Exploitation of underground bee nests by three sympatric consumers in Loango National Park, Gabon

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ABSTRACT

Honey represents a highly nutritious resource for animals, but is difficult to obtain given bees' defensive strategies. We investigated exploitation of the underground nests of stingless bees (*Meliplebeia lendliana*) by three sympatric consumers in Loango National Park, Gabon: the central African chimpanzee (*Pan troglodytes troglodytes*), forest elephant (*Loxodonta cyclotis*) and honey badger (*Mellivora capensis*). Given the differences in their respective morphological traits and sensory abilities, we hypothesized that chimpanzees would be more limited in digging out the bee nests, compared to the other two competitors, and would show behavioral strategies to overcome such constraints. Our dataset comprised camera trap footage recorded over 60 mo at 100 different bee nests. Chimpanzees visited the nests more often than the other consumers, showing a frequency of extraction success comparable to that observed in honey badgers, the most efficient digger. Both chimpanzees and honey badgers increased their extractive attempts across the dry season, whereas elephants did not. The soil hardness was greater during the dry season than the wet season and, possibly in order to compensate for this, chimpanzees showed a tendency toward digging at nests found in relatively softer soil. They also seemed to be inhibited by indirect cues left by other consumers, possibly as a risk-avoidance strategy. Overall, chimpanzees and honey badgers extracted the underground nests of stingless bees with similar frequencies, whilst forest elephants did so only occasionally. Moreover, chimpanzees can use tools and other behavioral strategies to overcome the physical limitations that may constrain their exploitation of this resource.

Key words: camera trapping; community ecology; honey consumption; *Loxodonta cyclotis*; *Mellivora capensis*; *Pan troglodytes troglodytes*; stingless bees; tool use.

HONEY REPRESENTS A HIGHLY VALUABLE DIETARY SUPPLEMENT FOR ANIMALS, being a concentrated source of sugars, vitamins, and minerals, as well as other chemically active compounds (Murray *et al.* 2001, Bogdanov *et al.* 2008, Vit *et al.* 2013). Having gained access to a bee nest, predators can also reach the brood, providing proteins and fat (Finke 2005). Honeybees (*Apis mellifera*) produce a high amount of honey, but it is obtainable at the cost of enduring bees' stings. Although stingless bees (Apidae: Meliponini) produce less honey than honeybees (Roubik 2006), their nests are a less risky target, provided that consumers can locate and reach the hidden chamber containing the honey and brood.

Stingless bees build their nests inside cavities, either in wood or underground, connected to the exterior through an entrance tube (Roubik 2006). The primary defense of nests consists of the matrix in which they are built, and their low visibility: the nest chamber can be located up to 2 m deep and the presence of a nest revealed only by its entrance tube, measuring 6–8 mm in diam and protruding 0.5–1 cm above the ground, favorably hidden by fallen foliage on the forest floor (de Portugal Araujo 1963). These features make locating and accessing nests a challenging task for nest predators, which represent the main cause of colony mortality; this evolutionary pressure may have shaped bee nesting behavior (Kajobe & Roubik 2006, Michener 2013).

In Africa, several mammals opportunistically raid these nests, with honey badgers and primates being the main threat in savanna and rain forest habitats respectively (Roubik 2006). Chimpanzees (*Pan troglodytes*) consume honey from both honeybees and stingless bees across their range, employing a variety of technological strategies to reach it (Sanz & Morgan 2009).

In Loango National Park (NP), Gabon, central African chimpanzees (*P. t. troglodytes*) use tools to extract the underground nests of *Meliplebeia lendliana* (Boesch *et al.* 2009), among other species. Camera traps were placed at known nest sites to observe chimpanzee behavior. Interestingly, footage revealed exploitation of the same resource by forest elephants (*Loxodonta cyclotis*) and honey badgers (*Mellivora capensis*), providing an opportunity to investigate patterns of exploitation by three consumers which differ greatly in their morphological traits and feeding ecology.

Honey badgers are specialized diggers (Rose *et al.* 2014), whilst elephants can use their tusks to dig into the soil. Nevertheless, chimpanzees can apply behavioral and tool-using strategies to compensate for their lack of physical adaptations to dig out nests. To detect the presence of food sources, elephants and honey badgers rely mainly upon olfaction (Begg 2001, Rizvanovic *et al.* 2013), while primates primarily rely on vision (Fobes 1982, but see Laska *et al.* 2000). Consumers (both con- and hetero-specific) may produce cues during their foraging activity, which persist in time and potentially are available to other individuals (Dall *et al.* 2005, Seppänen *et al.* 2007). For instance, non-human

animals can use such information when foraging (Galef & Giral-deau 2001). At each visit to an underground bee nest, the predator can either inspect it and leave, or start digging to reach it. If successful, the predator usually consumes the nest entirely and the bees leave. If not, the nest remains active, although potentially more visible and accessible.

In this study we: (1) tested which nest features limit the success of predators; (2) described the activity pattern of each consumer species around nests and test whether this followed a seasonal pattern; and (3) investigated which factors affected the extractive behavior of chimpanzees, the principal—and supposedly least proficient—consumer of these bees in rain forests.

We predicted that bees try to overcome predators by increasing uncertainty regarding the location of the underground nest chamber (represented by the distance and direction of the chamber from the entrance tube), rather than its depth, since both elephants and honey badgers are considered efficient diggers. We hypothesized that chimpanzees would be more limited than honey badgers and elephants by the structural features of bee nests.

Seasonal changes in environmental conditions may affect predators' activity patterns. We predicted that the hindrance represented by the soil in which nests are found will change with seasonal rainfall (assuming that soil hardness changes with seasonal variation in rainfall). Thus, less skilled diggers such as chimpanzees might concentrate their effort during the wet season, whereas soil hardness should not affect the visit patterns of the other two species. Alternatively, predators may intensify their attempts when a greater amount of honey and brood is available: stingless bees' food acquisition (and therefore honey storage and brood growth) correlates with floral abundance (Roubik 1982), which is typically negatively correlated with rainfall (Sommer *et al.* 2012). Under these circumstances, we expected all predators to increase their visits to nests during the dry season.

Finally, we predicted that chimpanzees should be more likely to dig when visual cues are available suggesting increased accessibility of a nest, namely signs of digging carried out by previous predators or presence of tools accumulated at a nest site following attempts by conspecifics (Fragaszy *et al.* 2013). We also considered the effects of indirect olfactory cues left by the previous visitor, prior to each chimpanzee visit. We hypothesized that apes could be either positively or negatively affected by such cues: the detection of a previous visitor could indicate the presence of a feeding resource, but also the presence of a potential competitor that would be preferable to avoid (Head *et al.* 2012 provide evidence of competitive exclusion between chimpanzees and elephants at this field site).

METHODS

FIELD SITE AND STUDY DESIGN.—Our field site is located in Loango NP, Gabon (2°04′S, 9°33′E), and covers an area of approximately 80 km² comprising mature, secondary, coastal and swamp forest and savanna. The mean annual rainfall is 2215 mm and mean daily temperature ranges between 22.9°C and 27.2°C. The long rainy season lasts from October to April, often interrupted by a brief dry season (December–January); the long dry season spans May to September (Head *et al.* 2011, 2012). The focal chimpanzee community was not habituated to human observers during this study. Their home range covers *ca* 36 km² (Head *et al.* 2013).

We used remote-sensor camera traps to monitor animal activity at opportunistically detected underground bee nests. We collected data on nest structure and other environmental variables (soil hardness at the nest site, rainfall, and phenological data).

CHARACTERISTICS OF BEE NESTS.—We monitored 100 underground nests of *M. lendliana*. Given the visual inconspicuousness of intact nests, we relied on evidence of activity by previous predators or noticed the bees flying in and out of the entrance tube to spot the nests. In only 22 cases were intact sites found. To locate the underground chamber, we repeatedly perforated the ground around the entrance tube with a metal stick, in concentric circles of increasing diameter, until the tip was retrieved with honey. We measured the horizontal distance between the entrance tube and this perforation point (cm; 'distance nest chamber-entrance tube'), the geographical direction of the nest relative to the entrance tube (in degrees from N) and the depth of the underground chamber (cm; 'chamber depth'). In some cases, the depth was measured after the nest had been extracted, by relying on the traces of the nest's protective layers that are usually left on the ceiling of the resulting hole (Fig. 1A, B). The underground chambers seemed randomly located relative to the entrance tube (Fig. 1C), possibly according to site-specific conditions (*e.g.*, soil hardness, presence of roots).

SOIL HARDNESS.—We measured soil hardness at 29 nests every 3 wk between July and December 2013. The measured nests were equally distributed across the area including our 100 focal nests and were representative of the variation in number of recorded visits by predators; both active and inactive nests (abandoned or extracted) were measured. We measured soil hardness by dropping a 5-kg weight three times from a height of 10 cm onto a metallic stick, which had previously been inserted 10 cm vertically into the soil around the entrance tube (or its assumed location, in the case of inactive sites). Soil hardness therefore expresses perforation into the ground (cm). We sampled at eight different points around the entrance tube, at a distance of 10 and 20 cm from the tube in each of the four cardinal directions (Fig. 1B). We slightly shifted the sampling points each time, to avoid sampling the same point repeatedly.

RAINFALL AND FLORAL PHENOLOGY.—Rainfall (mm) was recorded daily at the camp. We calculated the variable 'rain/d' (model 1; Table 1) as the amount of rainfall measured during the time elapsing between successive measurements of soil hardness, divided by the number of days concerned. The phenology of 64 different tree species (all recognized at minimum at the genus level) from 35 families, measuring ≥1 cm in dbh (range: 1–186 cm) was monitored monthly over 35 km along a trail system (Head *et al.* 2011). Of these, 24 species belong to families considered important food
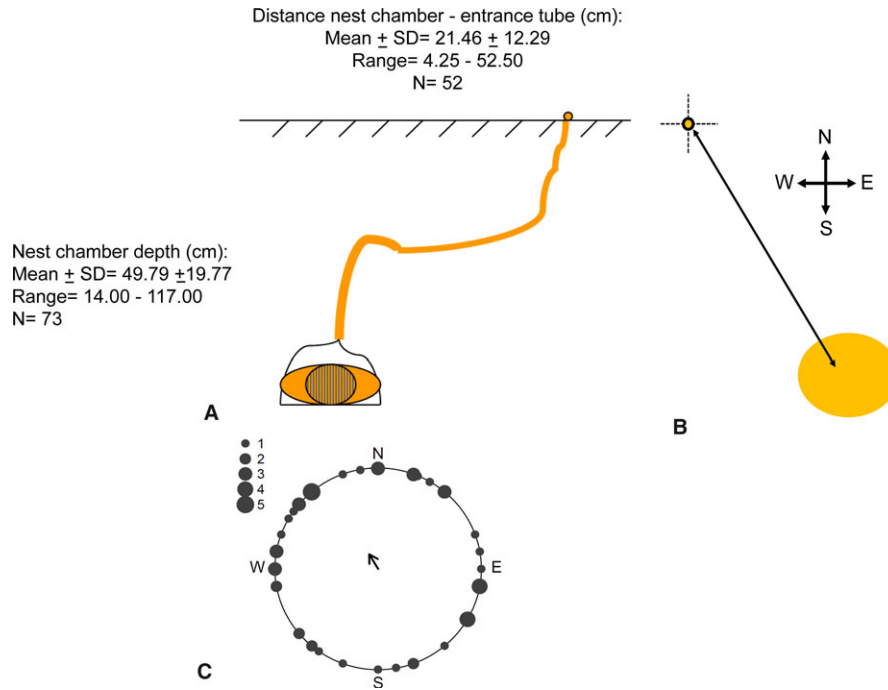
FIGURE 1. Description of underground stingless bee nests in Loango NP, Gabon: (A) schematic representation of nest structure (transversal view) and descriptive statistics for structural variables; (B) horizontal distance between the entrance tube and nest chamber, and the locations of soil hardness measurements around the entrance tube; (C) location (in degrees N) of the nest chamber relative to the entrance tube (N = 56 nests): the area of filled circles on the circumference represents the number of observations per direction.

TABLE 1. *Overview of models performed to investigate the consumption of underground stingless bee nests in Loango NP, Gabon. We report the exact formula used for each model, where test predictors are highlighted in bold, interactions are denoted by asterisks, random intercepts by (1\random effect), random slopes by (0 + predictor\random effect), and any offset terms indicated. In addition, we show results for the comparison of the full model versus the null model.*

Model	Formula	Full versus Null
1	Perforation into the ground (cm) ~ **rain/d * (habitat type + swamp presence) + elevation** + stick type + (1|nest site) + (1|nest condition) + (0 + stick type|nest site) + (0 + rain/d|nest site)	$\chi^2 = 47.553$, df = 6, $P < 0.001$
2A	Bee nest extracted by all consumers (yes/no) ~	$\chi^2 = 17.303$, df = 4, $P = 0.002$
2B	Bee nest extracted by chimpanzees (yes/no) ~	$\chi^2 = 15.007$, df = 4, $P = 0.005$
2C	Bee nest extracted by honey badgers (yes/no) ~	$\chi^2 = 5.672$, df = 4, $P = 0.225$
	chamber depth * distance nest chamber-entrance tube + average soil hardness + offset(total digging time)	
3A	N visits/mo (chimpanzee) ~	$\chi^2 = 9.688$, df = 2, $P = 0.008$
3B	N visits/mo (elephant) ~	$\chi^2 = 0.817$, df = 2, $P = 0.665$
3C	N visits/mo (honey badger) ~	$\chi^2 = 7.229$, df = 2, $P = 0.027$
	sine 15th d/mo + cos 15th d/mo + (1|yr) + (0 + sine 15th d/mo|yr) + (0 + cos 15th d/mo|yr) + offset (camera days/mo)	
4	Chimpanzee digging (yes/no) ~ time gap between visits * (**last visiting species + cumulative digging time**) + **average soil hardness per site + deviation soil hardness per site + floral availability + number of tools accumulated** + time since last human visit + total number social partners + age + (1|nest site) + (1|individual ID) + (1|visit ID) + (0 + average soil hardness per site|individual ID) + (0 + deviation soil hardness per site|nest site) + (0 + floral availability|nest site)	$\chi^2 = 23.731$, df = 10, $P = 0.008$

sources for African stingless bees (Kajobe 2013). Flower maturational stage was scored on an ordinal scale, from absent to mature. The number of trees monitored varied between 824 and 989 per year (average ± SD = 862.8 ± 70.9). From this dataset we extracted floral availability, used as a proxy for honey availability (model 4; Table 1).

VARIATION IN SOIL HARDNESS.—We investigated which factors influenced soil hardness (square-root transformed) using a Generalized Linear Mixed Model (GLMM; Baayen 2008) with Gaussian error distribution and identity link (model 1 in Table 1; $N = 1344$). The predictor 'habitat type' included two levels (open or closed secondary forest, distinguished based on a visibility estimate following Head *et al.* 2012), while the predictor 'swamp presence' accounted for the presence of swamps within 15 m of a nest. The elevation (m) of each nest site was extracted from a Digital Elevation Map of Gabon (USGS 2004). The control predictor 'stick type' had two values (during the study period the stick initially used to measure soil hardness broke and was replaced by another). 'Nest site' (29 nests), and 'nest condition' (seven levels: active, extracted by chimpanzee/elephant/honey badger, dug out by humans, abandoned by bees, or unknown reason for nest termination), were included as random effects. The model included the interactions between 'rain/d' and 'habitat type' and between 'rain/d' and 'swamp presence' as we assumed that rainfall had a differential effect upon soil hardness depending on these two parameters, as well as the appropriate random slopes terms (Barr *et al.* 2013). We did not account for slope steepness.

We predicted the values of soil hardness for each nest, for the whole period over which the nest was monitored. From these data, we calculated the average soil hardness for each nest and the soil hardness at the time of each chimpanzee visit (used in models 2 and 4; Table 1). To obtain predictions that were not conditional on any specific model, we fitted one model with each possible combination of the above-mentioned fixed effects (including the two interactions; models comprising an interaction also included the respective main effects), producing a total of 52 models. The predicted values of the response variable were calculated as the average of all predictions across all models, weighted by the Akaike weight of the respective model (Burnham & Anderson 2002). We assessed the accuracy of the predictions by using cross-validation. First, we fitted the same models as described above to a subset comprising 24 randomly selected nests and calculated the predicted values of soil hardness. Then we compared the predicted values for the five nests not included in the random selection with the measured soil hardness values for those five nests. We found that 95 percent of the predicted values deviated from the observed values by at most *ca* 11 cm (range of soil hardness values = 0.5–34.9 cm).

CAMERA FOOTAGE.—Video data were collected from April 2009 to March 2014, using camera traps (Sony Handycam with trailmaster 700V, Scoutguard 550 and Bushnell Trophy Cam). Sony cameras recorded continuously until no further movement was detected within a two-min interval; Scoutguard 550 and Bushnell Trophy Cam recorded one-min clips, and were re-activated as long as movement persisted with an inter-clip interval of one-second. Each camera was checked every 2 wk, the SD cards or tapes collected and replaced with empty ones, and the batteries changed. All cameras were placed at active nests and were removed once the nest had been extracted or there were no further signs of bee activity. The number of simultaneously monitored nests varied between 9 and 50. The unit of monitoring time used was 'camera day', indicating a day during which the camera trap functioned properly. A total of 20,935 camera days were obtained, with the monitoring period at a given nest ranging from 5 to 1810 camera days.

A 'visit' was defined as any instance when one or more individuals, of all those recorded in a video, belonging to any of the three predator species showed interest in the nest. A visit comprised one or more clips, provided the interval between consecutive clips was no more than 15 min. Each visit was classified as one of the following types: (1) 'exploration', when animals inspected the entrance tube, *e.g.*, smelled or scratched the surface; (2) 'digging', when animals removed soil by digging and/or using tools (ending in a successful extraction or not); and (3) 'visit after extraction', when animals visited a recently extracted nest with or without obtaining food from it. The duration of digging was scored using INTERACT 9 (MANGOLD 2010), and the overall duration of digging (sec) calculated as the sum of digging time per visit. Inter-observer reliability of digging duration was assessed by comparing the values obtained by two raters coding 15 video clips (five per species; Spearman's rho = 1, 0.7 and 0.9 for chimpanzee, elephant, and honey badger respectively). All chimpanzees were individually identified (Head *et al.* 2013). Our sample comprised 22 adult females, 30 juveniles/infants, 11 adult males, and 7 adolescents (age classes based on physical and behavioral criteria listed in Boesch & Boesch-Achermann 2000).

HONEY EXTRACTION.—We tested which environmental factors influenced the probability of extractions: first considering all three species of consumers combined, then considering chimpanzees and honey badgers separately (models 2A, B and C; Table 1). We could not test elephants due to their small number of extractions ($N = 2$). In each case we used a Generalized Linear Model (GLM) with binomial error distribution and logit link function (McCullagh & Nelder 1996; $N = 50$ nests for which data were available for all variables). We included the interaction between 'chamber depth' and 'distance nest chamber-entrance tube', as we assumed that nest depth had a differential effect upon extraction probability depending on how far the chamber was from the entrance tube. An offset term, 'total digging time' (sec), accounted for the duration of digging performed by any species at each site. All quantitative predictors were z-transformed (to a mean of zero and a standard deviation of one) and the offset term was log-transformed before fitting the model.

CONSUMER ACTIVITY PATTERNS.—We calculated the average time interval between visits at the same site, for each species separately, as the number of camera days between the first and the last visit at a given site divided by the number of visits recorded at that site after the initial visit. We tested the seasonality in monthly number of visits (across all nests), for each species separately (models 3A, B, and C; Table 1), using a GLMM with Poisson error structure and log link function ($N = 60$). Since we predicted a seasonal peak in predator activity, the effect of season

was included as a circular variable. The peak might occur either when the soil was softer (wet season) or alternatively when there was maximal honey storage (end of the dry season). We used the midpoint of each month (15th day) as a date to create the circular variable, which was calculated by transforming this date into radians. The model comprised the *sine* and the *cosine* of this variable. We accounted for the differential effect of season across years by including the random effect 'year' (six levels), as well as the relevant random slopes. Finally, 'camera days/mo' accounted for variation in monthly monitoring effort (log-transformed, included as an offset term).

Finally, we investigated which factors influenced the digging behavior of chimpanzees (model 4; Table 1), using a GLMM with binomial error structure and logit link function ($N = 307$). Since we expected that the cues left by a previous visitor would fade over time, we included the interaction between 'last visiting species' and the time elapsed between the occurrence of the previous visit and the visit of the chimpanzee ('time gap between visits'), as well as the interaction between the latter variable and 'cumulative digging time'. We controlled for cues left by researchers by including a variable expressing the time elapsed between each chimpanzee's visit and the last human visit at the site.

Floral availability was calculated as the monthly average floral maturational stage of all trees included in the phenology dataset, weighted by the crown diameter of each tree. To account for a possible time delay between the amount of available flowers and the storage of honey we included this variable in the model as the average floral availability over the 30 d prior to a visit (where the floral availability on any given day was taken to be the value for the respective month).

We tested for an effect of variation in soil hardness between sites by including the average value for each site, and for variation within each site by including the deviation of each value from the site-specific mean at the time of a chimpanzee's visit (van de Pol & Wright 2009). The values of soil hardness used per nest site and visit were taken from the predictive model described above. We controlled for the age class of the visiting individual (adult, adolescent, juvenile or infant) and for the number of social partners recorded in the videos. We included the random effects of site (44 levels), individual identity (68 levels) and visit (219 levels), and all relevant random slopes terms. Before running the model, we log-transformed the following predictors: 'time gap between visits', 'cumulative digging time', 'time since last human visit', 'total number of social partners' and 'number of tools accumulated' and then z-transformed all quantitative predictors.

MODEL IMPLEMENTATION.—We fitted all GLMMs using the functions lmer (model 1) or glmer (models 3 and 4) of the R-package lme4 (Bates *et al.* 2014), and the GLM (model 2) using the R-function glm. For GLMMs, correlations between random slopes and random intercepts were excluded to avoid models becoming too complex (Barr *et al.* 2013). For model 1, we verified the assumptions of normally distributed and homogeneous residuals by visually inspecting a qqplot and the residuals plotted against fitted values. When appropriate (models 1, 2, and 4), we excluded

the possibility of collinearity among predictors by inspecting Variance Inflation Factors (Field 2005) using the function vif of the R-package car (Fox & Sanford 2011), based on standard linear models excluding the random effects and interactions. Overdispersion was not detected in any of the Poisson models (model 3; dispersion parameters = 0.98, 1.77, 1.18 for models 3A, B, and C respectively). We assessed the stability of GLMMs by comparing the estimates derived from a model based on all data with those obtained from models based on subsets which excluded levels of the random effects one at a time. For the GLM, we inspected dfbeta-values (Field 2005). No issues were found in any model. In all cases, the overall significance of the full model (Forstmeier & Schielzeth 2011) was first tested by comparing it with a null model comprising only the control predictors, the offset terms (if present) and the random effects (for GLMMs), through a likelihood ratio test (R-function ANOVA with argument test set to 'Chisq'; Dobson 2002). When an interaction term had no significant effect (all $P > 0.14$, across all models), we ran a reduced model including only the main effects. P values for the individual effects were based on likelihood ratio tests comparing the full with respective reduced model (R-function drop1; Barr *et al.* 2013). All analyses were conducted in R (R Core Team 2014; v. 3.1.0).

RESULTS

SOIL HARDNESS.—The full model differed significantly from the null model (model 1; Table 1). The two interactions had no significant effect upon soil hardness (Table S1), but there was a significant main effect of rainfall; the measure of stick penetration into the ground was greater with increasing rainfall (estimate ± SE = 0.137 ± 0.013, $\chi^2 = 45.509$, df = 1, $P < 0.001$; Table S2; Fig. S1). Soil hardness varied greatly both within and across sites (Fig. S2), and the random effect 'nest site' had a significant effect ($\chi^2 = 133.77$, df = 1, $P < 0.001$).

UNDERGROUND BEE NEST EXTRACTIONS.—Nest features significantly affected the probability of a nest being extracted, when all consumer species were considered together (model 2A; Table 1). The interaction did not significantly affect the response (Table S3); the reduced model showed that the larger the distance between the entrance tube and the underground chamber the smaller the probability of successful extraction by any predator (estimate ± SE = −1.469 ± 0.414, $\chi^2 = 12.986$, df = 1, $P < 0.001$; Table S4). Chimpanzees' success at extracting nests was particularly affected by nest features (model 2B; Table 1), whilst honey badgers were not (model 2C; Table 1 and Table S5). The reduced model showed that chimpanzees were significantly limited by the distance between the entrance tube and the underground chamber (estimate ± SE = −1.145 ± 0.473, $\chi^2 = 7.469$, df = 1, $P = 0.006$; see Table S6 and S7 for results of the full and reduced models respectively).

CONSUMER ACTIVITY PATTERNS.—We recorded 730 visits. Of the 100 monitored nests, 14 were never explored nor was any digging

attempt by predators detected (Table 2); 18 nests were visited by all predator species, 41 nests visited by two species and 27 nests by only one species. Predator species differed in their time intervals between visits (Fig. S3). Chimpanzees accounted for 18 successful extractions (at 18 different sites), honey badgers 14 (14 different sites) and elephants 3 (three different sites), across the 33 sites at which extractions were observed. In all except two cases, the bees left the nest following a successful extraction. At the extracted sites, chimpanzees were successful in one out of two visits (median = 2, range = 1–7); honey badgers were mostly successful at their first visit (median = 1, range = 1–3), whereas elephants were the least successful predator (median = 8, range = 1–25). When considering both active and extracted nests, the average number of visits required to attain a success was higher for all predators (19.5, 3.7 and 76.7 visits for chimpanzees, honey badgers, and elephants respectively).

SEASONALITY.—Both chimpanzees and honey badgers increased their number of visits during the dry season (May to September), whilst elephants did not (models 3A, B, and C in Table 1; Fig. 2). Chimpanzees' visits peaked at the beginning of the rainy season (October).

CHIMPANZEE DIGGING BEHAVIOR.—Chimpanzees attempted to extract nests found with signs of digging by previous visitors and intact nests with similar probabilities (65.4% and 63.6%, respectively). Both cues left by previous predators and environmental factors had a significant effect on their extractive behavior (model 4; Table 1). The interactions did not significantly affect the response (Table S8). The identity of the previous species to visit a nest had a significant effect (χ^2 = 14.381, df = 2, P < 0.001; Table S9): chimpanzees were less likely to dig after a visit by honey badgers, compared to a previous visit by chimpanzees or elephants (Fig. S4). We found a tendency for chimpanzees to be more likely to dig at nests where the soil was, on average, relatively softer than elsewhere (estimate ± SE = 0.430 ± 0.288, χ^2 = 2.763, df = 1, P = 0.096; Table S9). The age class of the individual had a significant effect, with infants being significantly less likely to dig compared to older individuals (χ^2 = 10.934, df = 3, P = 0.012; Table S9).

DISCUSSION

Using an indirect monitoring method, we revealed the patterns of exploitation of underground stingless bee nests by three sympatric consumers. The main constraint for nest predators in success was the horizontal distance between the underground chamber and entrance tube of the nest. As predicted, the best defense for bees relied in creating uncertainty regarding the location of the nest chamber, rather than in its depth or the hardness of the surrounding soil. Chimpanzees were particularly limited by the former feature; as expected, none of the nest characteristics we considered to affect the success of honey badgers. We documented the exploitation of this resource by forest elephants, although at low levels. To our knowledge, neither bees nor their products have previously been reported to be consumed by this species (Tchamba & Seme 1993, Blake 2002, Morgan & Lee 2007).

In our study, chimpanzees and honey badgers exhibited comparable frequencies of extractions (51.4% and 40%, respectively), whereas elephants were rarely successful (8.6% of extractions). The tool-use behavior of chimpanzees possibly compensated for their lack of morphological specializations for digging. The three consumers revisited bee nests at different rates in the camera footage. Chimpanzees and elephants are present at comparable densities in Loango NP (1.72 and 1.37 individuals/km², respectively; Head *et al.* 2013); therefore, our results likely reflect a difference in their visiting behavior to bee nests. The same applies to honey badgers, as existing data indicate a low density (0.1–0.3 individuals/km²; Begg *et al.* 2008). Chimpanzees revisited the nests more often, compared to the other two predators, and needed repeated attempts before being successful. In contrast, honey badgers, specialized diggers, were highly successful at their first visit. Taken together, these results reflect differences in species-specific efficacy, likely linked to different digging abilities.

Chimpanzees and honey badgers increased their visits to bee nests during the dry months, confirming previous findings on seasonal honey consumption by both species (Fay & Carroll 1994, Vanderhaar & Hwang 2003, Sanz & Morgan 2009, 2013, Sommer *et al.* 2012). The dry season is typically a period of food

TABLE 2. *Overview of the number of visits, per predator species and visit type, recorded by camera traps placed at 100 underground stingless bee nests (see text for the operational definitions of visit types), and the number of nests visited by each species, in Loango NP, Gabon. The number of 'individual' visits represents the dataset for which the duration of digging behavior was coded.*

| Species | Visit type | | | Total | Individual visits | Visited nests |
	Exploration	Digging	Visit after extraction			
Chimpanzee	133	269	22	424	477	75
Elephant	190	45	14	249	281	54
Honey badger	27	25	5	57	63	34
Total	350	339	41	730	–	86[a]
Individual visits	370	392	59	–	821	–

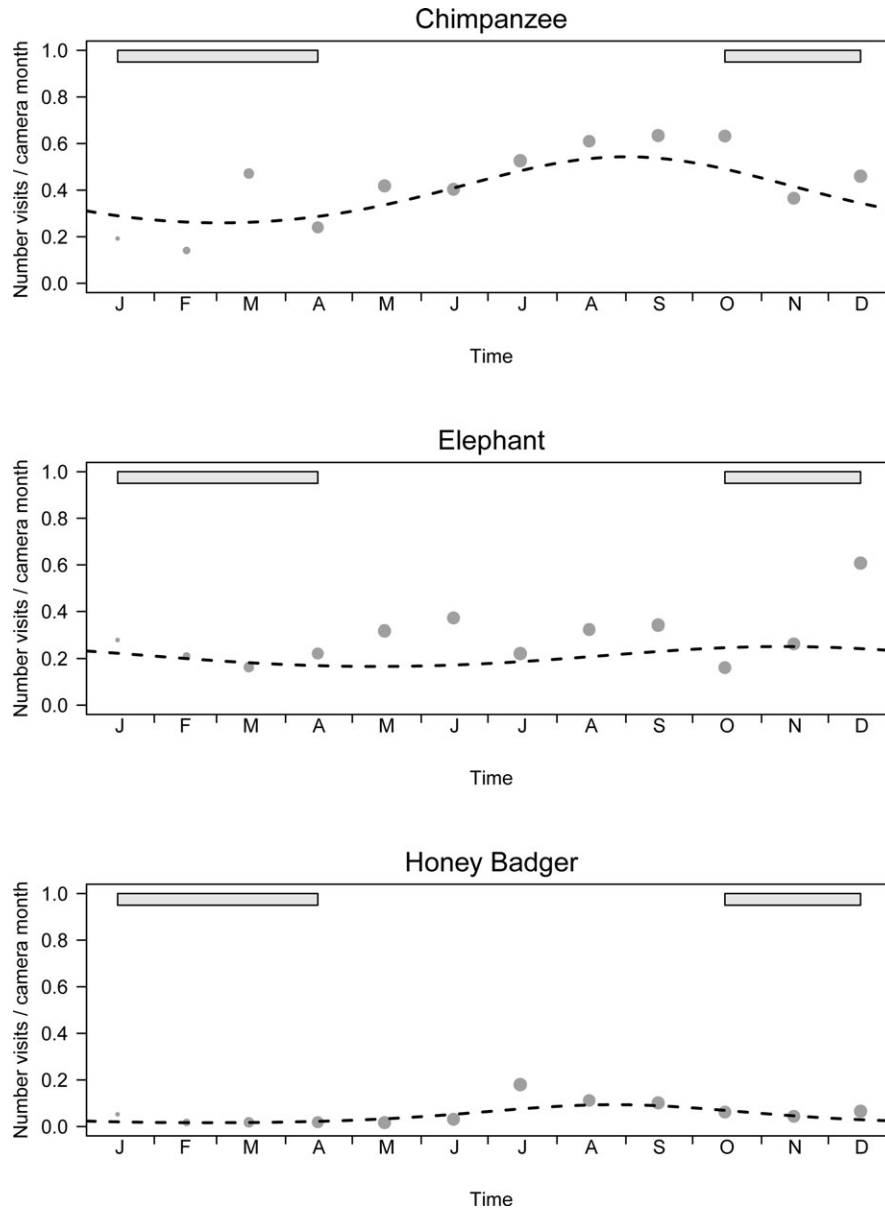[a]14 of the 100 monitored nests were never visited by any predator.

FIGURE 2. Seasonality of activity by different predator species at underground stingless bee nests; the plot shows the variation in number of visits (per camera month) across the year, and dashed lines indicate the fitted model; gray rectangles indicate the long rainy season.

scarcity for chimpanzees (*P. t. ellioti*: Hohmann *et al*. 2006, *P. t. troglodytes*: Sanz & Morgan 2013), thus, the exploitation of bee products during this period may represent an important addition to their diet. The same pattern (increased consumption of honey when fruit is scarce) is found for the Bulindi community, Uganda, although in this case it occurs during the rainy months (McLennan 2015). Interestingly, no correlation between rainfall and fruit availability was found at our site, and the consumption of fruit by chimpanzees is stable over the year (Head *et al*. 2011). The dry season presumably corresponds to the time when bee nests contain the maximum amount of resources (Roubik 1982), which probably peaks toward the end of the season.

Furthermore, during this period the forest floor is drier and more open, conditions which may make detection of nests easier, whether visually, via olfactory cues (*e.g.*, the greater quantity of stored honey could have an impact on the odor of nests), or by hearing the bees (Pascual-Garrido *et al*. 2013). A combination of these factors could explain the increase in chimpanzee visits to nests across the dry season, peaking at the beginning of the rainy season, when the honey was maximally available and the forest still very dry.

Chimpanzees' digging behavior seemed enhanced when they visit nests located in areas possessing, on average, softer soils than others. This possibly represented a behavioral strategy to

compensate for the fact that they increased their extractive effort during the dry season, when the soil is at its hardest. More puzzling is the negative effect of previous visits by honey badgers on chimpanzee behavior. Honey badgers, particularly females, can scent-mark foraging sites with urine, to regulate spatio-temporal separation of resource use among conspecifics (Begg 2001); we recorded this behavior on three occasions. Our result could reflect an olfactorily mediated aversive response of chimpanzees toward a potentially highly aggressive competitor, the honey badger (Begg 2001, Dominy *et al.* 2001). Infant chimpanzees seemed less eager to dig; such a tool-mediated foraging technique is likely acquired gradually over several years (Boesch-Achermann & Boesch 1993, Lonsdorf 2005, Humle *et al.* 2009). The acquisition of this technique will be the subject of future study.

In sum, the main cost of exploiting bee nests for chimpanzees is represented by the extractive effort. Nevertheless, overall they attained a comparable number of extractions to the most highly adapted digger species, the honey badger, which was the most efficient consumer. Chimpanzees seemed to prefer to dig at nests found in softer soils, which may facilitate their extraction. Although the yearly activity patterns of chimpanzees and honey badgers around bee nests overlapped, we assume that the competition between these two species is relatively low given the estimated local low density of the latter species. Also, chimpanzees seemed to avoid nests that have just been visited by honey badgers, which may reflect a behavioral strategy to avoid competitors.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

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

TABLE S1–S2. *Influence of environmental variables on soil hardness measured at underground stingless bee nests in Loango NP, Gabon.*

TABLE S3–S7. *Influence of environmental variables on the probability of an underground stingless bee nest being extracted in Loango NP, Gabon.*

TABLE S8–S9. *Influence of environmental variables and cues left by previous visits of competitors on the probability of digging behavior at bee nests by central African chimpanzees in Loango NP, Gabon.*

FIGURE S1. Influence of rainfall on soil hardness at underground stingless bee nests in Loango NP, Gabon.

FIGURE S2. Variation in soil hardness at the 29 underground stingless bee nests in Loango NP, Gabon, over 6 mo.

FIGURE S3. Time interval between visits to underground stingless bee nests for each predator species in Loango NP, Gabon.

FIGURE S4. Effect of the last species to visit a stingless bee nest upon the probability of digging behavior at that nest by central African chimpanzees.

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