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RESEARCH ARTICLE

Feeling a bit peckish: Seasonal and opportunistic insectivory for wild gorillas

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Abstract

Objectives: Insectivory likely contributed to survival of early humans in diverse conditions and influenced human cognitive evolution through the need to develop harvesting tools. In living primates, insectivory is a widespread behavior and frequently seasonal, although previous studies do not always agree on reasons behind this. Since western gorillas (*Gorilla gorilla*) diet is largely affected by seasonal variation in fruit availability, we aimed to test three non-mutually exclusive hypotheses (habitat use, frugivory and rainfall) to explain seasonality in termite feeding across age/sex classes in three habituated groups ($N_{\text{individuals}} = 27$) in Central Africa.

Materials and Methods: We used 4 years of ranging, scan and continuous focal sampling records of gorillas ($N_{\text{ranging days}} = 883$, $N_{\text{scans}} = 12,384$; $N_{\text{hours}} = 891$) in addition to 116 transects recording vegetation and termite mound distribution.

Results: Depending on the age/sex classes, we found support for all three hypotheses. Time spent in termite-rich vegetation positively impacted termite consumption in all age/sex classes, but subadults. Lengthier travels increased termite feeding in females but decreased it in subadults. Frugivory decreased termite consumption in adults. Daily rainfall had a positive effect on termite feeding and foraging in silverbacks and juveniles, but a negative effect in subadults. For females, rainfall had a positive effect on termite feeding, but a negative effect for termite foraging.

Discussion: In great apes, seasonal insectivory seems to be multifactorial and primarily opportunistic with important differences among age/sex classes. While insectivory has potentials to be traditional, it likely played a crucial role during primate evolution (including ours), allowing diet flexibility in changing environments.

KEYWORDS

feeding behavior, great apes, insectivory, seasonality, termites, western gorillas

1 | INTRODUCTION

Insect feeding played an important role in the development of early humans. Indeed, C3 and C4 isotopic signatures of robust

australopithecines show seasonal and annual variations in their diet (Sponheimer et al., 2006) and suggest that insects may have helped to fill suspected protein gaps (Lesnik, 2018; Sponheimer et al., 2006). In addition, bone tools dated to 1–2 million years ago associated with

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numerous *Paranthropus robustus* and early *Homo* remains showed wear patterns similar to those used in termite foraging (d'Errico & Backwell, 2009). Thus, insectivory in our ancestors triggered the cultural and cognitive abilities necessary to develop harvesting tools (Lesnik, 2018).

Many animal species consume insects for their high nutritional value (Bukkens, 1997). Insect energy and protein composition per unit mass are generally higher than most other food resources present in the environment (DeFoliart, 1989; Redford & Dorea, 1984; Rothman et al., 2014). Insectivory is widespread among primates (Raubenheimer & Rothman, 2013). Likely, this feeding behavior has been passed down from early primates, as evidenced by the presence of Acidic Mammalian Chitinase genes (CHIA) in all primate species genomes, including humans (Janiak et al., 2018). Due to the small size and mobility of insects, which limit the volume consumable by their predators (McGrew, 2001), highly insectivorous diets are only observed in a few primate species which have a body mass less than 1 kg (Kay, 1984); larger primates are mostly occasional insectivores (McGrew, 2001; Rothman et al., 2014). The majority of these large primates live in tropical forests with inter and intra-annual variations in rainfall and food availability (Chapman et al., 1999; Wright & van Schaik, 1994). High dietary flexibility, including occasional insectivory, allows larger primates to survive in a seasonally changing environment (Isbell & Young, 2007).

Great apes are thought to be specialized in the consumption of social insects as their high concentration in patchily distributed locations makes them easier to collect, and thus more profitable compared to other insect species (Fox et al., 2004; McGrew, 2001; Rothman et al., 2014; Tutin & Fernandez, 1992). The degree of great ape insect consumption differs between species (sympatric populations of *Pan troglodytes* and *G. gorilla*: Deblauwe, 2009; Deblauwe & Janssens, 2008; Tutin & Fernandez, 1992), between populations (e.g., *G. gorilla*: Cipolletta et al., 2007; Fuh et al., 2022) and among individuals of the same population depending on their age and sex class (e.g., *Pan troglodytes*: McGrew, 1983; Pruetz & Bertolani, 2007; e.g., *G. gorilla*: Cipolletta et al., 2007; Ganas & Robbins, 2004; Watts, 1989; e.g., *Pongo pygmaeus*: Fox et al., 2004). However, the study of insectivory in great apes has long been neglected likely because of its small nutritional contribution to their overall diet (McGrew, 1992, 2001). Although the main food component in the diet of the majority of great ape species is generally highly seasonal ripe fruit (Conklin-Brittain et al., 1998, 2000), in certain periods of the year some populations spend up to 10% of their feeding time consuming insects (e.g., *Pan troglodytes*: Bogart & Pruetz, 2011; e.g., *Gorilla gorilla*: Masi et al., 2015; e.g., *Pongo pygmaeus*: Fox et al., 2004). In terms of nutritional intakes, although representing only about 1% of the daily kcal requirements for chimpanzees and gorillas, ants and termites covered the entire daily Mg needs in chimpanzees and Fe in gorillas (Deblauwe & Janssens, 2008).

Great ape insectivory also tends to be seasonal (e.g., *Pan troglodytes*: Bogart & Pruetz, 2011; Goodall, 1968; e.g., *Gorilla* spp.: Cipolletta et al., 2007; Deblauwe, 2009; Fuh et al., 2022; Masi et al., 2015; Tutin & Fernandez, 1992), although it is not entirely clear why. While correlations between insect consumption and either fruit consumption, insect availability or rainfall have been tested (Bogart & Pruetz, 2011;

Cipolletta et al., 2007; Deblauwe, 2009; Doran et al., 2002; Fox et al., 2004; Goldsmith, 1999; Tutin & Fernandez, 1992) the results have been difficult to interpret given the complex interaction of ecological and nutritional factors affecting its variation (Cipolletta et al., 2007; Deblauwe, 2009; Tutin & Fernandez, 1992).

Due to inter- and intra-species differences, gorillas are an interesting taxon for investigating seasonal insectivory. While 3.3%–17.6% of mountain gorilla (*Gorilla b. beringei*) fecal samples show insect remains (Ganas & Robbins, 2004), in eastern lowland gorillas (*Gorilla beringei graueri*) this percentage reaches 30% (Yamagiwa et al., 1991, 1994). Similarly, in western gorillas (*G. g. gorilla*) insect remains have been observed in 30% of fecal samples collected over 7 years of monitoring in Gabon (Tutin & Fernandez, 1992). Western gorillas in particular are interesting for this purpose since they show large seasonal dietary variations across the year, particularly in fruit consumption (Doran et al., 2002; Masi et al., 2009, 2015; Remis, 1997a). In addition, previous studies showed their insect consumption also seems to be seasonal (Cipolletta et al., 2007; Deblauwe, 2009; Deblauwe et al., 2003; Goldsmith, 1999; Masi et al., 2015; Rogers et al., 1988; Tutin & Fernandez, 1992). However, the majority of these previous studies were based on indirect observations that likely underestimate the quantity of insects consumed (Cipolletta et al., 2007; Deblauwe, 2009; Deblauwe et al., 2003; Goldsmith, 1999; Rogers et al., 1988; Tutin & Fernandez, 1992). In addition, none of the studies that were based on direct observations of western gorilla feeding behavior (Doran-Sheehy et al., 2009; Fuh et al., 2022; Lodwick & Salmi, 2019; Masi et al., 2015) have investigated ecological variables that might trigger seasonal insectivory.

Previous studies hypothesized that the consumption patterns of the insects most eaten by western gorillas, termites, may change according to the time spent in termite-rich vegetation (Deblauwe, 2009; Tutin & Fernandez, 1992). Given the large seasonal changes in western gorilla diet (Doran et al., 2002; Fuh et al., 2022; Masi et al., 2015; Remis, 1997a, 1997b), likely habitat use also differs across the year. This led to the formulation of a *Habitat Use Hypothesis*. Indeed, when feeding mainly on fruit, western gorillas use more fruit-rich arboreal areas and less *Marantaceae*-rich herbaceous vegetation, which is poorer in termites because of the limited dense forest canopy (Cipolletta et al., 2007; Dibog et al., 1999; Eggleton et al., 2002). In addition, during periods of high fruit availability western gorillas travel more to locate fruiting trees (Cipolletta, 2004; Goldsmith, 1999; Masi et al., 2009), likely increasing the probability to encounter termite mounds (Deblauwe, 2009).

Since some previous studies found higher termite remains in gorilla feces during the rainy season, also a *Rainfall Hypothesis* has been formulated (Cipolletta et al., 2007; Deblauwe, 2009; Doran et al., 2002). Rainfall may cause variations in termite accessibility for gorillas. During dry seasons, soil-dwelling termites move deeper into the soil in search of moisture (Wood et al., 1982). In addition, gorillas break the termite mounds by hand and gain access to the inner termites (Cipolletta et al., 2007; Masi et al., 2022; Salmi et al., 2016; Tutin & Fernandez, 1983). Rains may soften the hard-outer layer of the termite mound rendering it easier to break open during the rainy season compared to the dry season (Cipolletta et al., 2007).

Finally, when western gorillas feed heavily on fruit, protein, fat and minerals intakes decrease (Lodwick & Salmi, 2019; Masi et al., 2015). They thus may need to implement their diet with more animal proteins from insects during the frugivory season. This *Frugivory Hypothesis* is supported by positive correlations found between fruit and insect consumption in previous studies on western gorillas (Deblauwe, 2009; Deblauwe & Janssens, 2008; Goldsmith, 1999; Kuroda et al., 1996). However, since other studies found no correlation (Cipolletta et al., 2007; Doran et al., 2002) or a negative one (Rogers et al., 1988) the effect of fruit eating on insect consumption remain unclear.

Relying on an unprecedented data set of over 4 years of direct observations of three habituated groups of wild western gorillas, we aim to shed light on the ecological correlates of seasonal insect (i.e., termite) feeding behavior in this species, including age/sex class differences. Specifically, we test the aforementioned three non-mutually exclusive hypotheses. First, we investigated whether areas rich with a mix of tree species (primary forest) had a greater amount of termite mounds than *Marantaceae*-rich herbaceous areas (secondary forest). If seasonal termite feeding in gorillas supports the *Habitat Use Hypothesis*, we would expect termite feeding to increase when gorillas are traveling further per day and when they spend more time in primary forest. If the *Rainfall Hypothesis* is supported, we would expect to find a positive correlation between gorilla termite consumption and daily rainfall. Finally, if the *Frugivory Hypothesis* is supported we predict termite consumption will increase with fruit consumption to compensate for this dietary deficiency.

Finally, we aim to investigate any age/sex classes differences in insect feeding in terms of the aforementioned Hypotheses. Since termites are limited and monopolizable food resources, if insect feeding is an opportunistic behavior in western gorillas (as suggested by Salmi et al., 2020), silverbacks should feed more on termites than other group members when the opportunity arises (i.e., when finding a termite mound on the path or in termite-rich vegetation), given their priority access over food (Masi et al., 2009; Remis, 1994). On the contrary, being the lowest ranking individuals with regards to food access (Fuh et al., 2022; Yamagiwa, 1992), subadults are expected to feed less on insects compared to other individuals. In terms of nutrition, if gorillas adjust insect feeding according to nutritional needs, we predict that juveniles and adult females will feed more on insects because of the greater nutritional needs for proteins, fats and other nutrients for growth and reproduction, respectively (Altmann, 2001; Masi et al., 2009; Nowell & Fletcher, 2007).

2 | METHODS

2.1 | Study area

Research was carried out at Bai Hokou (2°50' N, 16°28' E) and Mongambe (2°55' N, 16°23' E) in the Dzanga-Ndoki National Park (1222 km²), in south-western Central African Republic (CAR). The

park is part of the Dzanga-Sangha Protected Areas (DSPA), an integrated conservation and development project (Carroll, 1986), under the collaborative management of CAR Government and the World Wide Fund for Nature (WWF). All research below adhered to the protocols and legal requirements in CAR.

The climate in the study area shows marked seasonal variation in rainfall: the dry season is typically from December to February, when rainfall is less than 80 mm per month. September and October are generally the rainiest months (DSPA long-term data). The mean annual rainfall reaches 1700 mm (DSPA long-term data). Rainfall was measured daily at 6 a.m. and at 6 p.m. using a rain gauge at Bai Hokou camp in a remote area of the Park.

Bai-Hokou forest is a mosaic of vegetation of which six major types can be identified (modifying Cipolletta et al., 2007): (1) *primary forest* composed of mixed tree species with a dense forest canopy, (2) *primary forest with lianas* from *Haumania danckelmaniana*, (3) *secondary forest* rich in herbaceous vegetation dominated by *Marantacea* spp., (4) *monodominant forest* with a dense canopy composed almost entirely of *Gilbertiodendron dewevrei* trees, (5) *light gaps* (regenerating vegetation after treefalls), and (6) *clearing/riverine forest*.

2.2 | Distribution of *Cubitermes* spp. termite mounds and vegetation transects

The data on the distribution of *Cubitermes* spp. termite mounds was collected by AT, ShM and field assistants in 2004–2005 in the home-range of CAR 1 and CAR 2 groups. The surveyed area was divided into 500 × 500 m quadrants. In the diagonal of each quadrant, a 340 × 2 m belt transect was explored. The 340 m length was taken from an estimate of the best length to describe the plant diversity of the area. Along each transect we recorded: (1) vegetation type, (2) the distance occupied along the transect by each vegetation type, and (3) the number of *Cubitermes* spp. termite mounds found in each type of vegetation. These data consisted of 437 vegetation type segments distributed over 116 transects.

2.3 | Behavioral data sampling

Behavioral data were collected on three habituated groups of western gorillas, CAR 1 and CAR 2 group at Bai Hokou research site and CAR 3 group at Mongambe. The data collection was carried out during four study periods ($N_{\text{total}} = 535$ days): (1) from January to December 2005 (with a 1-month gap in May; $N_{2005} = 233$ days) by ShM on CAR 1, (2) from April to July 2008 and from November 2008 to March 2009 ($N_{2008-2009} = 155$ days) by ShM on CAR 1, (3) from July 2011 to January 2012 (with a 1-month gap in September; $N_{2005} = 63$ days) by TFN on CAR 1 and CAR 3, and (4) from June to November 2017 ($N_{2017} = 84$ days) by ASM on CAR 1, 2 and 3.

During all study periods, a focal individual (Altmann, 1974) was followed during half-days (7:00–12:00 a.m. or 12:00–05:00 p.m.) and sometimes a whole day, rotating the focal individuals to balance

sample size (see Electronic Supplementary Material, ESM, Table 1 for group compositions).

During three out of the four study periods, for the three study groups, scan sampling was used to record the focal animal's activity and the vegetation type in which it was located (Altmann, 1974); scans were taken every 5 min for the 2005 dataset and every 10 min for the 2008–2009 and 2017 datasets. Only focal sessions with more than three consecutive scans with the focal individual in visibility were used for the analyses. The resulting dataset, henceforth called *scan dataset*, comprised a total amount of 12,384 visual observation scans for all groups ($N_{\text{silverback}} = 4416$; $N_{\text{adult female}} = 4839$; $N_{\text{subadult}} = 1164$; and $N_{\text{juvenile}} = 1965$; see ESM Table 1 for the age/sex sample size per group).

In addition, during the 2008–2009, 2011, and 2017 study periods, continuous focal animal sampling (Altmann, 1974) was carried out, as such the activity of the focal individual was continuously recorded (but not the vegetation type). Focal animal samples with less than 20 min of observations were excluded from the analyses. The resulting dataset, henceforth called *continuous focal dataset*, comprised a total amount of visual observation time of 891 h for all groups ($h_{\text{silverback}} = 132$; $h_{\text{adult female}} = 289$; $h_{\text{subadult}} = 173$; and $h_{\text{juvenile}} = 297$; see ESM Table 1 for age/sex class sample size per group).

In both continuous and scan focal animal sampling, the activities were classified largely following Masi et al. (2009): feeding, foraging (including active searching for food and food processing), moving (including walking, running, climbing, not directly related with

foraging), resting (stationary, sitting down, sleeping, auto-grooming) and other (any social interactions, playing, vigilant surveillance). When the observed activity was feeding or foraging, the species and food type were noted with the help of knowledgeable Aka trackers.

2.4 | Daily journey length

For the study periods 2005 and 2008–2009, to measure the daily journey length of CAR 1 group, gorilla trails were plotted daily on a 1:20,000 map onto which a 250 × 250 m grid was superimposed with the help of a compass and an extensive mapped trail system marked every 100 m (as described in Cipolletta, 2004). The daily journey length was then calculated from the maps by measuring the distance traveled between each consecutive nest site (Cipolletta, 2004). In 2017, ranging data of each focal individual from all three groups were collected using a portable GPS device with track-log function set at every 18 m.

2.5 | Seasonal subdivision and statistical methods

2.5.1 | Seasonal insectivory

To assess whether insectivory by the gorillas followed a seasonal pattern, we fitted General Linear Mixed Models (GLMM; Bolker et al., 2009)

TABLE 1 Summary of the GLMM models used to investigate the effect of ecological and/or behavior variables on the insect feeding by western gorillas or on the termite abundance.

	Seasonal insectivory	Termite availability along vegetation types	The three hypotheses	Rainfall and termite feeding	Rainfall and termite foraging
Model type	GLMM	GLMM	GLMM	GLMM	GLMM
Dataset	Focal scan dataset	Transects dataset	Focal scan dataset	Continuous focal dataset	Continuous focal dataset
Response variable	Total number of scans of insect feeding and foraging per day	Number of termite mounds	Total number of scans of termite feeding and foraging per day	Time spent termite feeding per day	Time spent termite foraging per day
Test predictor(s)	Cosine of the day	1. Vegetation type 2. Distance of vegetation type within the transect	1. Age/sex classes 2. Age/sex classes: percentage of daily scans spent in termite-rich vegetations 3. Age/sex classes: daily journey length 4. Age/sex classes: daily rainfall 5. Age/sex classes: daily percentage of scans spent feeding on fruits	1. Age/sex classes 2. Age/sex classes: daily rainfall	1. Age/sex classes 2. Age/sex classes: daily rainfall
Random(s)	Week Subject identity Group	Transect identity	Week Subject identity Group	Week Subject identity Group	Week Subject identity Group
Offset term	Total number of daily scans	NA	Total number of daily scans	Total duration of continuous focal	Total duration of continuous focal
N	816	437	816	325	325

using the *scan dataset* (Table 1). This model estimated the sum of insect feeding and foraging scans per day as a function of the cosine of the day for a given study period (i.e., one turn of the trigonometric circle represents 1 year). To input the date variable into a cosine, we turned Julian date into a circular variable by dividing the trigonometric circle into a 365.25 day. To identify the best phase to consider given our data (i.e., which month should correspond to the trigonometrical zero), we compared the Akaike Information Criterion (AIC; Burnham et al., 2011) of models for which the considered trigonometric zero was set to each possible month (see ESM Material 1 for formula of the statistical model). The phase θ for which the AIC was minimized would indicate that the maximum ($\beta_1 > 0$) or the minimum ($\beta_1 < 0$) of insect feeding scan numbers per day occurred for that month. For instance, having a phase being null would mean that insectivory was at its most prevalent (or least prevalent, depending on β_1 sign) in January.

Once the seasonal pattern of insectivory was shown, we split the months of the different years (i.e., 2005, 2008–2009, and 2017) into *high-* and *low-insectivory season* based on whether they were above or below the average daily percentage of all insect feeding and foraging scans (from all study periods) (9.18%, $N = 5600$ for groups CAR 1, 2 and 3).

Since termites alone represented 94% of the insectivory scans in our dataset ($N = 517$ insects feeding scans, so termite represented 8.63% of the feeding and foraging scans), for the following analyses we have focused on termites only. We have assumed that the seasonality of termite feeding follows the same trends as that of other insectivory.

2.5.2 | Vegetation types and termite availability

To study the effect of the vegetation type on termite mound availability, we first fitted a GLMM (Bolker et al., 2009) using the number of termite mounds as the response variable and the six aforementioned vegetation types as fixed variables (Table 1). In addition, to control for unequal sample size we included the distance covered by each vegetation type along the transect as a fixed effect.

We then ran a post-hoc Bonferroni multiple comparison test to determine statistically significant differences in termite mound number ($p < 0.05$) among the different vegetation types. To do this, we used the function “*pairwise.t.test*” of the *stats* package specifying Bonferroni correction method for adjusting p -values in the ANOVA model. The results revealed two broad abundance categories of vegetation with termite mounds, a *termite-rich vegetation* (primary forest and its combination with liana secondary forest) and a *termite-poor vegetation* (all other vegetation types). For the following analyses, we then calculated the daily time spent in both these vegetation categories for each study group.

2.5.3 | Testing the three hypotheses

To test for the relative importance of the three aforementioned hypotheses (*Habitat Use Hypothesis*, *Rainfall Hypothesis*, and *Frugivory*

Hypothesis) on the daily sum of scans spent feeding and foraging on termites in relation to gorilla age/sex classes, we built a GLMM (Bolker et al., 2009) on the *scan dataset*, including the daily total number of scans spent feeding and foraging on termites as the response variable (Table 1). As fixed effects we included the age/sex classes and the interactions of age/sex classes with (1) the percentage of daily scans spent in termite-rich vegetation, (2) daily journey length (both testing for the *Habitat Use Hypothesis*), (3) daily rainfall (i.e., between 6 a.m. and 6 p.m.; *Rainfall Hypothesis*), and (4) and the daily percentage of scans spent feeding on fruits, henceforth called *frugivory scans* (*Frugivory Hypothesis*; see ESM Material for statistical choice explanations).

Finally, we used the more precise *continuous focal dataset* on all study groups to further investigate the *Rainfall Hypothesis*. We built two more GLMMs (Bolker et al., 2009) with response variables of the daily duration of observed time spent (1) feeding or (2) foraging on termites, respectively (Table 1). For each model, the daily rainfall, the age/sex classes and the interaction between them were included as fixed effects.

2.5.4 | General information on the statistical models

All models were run in R (R Development Core Team, version 1.4.1103 released on 2021-15-02). Statistical significance was set at an α level of 0.05. All GLMM models were ran with Poisson error structure and logarithmic link function. Since our dataset contained many zeros (when gorillas fed on other foods than insects or engaged in other activities), we used the “*glmmTMB*” function from the *glmmTMB* package (Brooks et al., 2017), specifying to take into account zero inflation in the intercept when building the model (with the *ziformula* argument set to “~1”). The absence of collinearity between the covariables in fixed effects (e.g., % of frugivory scans and rainfall) was first tested using the “*chart.Correlation*” function of the *PerformanceAnalytics* package, then all covariables were z-transformed to a mean of zero and a standard deviation of one.

All models could show spatial (i.e., vegetation types with regard to the local number of termite mounds) or temporal (i.e., insect/termite feeding behavior) autocorrelation unexplained by the predictors included in the models, leading to non-independent residuals (i.e., residuals obtained for data points sampled close to one another in space or time being more similar than residuals of more distant data points). To avoid this violation of the model assumptions, we included autocorrelation explicitly into the models by adding the transect identity or the week of the observation as random effects (weeks are specified in a calendar count continuous between 2005 and 2017: the first week begin on the 3rd January of 2005). This also allowed us to control for any significant differences between the four study periods, including the methodological differences (scan intervals of 5 and 10 min and daily journey length by quadrants or GPS). In addition, we included the focal subject and the group identity as random effects (see ESM).

Finally, to control for unequal sample size of daily scans and duration of the focal follows, the daily total number of scans or the daily total duration of continuous focal follows per individual were included as offset terms when using the *scan* or the *continuous focal dataset*, respectively (see [ESM](#) for explanations on this choice).

Each GLMM was validated. First, the significance of the full model was compared to the null model (comprising only the offset term and the random effects) using a likelihood ratio test (R function `anova` with argument `test = "Chisq"`; Forstmeier & Schielzeth, 2011). Then, we checked necessary assumptions (i.e., distribution of residuals, Q-Q plot, homoskedasticity and overdispersion) using the DHARMA package (Hartig, 2022) which pointed out no major issues, as well as the absence of correlation effects (maximum Variance Inflation Factor, VIF, close to 1, “vif” function from the *car* package; Fox & Weisberg, 2019).

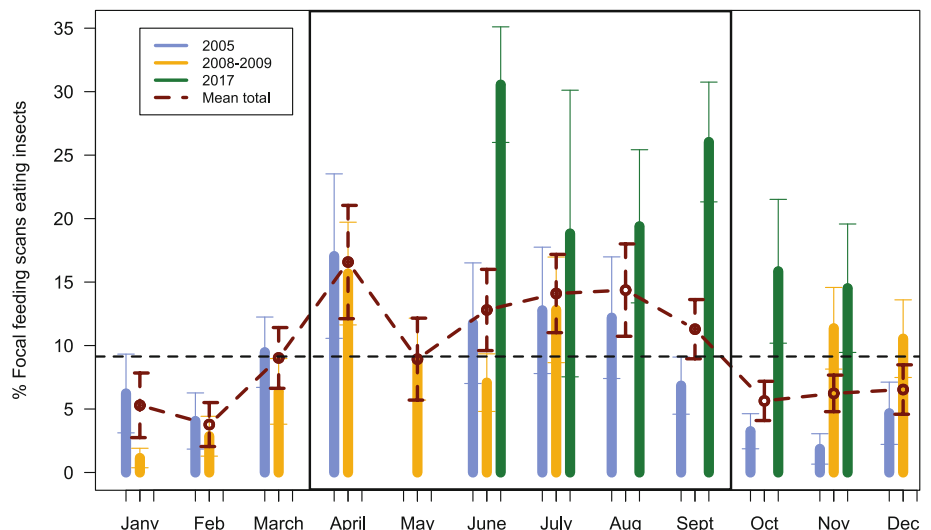
3 | RESULTS

3.1 | Seasonal insectivory

During the study periods of the *scan dataset*, the average daily percentages of insectivory during feeding and foraging scans was 9.1% ($N = 5597$ total feeding and foraging scans, min-max range of monthly average: 3.8%–16.6%; 2005: 7.4%, $N = 3596$, 1.9%–17.0%; 2008–2009: 9.0%, $N = 1338$, 1.1%–15.7%; 2017: 20.3%, $N = 663$, 14.5%–30.6%).

From the *scan dataset*, the daily number of insectivory scans significantly followed a seasonal cycle that peaked in June (best fit model for $\theta = 1 * \pi/6$, $\chi^2 = 5.49$, $df = 1$, $p = 0.02$). We thus split the months of all study periods into two seasons, based on whether they fell above or below the total average of daily insect feeding/foraging scans from all study periods combined: (a) March to September constituted the high-insectivory season, and (b) October to February the low-insectivory season (Figure 1; see [ESM](#) for average daily insectivory scan per season per study period).

FIGURE 1 Insect consumption from focal insectivory scans of the three study periods. The large square indicates the months that constitute the high insectivory season while the other months constitute the low insectivory season. The monthly average is shown in blue for 2005, yellow for 2008–2009 and green for 2017. The monthly average for all study periods combined is shown in dashed red while the dotted black line indicates the total average for all study periods. The error bars indicate the standard deviation.



During our three study periods, gorilla insectivory mainly consisted of feeding on termites of *Cubitermes* spp. (94.4%, $N = 516$ insectivory scans), followed by ants (5.6%, $N = 516$), most of which were weaver ants (*Oecophylla longinoda*; 4.5%, $N = 29$ ant feeding scans in feeding and foraging scans).

3.2 | Termite distribution and vegetation types

There was a clear impact of the different vegetation types on termite mounds abundance (likelihood ratio test: $\chi^2 = 48.9$, $df = 5$, $p < 0.001$, Table 2a). More specifically, post-hoc analysis revealed that termite mounds were more frequently found in primary forest and in primary forest with herbaceous lianas compared to secondary forest ($p < 0.001$) or light gaps and clearings ($p < 0.001$; see statistics in Table 2b). Presence of termite mounds did not differ between primary forest alone and primary forest with herbaceous lianas. In addition, no differences were found among the secondary forest, the monodominant forest, the light gap and the clearing/riverine forest (Table 2b).

Primary forest and primary forest with herbaceous lianas, henceforth termed *termite-rich vegetation*, represents 69.3% of the vegetation of the home ranges of CAR 1 and CAR 2 ($N = 39,269.5$ m). Together this termite vegetation category harbored 77.5% of all termite mounds ($N = 550$), while the others vegetation types combined, henceforth called *termite-poor vegetation*, represents 30.7% of the vegetation in these home ranges with 22.5% of termite mounds (see [ESM Table 2](#)).

3.3 | Age/sex classes and the three hypotheses

Age/sex classes differed in their daily termite consumption (both feeding and foraging scans) and in their response to the predictors (i.e., the percentage of daily scans spent in termite-rich vegetation, daily journey length, daily frugivory scans and daily rainfall; likelihood ratio test: $\chi^2 = 77.22$, $df = 19$, $p < 0.001$). Time spent in termite-rich

Term	Estimate	Std. error	Lower CI	Upper CI	χ^2 ^a	p-value
Intercept	-2.073	1.037	-4.104	-0.041	48.93	0.046
Secondary forest ^b	1.372	1.041	-0.668	3.411	48.93	0.187
Light gap ^b	1.275	1.052	-0.787	3.337	48.93	0.226
Monodominant forest ^b	1.507	1.060	-0.570	3.583	48.93	0.155
Primary forest ^b	2.131	1.037	0.098	4.163	48.93	0.040
Primary forest with liana ^b	2.254	1.036	0.223	4.284	48.93	0.030
Vegetation distance ^c	0.376	0.054	0.270	0.483	39.12	<<0.001

^aDegree of freedom are five for the vegetation type variable and one for the vegetation distance variable.

^bVegetation types was dummy coded with *clearing/riverine forest* being the reference category.

^cZ-transformed; mean and standard deviation of the original variable were 89.86 and 73.47, respectively.

TABLE 2a Results from GLMM testing termite mound repartition within the vegetation type.

TABLE 2b Results from post-hoc Bonferroni multiple comparison test testing termite mound distribution within the vegetation types.

	Clearing/riverine forest	Monodominant <i>G. dewevrei</i> forest	Light gap	Primary forest	Primary and liana secondary forest
Monodominant <i>G. dewevrei</i> forest	1.000				
Light gap	1.000	1.000			
Primary forest	0.041	0.027	<<0.001		
Primary and liana secondary forest	0.067	0.055	5	1.000	
Secondary forest	1.000	1.000	1.000	<<0.001	

vegetation had a positive impact on the daily termite consumption of silverbacks, adult females and juveniles but not of subadults (see Table 3 for statistics). Daily rainfall had a significant negative influence on daily termite consumption for subadults only (Table 3 and see ESM Methods 2). The daily percentage of frugivory had a negative influence on daily termite consumption in adults only (Table 3). Finally, while for adult females the daily journey length had a positive effect on daily termite consumption, for subadults the effect was negative (Table 3). No significant effect was found for the other age/sex classes.

3.4 | Further testing of the rainfall hypothesis

The negative effect of rainfall on gorilla termite consumption may be the result of western gorillas being relatively inactive during heavy rains. Therefore, we further tested the *Rainfall Hypothesis* using the *continuous focal dataset* (from study periods 2008–2009, 2011–2012, and 2017). Since we supposed that increased daily rainfall would increase the time spent feeding on termites but would decrease the time spent foraging (as the rain would soften the mound making it easier to detach from the tree), we tested the effect of rainfall on termite feeding and foraging, separately. The two models (i.e., termite *foraging* and *feeding*) revealed that both daily termite feeding and foraging were clearly impacted by the daily rainfall, with differences among the sex/age classes (likelihood ratio test: feeding, $\chi^2 = 83,079$, $df = 8$, $p < 0.001$; foraging, $\chi^2 = 126,085$, $df = 8$, $p < 0.001$). In the termite *feeding* model, the daily rainfall *positively* affected the time

spent feeding on termites for adults and juveniles (Table 4a). In subadults, a significant *negative* impact was found (Table 4a). In the termite *foraging* model, the daily rainfall also had a *positive* effect on time spent foraging in silverbacks and tended to do so in juveniles (Table 4b). However, a *negative* effect was found for adult females and subadults (Table 4b).

4 | DISCUSSION

To explain seasonal insect (termite) consumption in western gorillas, we found support for all three hypotheses (the *Habitat Use Hypothesis*, the *Rainfall Hypothesis*, and the *Frugivory Hypothesis*) in relation to the different age/sex classes (Table 5). In support of the *Habitat Use Hypothesis* we found that time spent in termite-rich vegetation *positively* impacted termite consumption in all age/sex classes, except for subadults. In addition, when the group traveled longer distances females fed opportunistically on termites, while subadults appeared disadvantaged by such journeys. In support of the *Frugivory Hypothesis*, when gorillas were more frugivorous, adults spent less time feeding on termites. The results for the *Rainfall Hypothesis* were less straightforward. Daily rainfall had a negative impact on termite consumption (both feeding and foraging) in subadults and a positive impact on silverbacks and juveniles. In contrast, females spent more time feeding and less time foraging when daily rainfall increased.

Termite consumption (foraging and feeding) by gorillas was clearly seasonal on a monthly scale. The months of the high-insectivory season (March–September) overlapped with both the high fruit seasons

TABLE 3 Results from GLMM testing age/sex differences in predictor variable effects.

Term	Estimate	Std. error	Lower CI	Upper CI	Z value	p-value
Intercept	-2.411	0.209	-2.821	-2.001	-11.523	<<0.001
Adult females ^a	-0.426	0.231	-0.878	0.026	-1.847	0.065
Subadults ^a	-0.366	0.307	-0.968	0.236	-1.192	0.233
Silverbacks ^a	-0.356	0.256	-0.857	0.145	-1.392	0.164
Juveniles: % daily scans in termite-rich vegetation ^b	0.704	0.205	0.303	1.105	3.441	<<0.001
Adult females: % daily scans in termite-rich vegetation ^b	0.379	0.139	0.106	0.653	2.721	0.007
Subadults: % daily scans in termite-rich vegetation ^b	0.241	0.257	-0.262	0.744	0.939	0.348
Silverbacks: % daily scans in termite-rich vegetation ^b	0.409	0.172	0.072	0.746	2.378	0.017
Juveniles: Daily rainfall ^c	-0.042	0.242	-0.517	0.432	-0.175	0.861
Adult females: Daily rainfall ^c	-0.200	0.147	-0.490	0.089	-1.357	0.175
Subadults: Daily rainfall ^c	-1.312	0.656	-2.598	-0.027	-2.001	0.045
Silverbacks: Daily rainfall ^c	-0.004	0.176	-0.381	0.310	-0.201	0.840
Juveniles: % daily frugivory scans ^d	0.175	0.379	-0.567	0.918	0.463	0.643
Adult females: % daily frugivory scans ^d	-1.010	0.206	-1.414	-0.607	-4.909	9.1e-07
Subadults: % daily frugivory scans ^d	-0.172	0.374	-0.904	0.560	-0.461	0.645
Silverbacks: % daily frugivory scans ^d	-0.774	0.282	-1.327	-0.221	-2.742	0.006
Juveniles: Daily journey length ^e	0.017	0.150	-0.277	0.310	0.110	0.912
Adult females: Daily journey length ^e	0.207	0.065	0.080	0.335	3.194	0.001
Subadults: Daily journey length ^e	-0.425	0.198	-0.814	-0.036	-2.140	0.032
Silverbacks: Daily journey length ^e	0.082	0.086	-0.087	0.251	0.949	0.342

^aAge/sex classes was dummy coded with juveniles being the reference category.

^bZ-transformed; mean and standard deviation of the % daily scans in termite-rich vegetation original variable were 0.486 and 0.368, respectively.

^cZ-transformed; mean and standard deviation of the Daily rainfall original variable were 1.769 and 5.564, respectively.

^dZ-transformed; mean and standard deviation of the % daily frugivory scans original variable were 0.175 and 0.271, respectively.

^eZ-transformed; mean and standard deviation of the Daily journey length original variable were 1868 and 760.7, respectively.

(Figure 2; June–September as defined by Masi et al., 2009) and to a larger extent with the rainy season (March–November). Our results from direct observations corroborate most of the previous results that used indirect methods, which found higher termite consumption in western gorillas during rainy months (Deblauwe, 2009; Doran et al., 2002; Goldsmith, 1999; Rogers et al., 1990) and/or during months of high frugivory (Deblauwe, 2009; Goldsmith, 1999). However, the insectivory season did not coincide exactly with periods of high frugivory (which starts later) nor with the rainy season (which lasts longer). This suggests that other factors rather than solely fruit consumption and rainfall affect termite feeding behavior in western gorillas. This may also contribute to explaining the ambiguous results for the Frugivory Hypothesis found by previous studies (Deblauwe, 2009; Deblauwe & Janssens, 2008; Goldsmith, 1999).

4.1 | Habitat use hypothesis

Termite consumption may be influenced by gorilla habitat use. Indeed, we found that termite mounds of *Cubitermes* spp. were not evenly distributed across the gorillas' home ranges, being more abundant in primary forest and primary forest with herbaceous lianas. These results are in line with studies on soil-feeding termites in wet environments

that show their higher abundance in vegetation with high canopies and with high diversity of plant taxa (Dibog et al., 1999; Eggleton et al., 1996; Eggleton et al., 2002; Gillison et al., 2003). Openings within the forest canopy generate microclimatic conditions, such as direct sun light, temperature and humidity fluctuations, which may impede the colonization of soil feeding termites (Jones, 2000; Jones et al., 2003). This may explain why we found that other vegetation types such as light gaps, clearings and secondary vegetation were poorer in termite mounds in comparison to primary forest vegetation. However, depending on the termite species (Ahmed et al., 2011) many other environmental and biological factors can influence termite mounds distribution, such as soil composition, inter and intra-species competition, and most importantly proximity to old termite mounds (Dangerfield, 1990).

As expected, time spent in termite-rich vegetation had a positive impact on termite consumption for all age/sex classes, except subadults (Table 5). Time spent in termite-rich vegetation, which provide also fruiting and leafing trees, increases the likelihood that gorillas find termite mounds. Gorillas seem to take advantage of this opportunity by feeding more on termites. Insect availability was also an important factor affecting insect consumption in previous studies (Cipolletta et al., 2007; Deblauwe, 2009; Deblauwe et al., 2003) corroborating the opportunistic nature of termite feeding in gorillas. Since time

TABLE 4 Results from the two GLMM testing the effect of *Daily rainfall* on termite *feeding* (a) and *foraging* (b) behavior from *continuous focal dataset*.

Term	Estimate	Std. error	Lower CI	Upper CI	Z-value	p-value
(a) Feeding model						
Intercept	-3.479	0.296	-4.059	-2.900	-11.77	<<0.001
Daily rainfall ^a	0.032	0.008	0.017	0.046	4.21	<<0.001
Adult females ^b	0.758	0.461	-0.145	1.661	1.65	0.100
Subadults ^b	1.894	0.054	1.789	2.000	35.07	<<0.001
Silverbacks ^b	0.883	0.599	-0.291	2.057	1.47	0.141
Adult females: Daily rainfall ^a	0.102	0.011	0.081	0.122	9.63	<<0.001
Subadults: Daily rainfall ^a	-1.289	0.035	-1.356	-1.221	-37.35	<<0.001
Silverbacks: Daily rainfall ^a	0.568	0.010	0.549	0.588	56.46	<2e<<0.001
(b) Foraging model						
Intercept	-4.265	0.316	-4.885	-3.645	-13.484	<<0.001
Daily rainfall ^a	0.035	0.018	-0.001	0.070	1.921	0.055
Adult females ^b	-0.029	0.436	-0.884	0.827	-0.065	0.948
Subadults ^b	-0.246	0.173	-0.585	0.093	-1.421	0.155
Silverbacks ^b	-0.472	0.566	-1.581	0.638	-0.834	0.405
Adult females: Daily rainfall ^a	-0.208	0.026	-0.259	-0.157	-7.991	1.4e
Subadults: Daily rainfall ^a	-1.280	0.143	-1.561	-0.999	-8.935	<<0.001
Silverbacks: Daily rainfall ^a	0.590	0.028	0.535	0.644	21.345	<<0.001

^aZ-transformed; mean and standard deviation of the *Daily rainfall* original variable were 1.518 and 5.592, respectively.

^bAge/sex classes was dummy coded with juveniles being the reference category.

spent in termite-rich vegetation is likely seasonal, increasing with fruit consumption from trees, this is likely a crucial factor affecting termite seasonality. In the case of one-male polygynous societies, as in western gorillas, subadults are the lowest ranking individuals in the group (Yamagiwa, 1992) and the least tolerated by adults at feeding sites (Masi et al., pers. obs.). Thus, they would be unlikely to profit from being in termite-rich vegetation as even if they located a termite mound, the takings may be stolen by higher-ranking adults. Moreover, since termite-rich vegetation are also fruit-rich habitats, this may explain the correlations found between fruit and termite consumption in previous studies (Deblauwe, 2009; Deblauwe & Janssens, 2008; Goldsmith, 1999; Kuroda et al., 1996).

Adult females were the only individuals positively influenced by daily journey length in terms of termite consumption (Table 5). The further they traveled the more they fed opportunistically on termites found along their way. The longer daily travel distances during high frugivory months (Cipolletta et al., 2007; Goldsmith, 1999; Masi et al., 2009; Remis, 1997b) could thus trigger seasonal insectivory in adult females. On the contrary, subadult termite feeding behavior was negatively affected by daily travel (Table 5). When an adult female finds a termite mound on the path and stop to feed on termites, it is highly likely that the whole group would wait for her. This is not the case for subadults, who are more peripheral to the group (Masi, pers. obs.). Both subadults and juveniles (who are more central in the group but nevertheless waited for by adults) are more likely to be displaced by the adults who monopolize termite mounds (Masi et al., 2009, see

Video 1 in ESM). This may explain the negative effect of daily journey length for subadults and the absence of an effect for juveniles. For silverbacks, although we studied three rare habituated groups of western gorillas, this species has only one silverback per group, so the low number of individuals falling in this class ($N = 3$) may affect significance of results.

4.2 | Frugivory hypothesis

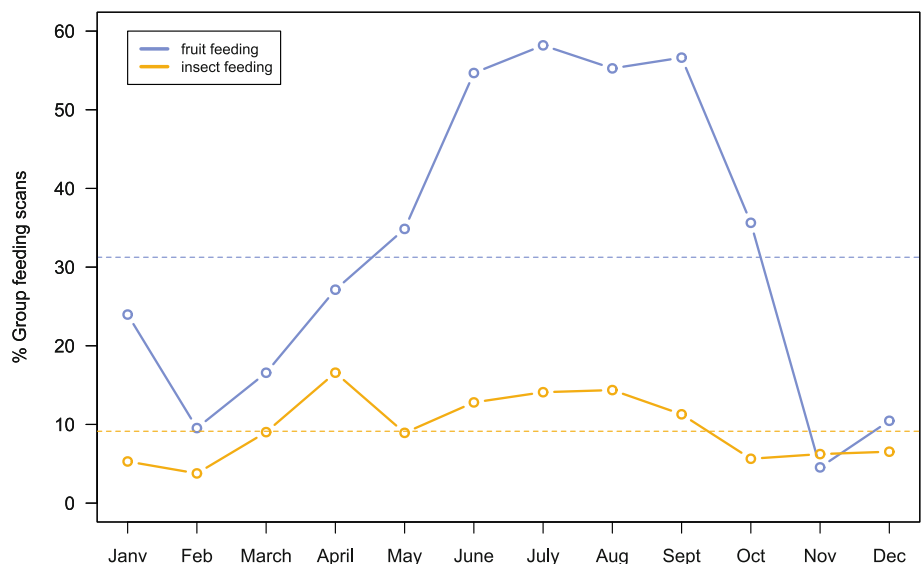
In adults, daily termite consumption was negatively influenced by daily fruit consumption (Table 5). During the high-insectivory season, gorillas are likely constrained by two tendencies: allocating time to insect or to fruit consumption. This seems to differ according to the age/sex classes' nutritional needs. During the study periods, all adult females of the three study groups were lactating. Their main need was thus to maximize readily accessible energy (similar for both human and non-human primates, Dufour & Sauther, 2002), mainly through the ingestion of sugars when fruit is abundant (Masi et al., 2015). Consequently, when the group was in primary forest where fruit and termites were abundant, adults may have prioritized readily accessible energy by feeding more on abundant fruit (Nogueira, 1996), which also allow to maintain group cohesion. On the contrary, since animal proteins are crucial for growth in subadults and juveniles (Rothman et al., 2008), they continued to feed on termites even when fruit was highly available (Masi et al., 2009). Indeed, insect

TABLE 5 Summary of the study results and their interpretation for the different hypotheses according to sex and age classes.

Hypothesis name	Tested variable	Effects depending on sex and age classes	Explanations
Habitat use hypotheses	Time spend in termite rich vegetation	Juveniles: + Subadults: / Adult females: + Silverbacks: +	Time spent in termite-rich vegetation increases the likelihood that gorillas find termite mounds. Gorillas seem to take advantage of this opportunity by feeding more on termites.
	Daily journey length	Juveniles: / Subadults: - Adult females: + Silverbacks: /	When an adult female finds a termite mound on the path and stop to feed on termites, it is highly likely that the whole group would wait for her. This is not the case for subadults, who are more peripheral to the group.
Frugivory hypotheses	Daily fruit consumption	Juveniles: / Subadults: / Adult females: - Silverbacks: -	When the group was in primary forest where fruit and termites were abundant, adults may have prioritized readily accessible energy by feeding more on fruit. On the contrary, since animal proteins are crucial for growth in subadults and juveniles, they continued to feed on termites even when fruit was highly available.
Rainfall hypotheses	Daily rainfall on time spend foraging on termites	Juveniles: + Subadults: - Adult females: - Silverbacks: +	The study groups were observed to rush to break termite mounds just after rain. Rainfall may soften termite mounds rendering them easier to break for the gorillas. Thus, adult females would have needed less time to detach a termite mound. The silverback being double the size of the females would have simply engage more in detaching mounds. And the juveniles would have benefit from the available pieces. The negative effect of rainfall on time spent feeding for subadults underline the ability of subordinates to develop counterstrategies (to forage on alternative food) to limit the costs of contest competition.
	Daily rainfall on time spend feeding on termites	Juveniles: + Subadults: - Adult females: + Silverbacks: +	

Note: The “+” sign indicates that the tested variables had positive effects on termite consumption, the “-” sign indicates negative effects, while the “/” sign indicates that no significant effect was found.

FIGURE 2 Fruit and insect consumption from group feeding scans of the three study periods. In blue: the average percentage of fruit by feeding scans per month; blue dashed horizontal line: the average percentage of fruit in feeding scans by all study periods; in yellow: the average percentage of insect by feeding scans per month; yellow dashed horizontal line: the average percentage of insect by feeding scans of all study periods.



consumption may depend on seasonal daily food intake, and could particularly be associated with decreasing intakes of proteins, fats and major minerals at a daily scale (Deblauwe, 2009; Goldsmith, 1999).

Therefore, although periods of high insectivory and high frugivory overlap enough to have led previous studies to find a positive correlation between frugivory and insectivory (Deblauwe, 2009; Deblauwe &

Janssens, 2008; Goldsmith, 1999; Kuroda et al., 1996), this relationship could heavily depend on the study group's composition in terms of age/sex classes. This may explain why previous results have been contradictory, highlighting an indirect relationship between insectivory and frugivory triggered by the seasonal changes in gorilla habitat use.

4.3 | Rainfall hypothesis

Since rainfall may soften termite mounds rendering them easier to break for the gorillas (Cipolletta et al., 2007), and since the study groups were observed to rush to break termite mounds just after rains, the negative impact of daily rainfall on termite consumption for subadults and the absence of it in the first model using scans for the other group members was unexpected. Since these could have been artifacts of our lower observation time of the gorillas or of their inactivity during heavy rains (which affects scan more than continuous sampling data), we further investigated the link between rainfall and termite consumption by using a more detailed dataset based on continuous activity sampling of the focal individuals (Altmann, 1974). In this second analysis, rainfall had a positive effect on time spent *feeding* on termites in all age/sex classes, but the opposite was true for subadults (Table 5). Such a positive relationship corroborates previous results on more insect remains being found in gorilla feces during the rainy season (Doran et al., 2002; Goldsmith, 1999; Rogers et al., 1990; Tutin & Fernandez, 1992). The negative effect of rainfall on time spent *feeding* for subadults was surprising. This may underline the ability of subordinates to develop counterstrategies such as foraging more peripherally and/or on alternative food to limit the costs of contest competition, as has been observed in other animal species (birds: Bugnyar & Kotrschal, 2004; ungulates: Hewitson et al., 2007; Held et al., 2010). Rainfall decreased time spent *foraging* on termites in adult females and subadults (Table 5), supporting the hypothesis of rainfall softening termite mounds (Cipolletta et al., 2007). Termites thus become more accessible and profitable for both adult females and subadults. On the contrary in silverbacks, rainfall had a positive effect on termite foraging time. Being double the size of the females (Smith & Jungers, 1997), silverbacks often detach very large termite mounds from trees which they and other group members can profit from. Therefore, compared to other group members silverbacks may forage more on termites simply because they engage more in detaching mounds when rains soften them (however, given the small size of three silverbacks studied, generalization should be taken with caution).

4.4 | Putative termite feeding traditions

Even though we identified a common pattern of termite feeding in response to different ecological factors of the different age/sex class, it is possible that traditional differences in termite feeding may also exist among groups. In great apes, cultural traits have been observed in relation to feeding habits (van Schaik et al., 2003; Whiten

et al., 1999). Despite the consistent publication of literature on chimpanzee and orangutan culture, gorillas have been rather overlooked, particularly in terms of traditions linked to feeding behavior (Robbins et al., 2016). Since in all our analyses “group” was always a factor significantly affecting insect consumption (when controlling for variability between study years), this underlines differences among our study groups. Group differences in feeding patterns could also be the result of different food availability (either of termites or other insect species) within each home range. Since two of the study groups' home ranges overlapped, we think this is unlikely to be the reason for the observed differences (however, since the overlap is not complete further investigation is needed to confirm this hypothesis). The absence of termite consumption in other western gorilla groups (Gabon: Robbins et al., 2022; Cameroun: WWF long-term data in Campo Ma'an) despite the presence of *Cubitermes* spp. in the forest, corroborates this hypothesis. Furthermore, western gorillas in Congo Republic showed tool use and behavioral innovation while feeding on termites (Masi et al., 2022). Studying inter-population differences will increase our understanding of how environmental and/or cultural variables could influence insect feeding patterns among great apes.

5 | CONCLUSIONS AND EVOLUTIONARY PERSPECTIVES

In western gorillas, termite consumption is primarily driven by the opportunity of finding a termite mound, particularly in adults. However, it is also influenced both by nutritional and meteorological variables. We showed how ecological predictors such as habitat use, daily journey length, fruit consumption, and rainfall can concurrently explain the seasonal pattern of termite consumption observed in gorillas. In addition, these variables triggered important differences among the age/sex classes in terms of termite consumption. These differences and the multifactorial nature of seasonal insectivory in great apes has likely contributed to the ambiguous results in previous studies.

This study underlines the importance of insects to gorilla diet, conferring a degree of flexibility which in turn allows them to cope with seasonal changes in the availability of nutrients and diverse forest habitats (Cipolletta, 2004; Masi et al., 2015). Although the environment of South African australopithecines was different from the dense forests in which great apes live today (Vrba, 1975), diets were quite similar and showed similar diversity (Scott et al., 2005). Increasing our understanding of insect eating in great apes allows us to shed light on the importance of insectivory among early humans (Lesnik, 2018). Isotopic signatures of *Paranthropus robustus* show even more extreme seasonal variations in their diet than those observed in savanna chimpanzees (Lesnik, 2018; Sponheimer et al., 2006). In addition, since its diet was mostly composed by protein-poor plant parts, the intake of protein-rich insects certainly has played an important role in the nutrition of our ancestors (Lesnik, 2018). Like for gorillas, insect feeding was likely an opportunistic behavior influenced by biological and environmental factors whose impact on individuals

depended on their age and sex class. In this framework, insect feeding may have been particularly advantageous for female australopithecines (Backwell & d'Errico, 2008). Optimizing insect intake may have been an incentive to develop tools to harvest them, as shown by their bone tools (d'Errico & Backwell, 2009).

Finally, soil-feeding termites like most insects, are sensitive to habitat disturbance which can reduce vegetation biodiversity (Ahmed et al., 2011; Gillison et al., 2003). Since insects are nutritionally important for endangered great apes (IUCN, 2016) and the tropical forest ecosystem, it is of crucial importance to preserve high insect biodiversity. Given current global climate change, as well as anthropogenic deforestation and land encroachment, that exacerbate seasonal inter-annual variability of forest phenology and food shortages (Bush et al., 2020; Chapman et al., 2005), animal feeding behavior and survival could greatly be at risk.

AUTHOR CONTRIBUTIONS

Claire Auger: Conceptualization (supporting); formal analysis (lead); investigation (equal); methodology (lead); writing – original draft (lead). **Chloé Cipolletta:** Data curation (supporting); resources (supporting); writing – review and editing (supporting). **Angelique Todd:** Data curation (lead); methodology (supporting); resources (supporting); writing – review and editing (equal). **Terence Fuh:** Data curation (supporting); resources (supporting); writing – review and editing (supporting). **Andrea Sotto-Mayor:** Data curation (lead); resources (lead); writing – review and editing (supporting). **Emmanuelle Pouydebat:** Formal analysis (supporting); funding acquisition (lead); project administration (equal); supervision (equal); validation (supporting); writing – review and editing (equal). **Shelly Masi:** Conceptualization (lead); data curation (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); resources (lead); supervision (lead); validation (lead); writing – review and editing (lead).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, Shelly Masi, upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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