *Landolphia owariensis* | *FR* | 100 | 0.015 | 0 | 0 | 0.138 | 0.007 | ND |
| Apocynaceae | *Landolphia* sp. | *ST* | 85.3 | 0.014 | 0.024 | 0 | 0 | 0 | ND |
| Apocynaceae | *Rauvolfia vomitoria* | *U* | 90.7 | 0.025 | 0.045 | 0 | 0 | 0 | ND |
| Aracaceae | *Elaeis guineensis* | *FR, N, ST* | 87.3 | 0.193 | 0.181 | 0.171 | 0.296 | 0.187 | ND |
| Aracaceae | *Laccosperma laeve* | *FR, S, RO* | 94 | 0.027 | 0.003 | 0 | 0 | 0.087 | ND |
| Aracaceae | *Laccosperma secundiflorum* | *FR, ST* | 46.7 | 0.219 | 0.073 e | 0.069 d | 0 f | 0.601 d,e,f | LR |
| Aracaceae | *Raphia vinifera* | *FR, S, N, RO, ST* | 84.7 | 0.192 | 0.32 b,c,e | 0.034 b | 0 c | 0.04 e | LD |
| Aracaceae | *Sclerosperma mannii* | *FR, ST* | 97.3 | 0.01 | 0 | 0 | 0 | 0.033 | ND |
| Aspleniaceae | *Asplenium africanum* | *RO* | 96 | 0.002 | 0.003 | 0 | 0 | 0 | ND |
| Balanophoraceae | *Thonningia sanguinea* | *F* | 100 | 0.002 | 0 | 0 | 0 | 0.007 | ND |
| Burseraceae | *Aucoumea klaineana* | *L, FR, S, R* | 33.3 | 0.025 | 0.003 | 0 | 0.158 | 0.027 | ND |
| Burseraceae | *Dacryodes edulis* | *FR* | 98 | 0.012 | 0.003 | 0 | 0.099 | 0 | ND |
| Caesalpiniaceae | *Hylodendron gabunense* | *L, S* | 72 | 0.188 | 0.334 b,c,e | 0 b | 0 c | 0.007 e | LD |
| Capparaceae | *Pentadiplandra brazzeana* | *FR* | 100 | 0.025 | 0 | 0 | 0 | 0.087 | ND |
| Chrysobalanaceae | *Parinari excelsa* | *FR, ST* | 94 | 0.095 | 0 b | 0.857 a,b,d | 0.435 a | 0.013 d | SR |
| Commelinaceae | *Palisota ambigua* | *L, F, FR, RO, ST* | 46 | 0.176 | 0.059 c | 0 a | 0.948 a,c,f | 0.174 f | SD |
| Commelinaceae | *Palisota hirsuta* | *L, ST* | 57.3 | 0.025 | 0.038 | 0 | 0 | 0.013 | ND |
| Connaraceae | *Agelaea pentagyna* | *L, RO, ST* | 36.7 | 0.012 | 0.021 | 0 | 0 | 0 | ND |
| Connaraceae | *Agelaea rubiginosa* | *B, L, FR, RO, ST* | 52 | 0.124 | 0.122 | 0.274 | 0.375 | 0.013 | ND |
| Connaraceae | *Cnestis corniculata* | *G, L, F, FR, S, RO, ST* | 75.3 | 0.3 | 0.285 | 0.583 | 0.593 | 0.174 | ND |
| Connaraceae | *Cnestis ferruginea* | *B, L, F, FR, RO* | 71.3 | 0.116 | 0.157 | 0.24 | 0.02 | 0.047 | ND |
| Connaraceae | *Cnestis* sp. | *L, RO* | 46 | 0.01 | 0.003 | 0.069 | 0.04 | 0 | ND |
| Cucurbitaceae | *Cogniauxia podolaena* | *FR* | 100 | 0.004 | 0 | 0 | 0 | 0.013 | ND |
| Cyatheaceae | *Cyathea camerooniana* | *ST* | 100 | 0.006 | 0.01 | 0 | 0 | 0 | ND |
| Cyperaceae | *Rhynchospora corymbosa* | *U* | 100 | 0.004 | 0 | 0.069 | 0 | 0 | ND |

(Continues)

**TABLE 1** (Continued)

| Botanical family | Species | Plant parts | *Ri* (%) | All seasons | LD | SR | SD | LR | Note |
|---|---|---|---|---|---|---|---|---|---|
| Cyperaceae | *Scleria boivinii* | *L, FR* | 54.7 | 0.259 | 0.15 | 0.514 | 0.514 | 0.334 | ND |
| Dichapetalaceae | *Dichapetalum cf. umbellatum* | *FR* | 66 | 0.017 | 0 | 0.034 | 0.158 | 0 | ND |
| Dilleniaceae | *Tetracera alnifolia* | *FR, S* | 40.7 | 0.087 | 0.108 | 0.069 | 0 | 0.08 | ND |
| Euphorbiaceae | *Alchornea floribunda* | *L, FR, RO, ST* | 59.3 | 0.317 | 0.111 c | 0.377 a | 2.094 a,c,f | 0.1 f | SD |
| Euphorbiaceae | *Bridelia ferruginea* | *FR, ST* | 98.7 | 0.008 | 0.014 | 0 | 0 | 0 | ND |
| Euphorbiaceae | *Croton mayumbensis* | *FR* | 98.7 | 0.041 | 0 | 0 | 0 | 0.14 | ND |
| Euphorbiaceae | *Croton sylvaticus* | *FR, S* | 94.7 | 0.112 | 0 e | 0 d | 0 f | 0.387 d,e,f | LR |
| Euphorbiaceae | *Macaranga schweinfurthii* | *F, FR, S* | 94.7 | 0.01 | 0.003 | 0 | 0.02 | 0.02 | ND |
| Euphorbiaceae | *Macaranga spinosa* | *FR* | 88.7 | 0.085 | 0 c | 0 a | 0.751 a,c,f | 0.04 f | SD |
| Euphorbiaceae | *Maesobotrya klaineana* | *FR* | 69.3 | 0.039 | 0 | 0 | 0.099 | 0.1 | ND |
| Euphorbiaceae | *Maesobotrya staudtii* | *FR* | 95.3 | 0.01 | 0.017 | 0 | 0 | 0 | ND |
| Euphorbiaceae | *Manniophyton fulvum* | *ST* | 74.7 | 0.035 | 0.063 | 0 | 0 | 0 | ND |
| Euphorbiaceae | *Plagiostyles africana* | *B, FR, S* | 72.7 | 0.145 | 0 c | 0.309 a | 1.304 a,c,f | 0 f | SD |
| Euphorbiaceae | *Ricinodendron heudelotii* | *FR, S* | 94 | 0.066 | 0.07 | 0 | 0 | 0.094 | ND |
| Euphorbiaceae | *Uapaca guineensis* | *FR, S, ST* | 44 | 0.615 | 0.974 c,e | 1.132 a,d | 0.02 a,c | 0.027 d,e | |
| Euphorbiaceae | *Uapaca mole* | *U* | 90.4 | 0.006 | 0 | 0 | 0 | 0.02 | ND |
| Fabaceae | *Calopogonium mucunoides* | *F, FR* | 98 | 0.043 | 0.077 | 0 | 0 | 0 | ND |
| Flacourtiaceae | *Oncoba welwitschii* | *FR* | 84.7 | 0.041 | 0 | 0 | 0.059 | 0.12 | ND |
| Gramineae | *Hyparrhenia diplandra* | *L* | 95.3 | 0.054 | 0.035 | 0.514 | 0.059 | 0 | ND |
| Gramineae | *Jardinea gabonensis* | *L* | 99.3 | 0.014 | 0.007 | 0.069 | 0.059 | 0 | ND |
| Gramineae | *Olyra latifolia* | *L, FR, ST* | 90 | 0.162 | 0.125 | 0.309 | 0.375 | 0.134 | ND |
| Gramineae | *Paspalum scrobiculatum* | *FR* | 98 | 0.006 | 0.01 | 0 | 0 | 0 | ND |
| Gramineae | *Setaria megaphylla* | *L* | 100 | 0.004 | 0 | 0.069 | 0 | 0 | ND |
| Gramineae | *Setaria* sp. | *U* | 99.3 | 0.01 | 0 | 0 | 0 | 0.033 | ND |
| Gramineae | *Urelytrum fasciculatum* | *L* | 44 | 0.002 | 0.003 | 0 | 0 | 0 | ND |
| Irvingiaceae | *Chrysophyllum africanum* | *FR* | 98.7 | 0.008 | 0 | 0 | 0 | 0.027 | ND |
| Irvingiaceae | *Chrysophyllum lacourtianum* | *FR, S* | 99.3 | 0.046 | 0.083 | 0 | 0 | 0 | ND |
| Irvingiaceae | *Irvingia grandifolia* | *FR, S* | 99.3 | 0.025 | 0 | 0 | 0.138 | 0.04 | ND |
| Irvingiaceae | *Klainedoxa gabonensis* | *FR* | 98.7 | 0.023 | 0 | 0 | 0 | 0.08 | ND |
| Lauraceae | *Persea americana* | *FR, N* | 99.3 | 0.008 | 0 | 0 | 0.079 | 0 | ND |
| Lecythidaceae | *Petersianthus macrocarpus* | *R* | 100 | 0.01 | 0.017 | 0 | 0 | 0 | ND |
| Leguminosae-Caesalpinoideae | *Berlinia bracteosa* | *F, S* | 96 | 0.064 | 0.021 | 0 | 0.533 | 0 | ND |
| Leguminosae-Caesalpinoideae | *Berlinia confusa* | *S* | 99.3 | 0.004 | 0.007 | 0 | 0 | 0 | ND |
| Leguminosae-Caesalpinoideae | *Dialium corbisieri* | *L* | 84 | 0.004 | 0 | 0 | 0.04 | 0 | ND |
| Leguminosae-Caesalpinoideae | *Dialium dinklagei* | *L, ST* | 62.7 | 0.147 | 0.17 | 0.549 | 0.119 | 0.033 | ND |
| Leguminosae-caesalpinoideae | *Dialium tessmannii* | *L* | 88 | 0.006 | 0.007 | 0 | 0.02 | 0 | ND |
| Leguminosae-Caesalpinoideae | *Distemonanthus benthamianus* | *L* | 94.7 | 0.008 | 0 | 0.069 | 0.02 | 0.007 | ND |

(Continues)

**TABLE 1** (Continued)

| Botanical family | Species | Plant parts | *Ri* (%) | All seasons | LD | SR | SD | LR | Note |
|---|---|---|---|---|---|---|---|---|---|
| Leguminosae-Mimosoideae | *Parkia bicolor* | *FR, S* | 99.3 | 0.054 | 0 | 0 | 0.119 | 0.147 | ND |
| Leguminosae-Mimosoideae | *Parkia filicoidea* | *S* | 100 | 0.023 | 0 | 0 | 0 | 0.08 | ND |
| Leguminosae-Mimosoideae | *Tetrapleura tetraptera* | *FR* | 100 | 0.002 | 0.003 | 0 | 0 | 0 | ND |
| Leguminosae-Papilionoideae | *Angylocalyx* sp. | *B* | 100 | 0.002 | 0.003 | 0 | 0 | 0 | ND |
| Leguminosae-Papilionoideae | *Dalhousiea africana* | *RO* | 82 | 0.014 | 0.024 | 0 | 0 | 0 | ND |
| Leguminosae-Papilionoideae | *Eriosema glomerata* | *FR* | 99.3 | 0.008 | 0.014 | 0 | 0 | 0 | ND |
| Marantaceae | *Halopegia azurea* | *ST* | 95.3 | 0.023 | 0.003 | 0 | 0 | 0.073 | ND |
| Marantaceae | *Haumania danckelmaniana* | *L, FR, S, ST* | 62 | 0.511 | 0.285 | 0.652 | 1.186 | 0.688 | ND |
| Marantaceae | *Haumania liebrechtsiana* | *L, F, FR, S, RO, ST* | 68.7 | 1.174 | 1.312 | 0.96 | 1.225 | 0.935 | ND |
| Marantaceae | *Megaphrynium macrostachum* | *L, F, FR, N, RO, ST* | 41.3 | 2.478 | 2.018 | 3.327 | 4.821 | 2.404 | ND |
| Marantaceae | *Sarcophrynium brachystachyum* | *FR, RO, ST* | 72 | 0.087 | 0.129 | 0 | 0 | 0.053 | ND |
| Marantaceae | *Trachyphrynium braunianum* | *U* | 78.7 | 0.01 | 0.014 | 0 | 0 | 0.007 | ND |
| Melastomataceae | *Dichaetanthera africana* | *L, RO, ST* | 62.7 | 0.035 | 0.017 | 0.412 | 0.02 | 0 | ND |
| Melastomataceae | *Dissotis multiflora* | *L* | 96.7 | 0.031 | 0.014 | 0.137 | 0.158 | 0 | ND |
| Melastomataceae | *Medinilla mirabilis* | *L, FR* | 74.7 | 0.01 | 0 | 0 | 0 | 0.033 | ND |
| Melastomataceae | *Ochthocharis dicellandroides* | *L* | 96.7 | 0.025 | 0.007 | 0 | 0 | 0.073 | ND |
| Melastomataceae | *Tristemma mauritianum* | *L, FR* | 90 | 0.021 | 0.021 | 0 | 0 | 0.033 | ND |
| Meliaceae | *Carapa procera* | *S* | 86.7 | 0.002 | 0 | 0 | 0 | 0.007 | ND |
| Mimosaceae | *Albizia gummisera* | *B, RO* | 93.3 | 0.012 | 0.003 | 0.171 | 0 | 0 | ND |
| Mimosaceae | *Pentaclethra eetveldeana* | *F, S, R, RO* | 47.3 | 0.074 | 0.073 | 0.24 | 0.119 | 0.027 | ND |
| Mimosaceae | *Pentaclethra macrophylla* | *L, F, FR, S, R, RO, ST* | 69.3 | 1.118 | 1.781 c,e | 0.96 | 0.296 c | 0.154 e |  |
| Mimosaceae | *Piptadeniastrum africanum* | *L, FR, RO* | 64.7 | 0.01 | 0.01 | 0 | 0.02 | 0.007 | ND |
| Mimosaceae | *Pseudoprosopis gilletii* | *L, ST* | 80 | 0.015 | 0.021 | 0 | 0.02 | 0.007 | ND |
| Moraceae | *Ficus mucuso* | *FR* | 98.7 | 0.046 | 0.083 | 0 | 0 | 0 | ND |
| Moraceae | *Musanga cecropioides* | *L, F, FR* | 95.3 | 0.474 | 0.543 b | 0.343 b | 0.415 | 0.387 |  |
| Moraceae | *Myrianthus arboreus* | *FR, RO, ST* | 84.7 | 0.05 | 0.017 b | 0.617 a,b,d | 0.02 a | 0.013 d | SR |
| Musaceae | *Musa paradisiaca* | *FR* | 100 | 0.004 | 0 | 0 | 0 | 0.013 | ND |
| Myristicaceae | *Pycnanthus angolensis* | *S* | 84 | 0.019 | 0.021 | 0.137 | 0 | 0 | ND |
| Myristicaceae | *Scyphocephalium ochocoa* | *FR* | 99.3 | 0.008 | 0 | 0 | 0 | 0.027 | ND |
| Nymphaeaceae | *Nymphaea maculata* | *WH* | 99.3 | 0.226 | 0.365 b,c,e | 0.034 b | 0.079 c | 0.047 e | LD |
| Ochnaceae | *Ochna afzelii* | *L* | 80.7 | 0.002 | 0.003 | 0 | 0 | 0 | ND |
| Orchidaceae | *Stanhopea hernandezii* | *L, ST* | 99.3 | 0.004 | 0.007 | 0 | 0 | 0 | ND |
| Pandaceae | *Microdesmis haumaniana* | *FR, ST* | 41.3 | 0.033 | 0.003 | 0 | 0.277 | 0.013 | ND |
| Papillonaceae | *Popowia* sp. | *L* | 31.5 | 0.002 | 0.003 | 0 | 0 | 0 | ND |
| Passifloraceae | *Barteria fistulosa* | *G, L, FR, ST* | 69.3 | 0.015 | 0.014 | 0.069 | 0 | 0.013 | ND |
| Piperaceae | *Piper guineensis* | *L, RO* | 80.7 | 0.008 | 0.003 | 0 | 0 | 0.02 | ND |

(Continues)

**TABLE 1** (Continued)

| Botanical family | Species | Plant parts | *Ri* (%) | All seasons | LD | SR | SD | LR | Note |
|---|---|---|---|---|---|---|---|---|---|
| Rubiaceae | *Craterispermum cerinanthum* | *L, FR* | 84 | 0.087 | 0.111 | 0.171 | 0 | 0.053 | ND |
| Rubiaceae | *Geophila afzelii* | *FR, RO, ST* | 53.3 | 0.139 | 0.09 | 0 | 0 | 0.307 | ND |
| Rubiaceae | *Lasianthus batangensis* | *L, FR* | 59.3 | 0.286 | 0.202 | 0.103 | 0.02 | 0.574 | |
| Rubiaceae | *Lasianthus* sp. | *FR* | 85.3 | 0.006 | 0 | 0 | 0 | 0.02 | ND |
| Rubiaceae | *Morinda morindoides* | *L, FR* | 52 | 0.014 | 0.007 | 0 | 0 | 0.033 | ND |
| Rubiaceae | *Mussaenda debeauxii* | *FR* | 98 | 0.01 | 0 | 0 | 0.02 | 0.027 | ND |
| Rubiaceae | *Mussaenda soyauxii* | *B, FR* | 92.7 | 0.012 | 0.007 | 0 | 0.02 | 0.02 | ND |
| Rubiaceae | *Nauclea latifolia* | *FR* | 100 | 0.014 | 0.024 | 0 | 0 | 0 | ND |
| Rubiaceae | *Pausinystalia johimbe* | *L* | 77.3 | 0.002 | 0 | 0.034 | 0 | 0 | ND |
| Rubiaceae | *Pseudosabicea milbraedii* | *FR* | 92.7 | 0.029 | 0 | 0 | 0 | 0.1 | ND |
| Rubiaceae | *Psychotria gilletii* | *L, F, FR, ST* | 76 | 0.106 | 0.164 e | 0.069 | 0.099 | 0.007 e | |
| Rubiaceae | *Psychotria stenostegia* | *FR, ST* | 90.7 | 0.106 | 0.157 | 0 | 0 | 0.067 | ND |
| Rubiaceae | *Spermacoce latifolia* | *L, FR, ST* | 98.7 | 0.066 | 0.115 | 0 | 0 | 0.007 | ND |
| Rubiaceae | *Tricalysia cf. breteleri* | *L, F, FR, RO* | 58.7 | 0.17 | 0.122 b | 0.755 a,b | 0.178 a | 0.147 | |
| Sapindaceae | *Ganophyllum giganteum* | *FR* | 99.3 | 0.031 | 0 | 0 | 0 | 0.107 | ND |
| Selaginellaceae | *Selaginella myosurus* | *L, ST* | 66 | 0.044 | 0.042 | 0.274 | 0.059 | 0 | ND |
| Smilaceae | *Smilax anceps* | *L, F, FR, RO, ST* | 43.3 | 0.302 | 0.285 | 0.343 | 0.158 | 0.374 | ND |
| Sterculiaceae | *Leptonychia echinocarpa* | *FR* | 94 | 0.031 | 0.049 | 0 | 0 | 0.013 | ND |
| Violaceae | *Rinorea cerasifolia* | *FR* | 100 | 0.008 | 0.003 | 0 | 0.059 | 0 | ND |
| Zingiberaceae | *Aframomum alboviolaceum* | *F, FR, ST* | 85.3 | 0.097 | 0.115 | 0.034 | 0 | 0.107 | ND |
| Zingiberaceae | *Aframomum cf. polyanthum* | *F, FR, ST* | 90.7 | 0.13 | 0.035 e | 0 d | 0.099 f | 0.347 d,e,f | LR |
| Zingiberaceae | *Aframomum daniellii* | *L, F, FR, RO, ST* | 71.3 | 0.936 | 0.574 | 1.509 | 1.442 | 1.349 | ND |
| Zingiberaceae | *Aframomum* sp. | *FR* | 90 | 0.035 | 0.003 | 0 | 0.02 | 0.107 | ND |
| Zingiberaceae | *Costus afer* | *ST* | 96.7 | 0.017 | 0.007 | 0 | 0 | 0.047 | ND |
| Zingiberaceae | *Costus* sp. | *F* | 96.7 | 0.004 | 0.007 | 0 | 0 | 0 | ND |
| Zingiberaceae | *Renealmia cincinnata* | *FR* | 97.3 | 0.033 | 0.003 | 0 | 0 | 0.107 | ND |
| Zingiberaceae | *Renealmia macrocolea* | *F, FR, ST* | 84 | 0.226 | 0.153 e | 0 d | 0.02 f | 0.481 d,e,f | LR |
| – | *Indet1* | – | 100 | 0.002 | 0 | 0 | 0.02 | 0 | ND |
| – | *Indet2* | – | 99.3 | 0.004 | 0 | 0 | 0.04 | 0 | ND |
| – | *Indet3* | – | 96.7 | 0.006 | 0 | 0 | 0.059 | 0 | ND |
| – | *Indet4* | – | 100 | 0.008 | 0 | 0 | 0.079 | 0 | ND |
| – | *Indet5* | – | 100 | 0.002 | 0 | 0 | 0.02 | 0 | ND |
| – | *Indet6* | – | 100 | 0.002 | 0 | 0 | 0 | 0.007 | ND |
| – | *Indet7* | – | 90.7 | 0.004 | 0.007 | 0 | 0 | 0 | ND |

Seasonal frequencies are presented (number of times an item was consumed per hour). These frequencies are based on all the focals performed on the 57 studied animals across all four seasons or per season (with LR: long rainy, LD: long dry, SR: short rainy, SD: short dry).

Plant parts consumed: B, bark; F, flower; FR, fruit; G, gall; L, leaf; N, nut; R, resin; RO, root; S, seed; ST, stem; WH, whole plant; U, unknown.

Lowercase letters identify plant species responsible for the significant differences observed across pairs of seasons (pairwise comparisons across the four seasons using the SIMPER function: a, SR-SD; b, SR-LD; c, SD-LD; d, LR-SR; e, LR-LD; f, LR-SD). The column "Note" identifies plant species that did not contribute the most to the variance observed across season (ND), or the ones that were almost exclusively consumed during one season (the acronym of the season is given); empty cells indicate intermediate cases. Note that the 10 species that contributed the most to the variance were retrieved from a data set restricted to the animals observed for more than 1 hr per season (*N* = 45 animals observed during one to four seasons).

(>0.10 occurrence/hr) and those that were rarely consumed (<0.10 occurrence/hr). This threshold represented the averaged frequency of consumption across all consumed species.

These frequencies of consumption were highly correlated to the number of bites recorded per hour for each consumed item ($R^2$ = 51.5%). We chose to consider the former rather than the latter measurement because frequencies were less subjective to retrieve than the number of bites.

### 2.6.3 | Plant consumption

For each studied individual, we calculated, as above, the frequencies of plant consumption per hour across all four seasons (121 individual. seasons, 45 individuals). We compared the composition of the mandrill's diet across individuals using multivariate analyses (Vegan package version 2.4-3; R software) as parametric statistics were impossible to implement because of over-dispersed data (the mandrill's diet was highly diverse with many plant species consumed in low frequencies overall). We performed analyses of variance using distance matrices and permutation tests (10,000 iterations) with pseudo-*F* ratios (adonis function) based on all plant species consumed. Adonis is similar to permutational MANOVA or nonparametric MANOVA (Anderson, 2001; McArdle & Anderson, 2001) and because its inputs are linear predictors, it is a robust alternative both to the parametric MANOVA and to ordination methods. Moreover, it allows comparing animals based on their full diet rather than on a few items. We standardized the frequencies of consumption and considered the Bray–Curtis index to calculate dissimilarities across individual diets. This index is particularly useful when the probability of detection of a plant species is <1 because it gives more weight to a detection than to an absence of detection.

We first studied the effect of seasonality on the mandrill's diet using the four seasons as defined above. We controlled for a possible individual effect by adding a "strata" statement in the adonis function (which constrained permutations to defined groups; note that removing this strata statement did not impact our results). For each season, we then studied the influence of individual's sex and age on the mandrill's diet as defined above. In all these models based on frequencies of consumption, we further controlled for a possible effect of the total focal time (in hours) performed on each studied animal. Indeed, the number of plant species consumed was correlated to this focal time because of the extreme diversity of the mandrill's diet. Whatever the total focal time we performed (between 1 and 12.24 hr per season across the studied animals), an asymptote was never reached. In other words, the more an animal was observed, the higher the number of consumed species.

When an effect of the studied explanatory variables was found to be significant, we further tested for the homoscedasticity of the data by considering the "betadisper" function (an analogue of, e.g., Levene's test for homogeneity of variances). Homoscedasticity was verified for all the significant variables found (not shown). Nonmetric multidimensional scaling (NMDS; metaMDS function, Vegan package) was used to visualize similarities among individuals by finding the best two-dimensional representations of the distance matrix. We finally performed a similarity percentage (SIMPER) analysis. SIMPER (Clarke, 1993) is based on the decomposition of Bray–Curtis dissimilarity index. The SIMPER function performs pairwise comparisons of groups of sampling units and finds the average contributions of each species to the average overall Bray–Curtis dissimilarity. This analysis was used to identify the plant species that contributed most strongly to the dissimilarity observed across, for example, seasons. However, because most of the plant species consumed contributed slightly to the variance in the mandrill's diet, we only provided results based on the 10 plant species that contributed the most to this variance.

### 2.6.4 | Animal consumption

For each studied animal, we analyzed the frequencies of animal consumption per hour across all four seasons (121 individual.seasons, 45 individuals), using a General Linear Mixed Model (LMM, proc GLIMMIX, SAS V4). Data were first ln-transformed to fit to a Gaussian distribution. We tested for possible effects of the season, individual's sex and class of age, as defined above. In this model, we also considered individual's identity as a random effect as well as all first-order interactions except the interaction between season and age class because of the non-representation of some categories. We kept the full model excluding non-significant interactions. When a significant effect was found, we further tested for pairwise differences in least square means using the lsmeans function (proc GLIMMIX, SAS V4). We visually checked that data were not over-dispersed.

## 3 | RESULTS

### 3.1 | Generalities about the mandrill's diet

Over the studied period, mandrills spent 56.2% of their time foraging. All individuals foraged more during the long dry season than during any other season and this effect tended to persist during the succeeding short rainy season (Table 2). Females tended to spend more time foraging than males across all seasons, as did juveniles compared to adults and to a lesser extent, adolescents (Table 2). We further found a significant effect of individual's age and sex with adult males spending the least time foraging overall (Table 2).

The 57 studied mandrills consumed a total of 147 plant species belonging to 47 botanical families (Table 1). Mandrills mostly consumed these plant species (rate of consumption across all consumed items: 74.1%) compared to invertebrates (5.6%), vertebrates (<1%), and mushrooms (<1%). Finally, mandrills foraged on unidentified items collected from the ground on 19.3% of all occurrences. Mandrills ate 449 different plant parts with fruits being largely dominant (rate of consumption across all plant parts: 40.2%) in comparison with stems (23.7%), seeds/nuts (17.1%), or leaves (11.2%). Other items such as roots, barks, flowers, gums or honey were all rarely consumed (<5%; Table S1 for details about the frequencies of consumption of these plant parts across seasons, individual's age and sex).

The analysis of the species *Ri* showed that 46 plant species were abundant (*Ri* < 80) in mandrills' home range (Table 1). Among these 46 species, 22 were frequently consumed (>0.10 occurrence/hr, such as *Xylopia aethiopica* and *Pentaclethra macrophylla*), while 24 others were only rarely consumed (<0.10 occurrence/hr, such as

**TABLE 2** Percentages of time spent foraging across seasons and individual's age and sex

| | Averaged percentages of time spent foraging (±*SD*) | *F* | *p* |
|---|---|---|---|
| Season | LD: 68.7 ± 13 | 67.05 | **<.0001** |
| | SR: 50.8 ± 11 | | |
| | LR: 50.0 ± 10 | | |
| | SD: 46.4 ± 14 | | |
| Individual's sex | F: 59.1 ± 14 | 3.21 | .077 |
| | M: 52.4 ± 16 | | |
| Individual's age | JUV: 63.5 ± 0.15 | 6.44 | **.003** |
| | ADO: 49.0 ± 13 | | |
| | ADU: 55.4 ± 15 | | |
| Interaction between age and sex | F JUV: 61.2 ± 13 | 8.34 | **<.001** |
| | F ADO: 56.5 ± 23 | | |
| | F ADU: 58.9 ± 14 | | |
| | M JUV: 64.3 ± 16 | | |
| | M ADO: 48.1 ± 12 | | |
| | M ADU: 42.1 ± 9 | | |

These percentages were averaged across studied individuals. Data were restricted to the animals observed for more than 1 hr per season (*N* = 48 animals observed during one to four seasons corresponding to 131 individual.seasons).

Results from the statistical model (LMM) are also provided (*F*, *F*-statistics; *p*, *p*-values). Significant effects are shown in bold. Pairwise differences in least square means are as follows. Seasonal effect: LD significantly higher than all other seasons ($p < .0001$ in all instances); SR significantly higher than SD ($p = .030$); $p > .05$ in all other instances. Effect of individual's age: JUV significantly higher than ADU ($p < .001$) and slightly higher than ADO ($p = .069$); $p > .05$ in all other instances. Effect of the interaction between age and sex: M ADU significantly lower than all other categories ($p < .05$ in all instances) except than F ADO ($p > .05$); M JUV and F ADU significantly higher than M ADO ($p < .005$ in all instances); $p > .05$ in all other instances.

*Popowia* sp.; Table 1). By contrast, 11 other plant species were frequently consumed by mandrills (>0.10 occurrence/hr) while rare in their environment, such as *Renealmia macrocolea*, *Nymphaea maculata* or *Musanga cecropioides* (Table 1). Finally, all plant species that were considered as "absent" from the environment from the species rarity index (*Ri* = 100) were also rarely consumed (≤0.025 occurrence/hr). We identified three plant species that were frequently consumed all year-long (>0.50 occurrence/hr): two Marantaceae (*Haumania liebrechtsiana* and *Megaphrynium macrostachum*) and a Zingiberaceae (*Aframomum daniellii*). Mandrills consumed all plant parts of these three species including their roots, stems or flowers in addition to their fruits (Table 1).

During the whole study period, mandrills were observed consuming animal species on 669 occasions, representing a rate of consumption of 5.8% across all consumed items. Animal items mostly included insects (93.7%) such as caterpillars, ants, and termites. More rarely, mandrills fed on spiders (1.6%), amphibians (<1%), reptiles (1.2%) such as turtles and lizards, mammals (1.5%) such as rats and gazelles, or birds (<1%).

## 3.2 | Plant consumption

Seasonality explained almost 30% of the variance in the mandrill's diet (Adonis function; Table 3) which greatly differed across all four seasons. Indeed, we found no overlap in dietary similarities across seasons when considering the best dimensional representation of the distance matrix (Figure 1). When restricting the data set to the 10 plant species that contributed the most to the observed variance across seasons, pairwise comparisons across these seasons (SIMPER function) revealed that most species (125/147; Table 1) did not contribute or contributed very slightly to seasonal variations. By contrast, only a few plant species appeared to be consumed during a single season (Table 1).

Diet significantly or tended to differ between males and females during the two rainy seasons (Table 3), especially during the short rainy season where sex explained 13.5% of the variance. The 10 plant species that contributed the most to the variance observed between the sexes explained only small proportions of this variance, suggesting that several plant species were responsible for small sex differences, with two exceptions: *Plagiostyles africana* and *Craterispermum cerinanthum* were both more consumed by males and explained 4% of the variance between the sexes during the short rainy season (Table 4).

Diet also significantly differed across the three age classes defined but during the long dry season only (Table 3). As above, the 10 plant species that contributed the most to the variance observed across age classes did not explain more than 2.8% of this variance and only one species differed across all three age classes (*Psychotria gilletii*; Table 5). Additionally, a few plant species were consumed in large majority by one age class compared to the two others (juveniles: *Ficus mucuso*, *Geophila afzelii*, *Sarcophrynium brachystachyum*; adolescents: *Aframomum alboviolaceum*, *Laccosperma secundiflorum*, *Landolphia hirsuta*; adults: *Scleria boivinii*; Table 5).

## 3.3 | Animal consumption

The frequency of animal consumption highly varied across seasons ($F = 42.39$, $p < .0001$) and sexes ($F = 4.52$, $p = .037$), but not across age classes ($F = 0.48$, $p = .62$). Mandrills consumed equally frequently animal species both during the long rainy and the short dry seasons (difference in least square means between these two seasons: $p = .39$) but not during the short rainy season (all pairwise comparisons across seasons: $p < .029$). Females consumed more frequently animal species than males ($\bar{x} \pm SD$: 0.67 ± 0.64 *vs*. 0.53 ± 0.69 occurrence/hr in females and males, respectively).

# 4 | DISCUSSION

Our results showed that mandrills spent about half of their time foraging, with non-negligible variations observed across seasons and individual's age and sex. The mandrill's diet appeared also to be more diverse than previously reported (Gautier-Hion et al., 1999; Hoshino, 1985) with 147 plant species consumed over a 17-month period,

**TABLE 3** Determinants of the mandrill's (plant) diet

| | *N* | *F* | $R^2$ (%) | *p* | Stress value |
|---|---|---|---|---|---|
| All four seasons | 121 | 19.27 | 29.2 | **<.0001** | 0.19 |
| Long rainy | | | | | |
| Sex | 38 | 1.49 | 3.6 | .060 | 0.23 |
| Age class | | 1.20 | 5.8 | .16 | |
| Long dry | | | | | |
| Sex | 43 | 1.12 | 2.4 | .30 | 0.21 |
| Age class | | 1.80 | 7.8 | **.002** | |
| Short rainy | | | | | |
| Sex | 14 | 1.93 | 13.5 | **.012** | 0.21 |
| Age class | | 1.30 | 9.1 | .18 | |
| Short dry | | | | | |
| Sex | 26 | 0.71 | 2.8 | .81 | |
| Age class | | 1.17 | 9.3 | .22 | |

Significant effects (in bold) indicate higher diet similarity within classes than between classes (adonis function). *F*-statistics (*F*), percentage of variance explained ($R^2$), and *p*-values are provided. Sample sizes (*N*) give either the total number of individual.seasons (all seasons) or the number of individuals (for each of the four seasons). Stress values retrieved from the NMDS procedures are provided.

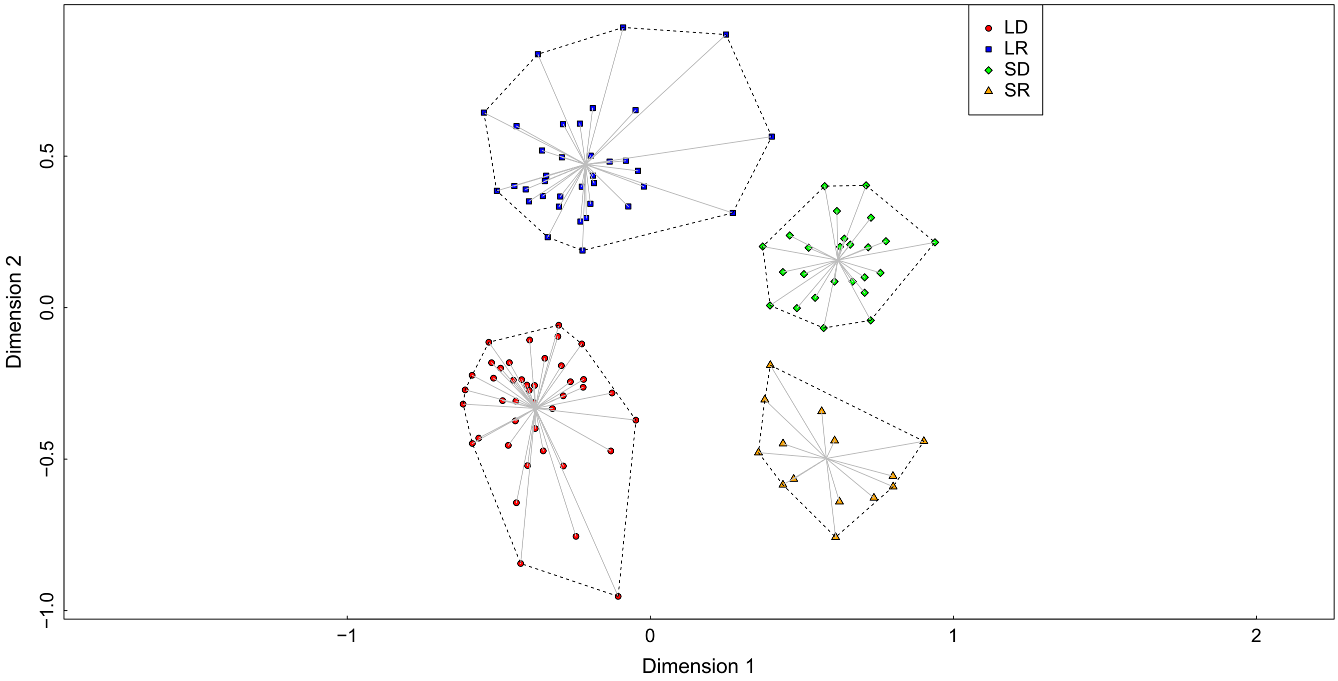

**FIGURE 1** Seasonal similarities in the mandrill's (plant) diet across individuals. Each data point represents an individual diet (individual frequency) during one given season based on non-metric multidimensional scaling. LD (dots, in red in the online version of the figure): long dry season; LR (squares, in blue online): long rainy season; SD (diamonds, in green online): short dry season; SR (triangles, in orange online): short rainy season. Data points are grouped (dashed lines) by season and the centroid of each group is indicated

representing almost 450 different plant parts. In addition to these numerous plant species, mandrills also consumed mushrooms and animal items. Mandrill appeared to be an omnivorous primate species with a frugivorous tendency, confirming earlier results (Gautier-Hion et al., 1999; Hoshino, 1985; Lahm, 1986; Norris, 1988; Rogers et al., 1996).

Most of the plant species in the diet of mandrills were either rare in their home range and little consumed or both abundant and frequently consumed as expected if mandrills were constrained by plant availability. This positive relationship between food availability and frequency of consumption has been observed in other frugivorous primates (Hladik, 1988; Meyers & Wright, 1993; Wrangham, Conklin-Brittain, & Hunt, 1998). On some occasions, however, mandrills rarely consumed some plant species that were abundantly present in the environment, probably reflecting an optimization of feeding strategies or an active avoidance due to, for example, plant toxicity. Conversely, mandrills were found to abundantly consume some plant

**TABLE 4** The 10 plant species contributing the most to the model's variance across individual's sex and season (short rainy [SR] and long rainy [LR] seasons)

| | Species | M | F | Variance explained (%) |
|---|---|---|---|---|
| SR | *Plagiostyles africana* | 1.04 | 0.13 | 4.5 |
| | *Craterispermum cerinanthum* | 0.82 | 0 | 4.3 |
| | *Hyparrhenia diplandra* | 0.15 | 0.65 | 3.6 |
| | *Smilax anceps* | 0.49 | 0.23 | 3.4 |
| | *Tricalysia cf. breteleri* | 1.03 | 0.47 | 3.3 |
| | *Dialium dinklagei* | 1.04 | 0.49 | 3.2 |
| | *Myrianthus arboreus* | 0.35 | 0.89 | 3.1 |
| | *Landolphia incerta* | 0.80 | 0.75 | 3.1 |
| | *Pentaclethra macrophylla* | 1.69 | 0.49 | 3.1 |
| | *Dichaetanthera africana* | 0.73 | 0.27 | 3.1 |
| LR | *Elaeis guineensis* | 0.19 | 0.17 | 2.2 |
| | *Renealmia macrocolea* | 0.47 | 0.51 | 2.2 |
| | *Aframomum cf. polyanthum* | 0.45 | 0.33 | 2.2 |
| | *Landolphia breviloba* | 0.07 | 0.17 | 2.1 |
| | *Croton sylvaticus* | 0.28 | 0.43 | 2.1 |
| | *Palisota ambigua* | 0.20 | 0.14 | 2.1 |
| | *Halopegia azurea* | 0.31 | 0 | 2.1 |
| | *Klainedoxa gabonensis* | 0.19 | 0.04 | 1.9 |
| | *Oncoba welwitschii* | 0.04 | 0.15 | 1.9 |
| | *Xylopia aethiopica* | 0.33 | 0.47 | 1.9 |

Averaged frequencies of consumption per sex (M: males, F: females) are presented. The proportion of variance explained by each plant species is provided. Averaged frequencies are sometimes close between sexes (e.g., SR: *Landolphia incerta*), indicating that the variance observed in one sex is high compared to the other sex.

species that were rare in their habitat. These results again highlight diet preferences in the studied animals. Intraspecific population surveys in several primates showed large variations in feeding habits that were unrelated to food availability, with local traditions and food profitability probably explaining such variations (Chapman & Fedigan, 1990; Richard, 1977). Indeed, important plant compounds, such as secondary compounds and mineral content, are probably crucial factors regarding feeding selectivity (Carrai, Borgognini-Tarli, Huffman, & Bardi, 2003; Cousins & Huffman, 2002; Ganzhorn, Klaus, Ortmann, & Schmid, 2003; Magliocca & Gautier-Hion, 2002; Oates, Swain, & Zantovska, 1977; Wrangham & Waterman, 1983). For example, plant species like *Musanga cecropioides* and *Rhynchospora corymbosa*, consumed by the studied mandrills, were also selected by chimpanzees and gorillas primarily for their mineral content (Magliocca & Gautier-Hion, 2002; Simmen & Hladik, 1998).

Primate ranging behavior is a trade-off between the energy obtained from food and the energy expended during the foraging process. The preferential frugivory that we report in mandrills is in accordance with the large home range that the study population occupied (approx. 10 km$^2$; Brockmeyer et al., 2015; see also: White et al., 2010, for home range estimates at the Lopé National Park) and its average day-range length (2.42 km/day; Brockmeyer et al., 2015). Home range sizes are generally larger in frugivorous primates than in folivorous primates because fruit distributions are generally patchier while leaves are evenly distributed in forested habitats (Clutton-Brock & Harvey, 1977). For example, two morphologically similar species of langurs showed different home ranges associated to different feeding behavior. The more frugivorous species (*Presbytis entellus*) ranged in an area of about 15 ha, triple the area occupied by the species (*P. senex*) living in the same habitat but that mainly fed on the leaves of *Adina cordifolia*, homogenously distributed in the area (Hladik & Hladik, 1972; and see: Ehlers Smith, Ehlers Smith, & Cheyne, 2013, for related results on Colobines).

By contrast with earlier studies on the feeding ecology of mandrills, our observational survey covered all four seasons characterizing Gabonese environment, albeit on a limited period of time (17 months). We found that mandrills spent more time foraging during the long dry season compared to any other season and that diet differed dramatically across the four seasons, again suggesting that diet was largely constrained by food availability. Several studies previously demonstrated that food items such as fruits and young leaves (first and fourth preferred plant parts in our study, respectively) were highly seasonal (Meyers & Wright, 1993; Van-Schaik, Terborgh, & Wright, 1993; Wrangham et al., 1998), possibly explaining the pronounced seasonal variations we found. While previous studies suggested that seasonal variations of food availability were less salient in Equatorial rainforests than in dryer tropical habitats (Hladik, 1978), a large-scale phenological survey of 175 plant species found in North-Eastern Gabon showed that fruit availability was highly dependent of the season (Gautier-Hion et al., 1985), in concordance with our findings. We found, however, that 15 species only contributed for most of the observed diet variation across all four seasons, with a large monopolization of 3–4 items per season. Moreover, throughout the year, mandrills consumed almost all the parts (fruits, flowers, young stems and roots) of a few core plant species. These species probably constituted the staple foods in the mandrill's diet. In tropical and Equatorial forests, fruits, seeds, flowers, nectar, and bark produced by a small set of plant species only (e.g., nectar of *Combretum assimile* in Peru: Terborgh & Stern, 1987; nectar of *Mabea fistulifera* in Brazil: Ferrari & Strier, 1992; fruits of *Polyalthia suaveolens* in Gabon: Gauthier-Hion & Michaloud, 1989; nectar of *Daniella pynaertii* in Republic of Congo: Gautier-Hion & Maisels, 1994) are available all year-long and constitute, as such, core plant resources for a wide range of animal species (Gilbert, 1980; Howe, 1977).

In our study, we also showed that mandrill's sex influenced feeding habits. First, females spent more time foraging than males, as observed in a captive population of mandrills where females foraged during 67% of their time compared to 57% in males (Norris, 1988). Sexual differences in feeding selectivity were also apparent during the rainy seasons: two of the 10 plant species that contributed the

**TABLE 5** Plant species contributing the most to the model's variance across individual's age classes (during long dry season)

| | Juveniles | Adolescent | Adults | Variance explained |
|---|---|---|---|---|
| *Aframomum alboviolaceum* | 0.07 a | 0.22 a,c | 0.09 c | a: 2.8%; c: 2.6% |
| *Agelaea rubiginosa* | 0.17 a | 0.16 a,c | 0.12 c | a: 1.9%; c: 2.0% |
| *Chrysophyllum lacourtianum* | 0.10 | | 0.08 | 1.8% |
| *Cnestis corniculata* | 0.14 | 0.56 | | 2.4% |
| *Dialium dinklagei* | 0.26 b | 0.13 c | 0.16 b,c | b: 2.0%; c: 2.0% |
| *Elaeis guineensis* | | 0.27 | 0.18 | 2.1% |
| *Ficus mucuso* | 0.24 a,b | 0.07 a | 0.08 b | a: 2.2%; b:2.1% |
| *Geophila afzelii* | 0.19 a,b | 0.05 a | 0.08 b | a: 2.0%; b: 1.9% |
| *Laccosperma secundiflorum* | 0.05 a | 0.14 a,c | 0.05 c | a: 1.9%; c: 2.1% |
| *Landolphia hirsuta* | 0.03 a | 0.10 a,c | 0.07 c | a: 2.2%; c: 2.6% |
| *Lasianthus batangensis* | 0.22 | | 0.21 | 1.8% |
| *Nymphaea maculata* | | 0.43 | 0.32 | 2.0% |
| *Psychotria gilletii* | 0.18 a,b | 0.11 a,c | 0.18 b,c | a: 2.0%; b: 1.9%; c: 1.9% |
| *Psychotria stenostegia* | 0.24 | | 0.14 | 1.9% |
| *Sarcophrynium brachystachyum* | 0.24 a,b | 0.08 a | 0.11 b | a: 2.0%; b: 2.0% |
| *Scleria boivinii* | 0.13 b | 0.05 c | 0.16 b,c | b: 1.9%; c: 2.2% |
| *Spermacoce latifolia* | 0.25 a,b | 0.03 a | 0.13 b | a: 1.9%; b: 1.9% |
| *Xylopia staudtii* | | 0.13 | 0.06 | 1.9% |

The 10 (plant) species that contributed the most to the model's variance are provided for pairwise comparisons. Averaged frequencies of consumption per age class are presented. The proportion of variance explained by each plant species is provided. Averaged frequencies are sometimes close across classes (e.g., *Psychotria gilletii*), indicating that the variance observed in one class is high compared to the other classes. Letters indicate significant differences across pairwise comparisons (a: juveniles-adolescents; b: juveniles-adults; c: adolescents-adults).

most to the variance observed between the sexes were never consumed by females while widely eaten by males (short rainy season: *Craterispermum cerinanthum* and long rainy season: *Halopegia azurea*). Overall, males showed a more diverse diet than females, probably explaining most of the dietary differences observed between the sexes. Indeed, 13 plant species (over 20) were more widely consumed by males, albeit females consumed 4.3 times more *Hyparrhenia diplandra* and 2.5 times more *Myrianthus arboreus* (mainly the leaves) than males during the short rainy season. In captivity, males also showed a more diverse diet than females perhaps because, in this early study, females fed more on grass than males (Norris, 1988). The sex differences that we report here are likely due to different physiological constraints and needs, either related to the prominent sexual dimorphism in this species or to the reproductive status of females or both. Differences in feeding habits may be due to the large body mass variations observed between sexes: in this population, females were on average three times lighter than males (M.J.E. Charpentier, personal observation). Their caloric needs were therefore certainly lower than males. Furthermore, females may have access to different food items, for example the ones situated on fine branches. Alternatively, fully grown males may also spend more time on the ground and spend more time feeding on lower levels of the forest, albeit in captivity males were observed to feed more on arboreal strata of the forest (Norris, 1988). The time dedicated to resting *vs*. feeding also differs between male and female primates (Clutton-Brock, 1977; Nakagawa, 2000), including in the studied mandrills (M.J.E. Charpentier, personal observation). Finally, in Cercopithecines, females may also preferentially consume food items rich in proteins, such as leaves, while males may prefer energetic food items such as fruits and flowers which are rich in carbohydrates that are easily digested (Cords, 1986; Gauthier-Hion, 1980; Harrison, 1983; Nakagawa, 2000). In our study, while we did not find a strong support for a higher consumption of leaves in females and of fruits in males (Table S1), we obtained some support for a higher protein-rich diet in females: studied female mandrills consumed more animal proteins than males, suggesting sex-related differential physiological needs. Similarly, adult female gorillas also generally consumed more plant proteins than silverback males, probably reflecting higher metabolic requirements of females due to pregnancy, lactation, and transport of infants (Rothman, Dierenfeld, Hintz, & Pell, 2008).

The mandrill's diet also differed across the three age classes defined during the long dry season where food availability was probably the lowest and juveniles also spent more time foraging than older animals. The effect of age observed in feeding preferences probably reflected distinct feeding strategies resulting from different nutritional needs. In addition, these effects may reflect different capacities in monitoring the environment as a function of age and/or an increased propensity to "try-and-taste" unknown food items in young individuals. Moreover, due to differences in body size and stature, younger animals may have more access to food located at the extremity of boughs (Clutton-Brock, 1977). A closer examination of the 10 plant species that contributed the most to the variance observed across age classes indicated that juveniles, and to a lesser extent adolescents, showed marked feeding preferences while adult diet seemed more equilibrated across these plant species. Juveniles, for example, fed largely more on *Dialium dinklagei*, *Ficus mucuso*, *Geophila afzelii*, *Sarcophrynium brachystachyum*, and *Spermacoce latifolia* than adolescents and adults did.

Taken together, our results called for further attention to these animal species that live in rather predictable and buffered environments such as the Equatorial forests. Such seasonal effects we report here may have shaped various life history traits in mandrills. This study sets therefore the first steps toward future analyses that will examine, for example, the nutritional contents of the consumed plant species to characterize finely optimal feeding strategies in this little studied species.

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