



RESEARCH ARTICLE - BEES

Patterns of Diversity and Distribution of Arboreal Social Bees' Beehives within Chimpanzees' Home Range in a Forest-Savanna Mosaic (Comoé National Park, Côte d'Ivoire)

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Abstract

The goal of this study was to explain the patterns of diversity and distribution of arboreal social bees nesting in forests of the Comoé National Park, within the home-ranges of wild chimpanzees, consumers of their honey. Investigations were done using a total of sixteen plots of one hectare each, established in three habitat types (mature forest island, secondary forest island and gallery forest). The diversity and distribution of arboreal social bees was assessed using visual searches. The exploitation of the beehives of these bees by chimpanzees was also evaluated using honey dipping tools as indicators. Five bee species belonging to two tribes, namely the Meliponini (*Meliponula ferruginea*, *Meliponula togoensis*, *Meliponula bocandei*, *Hypotrigona gribodoi*) and the Apini (*Apis mellifera*) were collected. Furthermore, frequent exploitation of the honey of stingless bees by chimpanzees was observed, excepted for *H. gribodoi*. Beehives of *Meliponula ferruginea* were identified as the most exploited ones by chimpanzees. A total of 114 beehives were found in the established plots leading to an estimated density of 2.4 beehives/ha within the study area. Among the surveyed habitats, mature forest island was found to harbor the highest beehives' density (4.2 beehives/ha), followed respectively by secondary forest island (1.9 beehives/ha) and gallery forest (1.1 beehives/ha). Finally, all bee species were found nesting in cavities of trees with a DBH ranging from 15 to 87.3 cm, with a special preference for *Dialium guinneense*. However, the DBH of the nesting trees and the beehives' height measured from the ground level, were found not significantly influencing the honey exploitation by chimpanzees. In sum bee species diversity and distribution might be the most important variables in the survival of chimpanzees within forest-savanna mosaic landscape.

Introduction

Invertebrates are included in the diet of many primates (Redford, 1987; Pruetz, 2006). Within the primates, chimpanzees

consume mainly social insects such as termites (*Macrotermes* spp., *Cubitermes* spp., *Thoracotermes* spp.), ants (*Dorylus* spp., *Oecophylla longinoda*, *Camponotus* spp.) and bees/honey (*Apis mellifera* and the Meliponini) (O'Malley & Power, 2012).



These invertebrates offer a large, clumped biomass and/or a high nutritional pay-off (McGrew, 2001; Deblauwe et al., 2003).

In African savannas, where chimpanzees have been studied extensively, it has been demonstrated that the consumption of insects by chimpanzees occurs seasonally. In Tanzania and Senegal, respectively located in eastern and western Africa, termites were for example found mainly included in their diet during rainy seasons (McBeath & McGrew, 1982; Goodall, 1986), while bees and honey were eaten during the late dry season (Pruetz, 2006). The consumption of honey by chimpanzees has been reported in many sites across Africa, suggesting the importance of bees as a significant food resource for these primates (McGrew, 1992; Sanz & Morgan, 2007; 2009). In fact, some populations of the chimpanzee subspecies have been found to prey upon brood and stored honey of Apini and Meliponini (Sommer et al., 2012). Many of these studies revealed the use of tools by the chimpanzees to collect the honey (Crickette & David, 2008; Boesch et al., 2009; McLennan, 2011; Sommer et al., 2012). Indeed, apart from humans, only orangutans (van Schaik, 2004) and chimpanzees (Sanz & Morgan, 2009) gain access to beehives using tools. Honey gathering using tools typically involves inserting probes in beehives. These probes can be modified to obtain frayed ends for honey dipping (Sommer et al., 2012). Indeed, such tools with brush-tips allow collecting up to six times more honey than those with unmodified tips (Tutin et al., 1995).

Like other great ape taxa, the western chimpanzee has come under enormous human pressures. For example, about 90% of the Ivorian chimpanzee population was lost mainly due to anthropogenic disturbances (Campbell et al., 2008). In this country, the chimpanzee populations are highly endangered since only those found in the Taï and Comoé national parks are considered as viable (Hoppe-Dominik, 1991; Marchesi et al., 1995). Recently, studies combining the use of camera trap videos and the indirect signs' observations along transects, revealed the importance of honey consumption by the chimpanzees of the Comoé National Park (Lapuenta et al., 2016). However, a lack of information was identified on (i) the diversity of bee species exploited by these chimpanzee populations, (ii) the density of beehives within the chimpanzees' habitats and (iii) the plant species on which these beehives are established.

Bees are recognized to exhibit a diverse array of nesting strategies closely dependent to the part of the habitat type, the nature of the used substrate to nest and the material required for the construction of the beehive (Roubik, 2006).

The most important role of these beehives is to protect colonies against environmental perturbations by maintaining a specific microclimate for brood development (Roubik, 2006; Siqueira et al., 2012; Pavithra et al., 2013). Social bees from the Apidae family, including honeybees, bumblebees, and stingless bees, often use pre-existing cavities of trees, ground and termite mounds for building their beehives (Potts et al., 2005; Roubik, 2006; Eardley et al., 2010).

We started this research with the following questions in mind: (1) which social bees' species produce honey consumed by chimpanzees of the Comoé National Park? In addition, (2) is there a selection of tree species by bees, for nidification within habitats? Finally, (3) does the habitat type has an effect on the availability of tree species with suitable nesting sizes for bees?

The overall goal of this study was to determine the patterns of diversity and distribution of arboreal social bee species' beehives within habitats of a Sudano-guinean savanna zone in order to assess their exploitation by the dwelling chimpanzee species. Specifically, it aimed at (i) assessing the diversity of arboreal social bees nesting in the home-ranges of chimpanzees within the Comoé National Park, (ii) determining the distribution and density of the beehives of these bee species within these habitats, (iii) identifying the preferred plant/tree species and the height of beehive' positioning in the identified bee species.

Materials and methods

Description of study area

This study was conducted in the Comoé National Park (CNP). This park covers around 11,500 km². It is a UNESCO World Heritage site and a Biosphere Reserve, located in the north-eastern part of Côte d'Ivoire in West Africa, between the 8°30' - 9°40' N and the 3°10' - 4°20' W. The CNP is covered by 91% of savanna habitats while gallery forests and forest islands cover around 8.4% of this park (Mühlenberg et al., 1990). These forests are the main chimpanzee habitats within this park.

The climate of the CNP is warm and dry, with a mean temperature of 27°C and an average annual precipitation oscillating around 1090 mm (Hennenberg, 2005). From November 2017 to July 2018, this study was concentrated on a study area of 900 km² that the Comoé Chimpanzee Conservation Project established since 2014 in the South-Western sector of the park. During this study, three forest types, which respective characteristics are described below, were surveyed:

- **Mature forest island (MFI):** this habitat is an old, never exploited semi-deciduous forest island submitted to a natural evolution which is now close to the final stages (aging, mortality) of the silvigenetic cycle. It is an open pool of trees, up to 35 m in height, with a recovery of at least 40% (Kouassi et al., 2014). This habitat is dominated by several species belonging to numerous plant families: Malvaceae (*Ceiba pentandra*, *Cola cordifolia*), Combretaceae (*Anogeissus leiocarpus*), Moraceae (*Antiaris toxicaria*, *Milicia excelsa*), Oleaceae (*Schrebera arborea*), Zygophyllaceae (*Balanites wilsoniana*), Ulmaceae (*Celtis zenkeri*, *C. integrifolia*), Fabaceae (*Dialium guineense*), Ebenaceae (*Diospyros mespiliformis*, *D. abyssinica*), Sapotaceae (*Pouteria alnifolia*, *Manilkara obovata*, *M. multinervis*), Dichapetalaceae (*Tapura fischeri*) (Lauginie, 2007).

The herbaceous layer is dominated by Poaceae family (*Oplismenus hirtellus*, *Cyrtococcum chaetophoron*, *Olyra latifolia* and *Centotheca lappacea*). This layer is sparse and has a height between 0 and 2 m (Kouassi et al., 2014).

- **Secondary forest island (SFI):** which is also a semi-deciduous forest island that has undergone different forms of anthropogenic disturbances at a given period; but regenerated over years (Aubréville, 1949). This habitat is also dominated by most of the same plant species of the mature forest island; but in a lower density. However, other species were exclusively encountered in this habitat (i.e. *Lannea welwitschii*, *Tetrapleura tetraptera*, *Zanthoxylum zanthoxiloides*, *Afraegle paniculata*) and woody liana belonging to two families; namely the Malpighiaceae (*Flabellaria paniculata*) and the Apocynaceae (*Alafia scandens*, *Landolphia hirsuta*, *Secamone afzelii*, *Baissea zygodoides*, *Cryptolepis sanguinolenta*) (Laugnie, 2007). The invasive plant species *Chromolaena odorata* (Asteraceae) is also abundant in this habitat.
- **Gallery forest (GF):** This habitat is located along the Comoé river. It presents a relatively closed pool of trees with a higher closed canopy of more than 30 m high. The recovery is between 40 and 70% for the upper stratum (Kouassi et al., 2014). The dominant tree species is *Cynometra megalophylla* (Caesalpiniaceae). However, other plant species are found in this habitat. They mainly belong to the families Euphorbiaceae (*Drypetes floribunda*, *D. gilgiana*, *Dichapetalum madagascariensis*), Rubiaceae (*Oxyanthus recemosus*), Fabaceae (*Dialium guinnense*), Loganiaceae (*Strychnos* sp.), Linaceae (*Hugonia planchonii*) and Annonaceae (*Xylopia parvifolia*). The herbaceous layer of this habitat dominated by three plant families namely Acanthaceae (*Elytraria marginata*), Poaceae (*Acroceras zizanioides*) and Cyperaceae (*Hypolytrum heteromorphum*). Its characteristics are identical to those of the forest island.

Sampling design

Bee beehives survey

Sixteen plots of one hectare each (100 m x 100 m) were established within each of the surveyed habitats. Visual searches of arboreal social bees' beehives were conducted in each plot, using a pair of binoculars when needed.

Trees with diameter at breast height (DBH) ≥ 15 cm, were considered as potential nesting ones (Darchen, 1972; Tornyie & Kwapong, 2015). For every encountered beehive, the tree DBH and height at which the entrance of bees is located above the ground level, were recorded using a measuring tape. For trees with large buttresses, the DBH measurements were taken just above these buttresses. The height of the bees' nests above the ground level was measured when located less than 6 m and just estimated when superior to this distance.

The density of potential nesting trees (with a DBH ≥ 15 cm) was calculated per habitat and per species surveyed. The density of beehives per species was also determined in these established plots. Some beehives were certainly missed, especially those located high in the canopy.

The field surveys were done during the sunny days in order to make easier the observation of foraging bees' flying in and out of their respective beehives. Bees' traffic and beehives entrances tubes were then searched in bases, on trunks and branches of all dead and live trees. The encountered beehives were all photographed and geo-referenced with a handheld GPS. For each beehive found, samples of worker individuals were collected using an insect aerial net and stored in Eppendorf tubes containing 70 % ethanol for future identification. The species identification of colonies nesting high in inaccessible tree trunks was done in situ using a pair of binoculars.

When a beehive was found in a tree cavity, this tree was identified at the species or morphospecies level. The identification of plant species was confirmed by the National Floristic Centre located of the Félix Houphouët-Boigny University (Abidjan, Côte d'Ivoire).

Identification of social bees which honey is exploited by chimpanzees

A recent study by Lapuente et al. (2016) showed the use of tools for the consumption of honey by the chimpanzee communities of the CNP. Based on these results, the chimpanzee honey dipping tools were used as indicators of beehives exploited by these primates. Comoé chimpanzees have been found to leave honey collection tools inserted in the beehive entrance or at the base of the trees where the beehive has been exploited. Therefore, we determined which beehives had been exploited by chimpanzees by the presence of used tools and traces of the exploitation such as honey dripping from the beehive entrance or remains of the honeycombs with chimpanzee teeth marks. We identified the used chimpanzee tools by the following characteristics: a portion of a branch cut to a determined length, stripped from leaves and lateral branches, often with a brush tip made by chimpanzees using their teeth and clear signs of wear from being used, such as frayed or blunt ends, remains of honey or wax, dirt left by the hand grip.

Identification of bees

Bees were first mounted, labeled and then identified using the determination keys of Eardley (2004) and (Eardley et al., 2010) under a low-power stereo binocular microscope. The reference collection of bee species of Central Côte d'Ivoire collected in the Lamto Scientific Reserve was also used during this work. Voucher specimens of all the identified species are available at the Lamto Research Station in Ecology.

Statistical analysis

The sampling efficiency of bees was tested by constructing sample-based species accumulation curves and recording the mean similarity between plots of the same habitat type. Indeed, accumulation curves were produced to show the evolution of the species richness in relation to the sampling effort. Using the program EstimateS 8.0.0 (Robert K. Colwell, Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT 06869-3043, USA; Website: <http://purl.oclc.org/estimates>), the observed and estimated species accumulation curves, respectively Sobs and Chao2, were constructed after randomizing 500 times the sample in order to ensure the statistical representation of the target assemblage. The diversity of bees' assemblages and its evenness are measured by Simpson's index. The Bray-Curtis index was calculated for the measurement of the β -diversity on one hand and the determination of the similarity of species composition between plots of each habitat type on the other hand. Based on the species composition of the surveyed habitats, a hierarchical Ascending Classification (HAC) was performed in order to test the similarity them. These indexes were run on Paleontological STatistics (PAST) version 3.09 (Hammer et al., 2001) at a significance level of 0.05. Levene's test for homogeneity of variance was used to test the distribution of our data before comparison between habitats. Due to the non-normal distribution of data and the heterogeneity of variances, non-parametric multivariate analysis of variance Kruskal-Wallis and post hoc test (pairwise Mann-Whitney) was used for comparison.

Results

Overall taxonomic structure of the observed bee species

A total of five bee species, belonging to the family Apidae, were found being regularly exploited by Comoé chimpanzees. Four of these species belong to three genera of Meliponini, the stingless bees (*Hypotrigona gribodoi* Magretti 1884, *Meliponula ferruginea* Lepeletier 1836, *Meliponula bocandei* Spinola 1853, *Meliponula togoensis* Stadelman 1895) and one to the Apini, the honeybees (*Apis mellifera* Latreille 1804).

Sampling efficiency during this study

The accumulation curves of the estimated and observed species richness were similar in all the surveyed habitats (Fig 1), suggesting a good estimate of the expected species richness of these habitats. Indeed, 100 % of the expected species of each of the surveyed habitat were sampled (Table 1).

Table 1. Metrics of arboreal social bees' diversity in the visited habitats.

Habitat Types	Species richness	Sampled Coverage	Simpson's Index	Evenness's Index	Abundance
MFI	5	100	0.76	0.91	67
SFI	5	100	0.56	0.62	30
GF	5	100	0.73	0.84	17

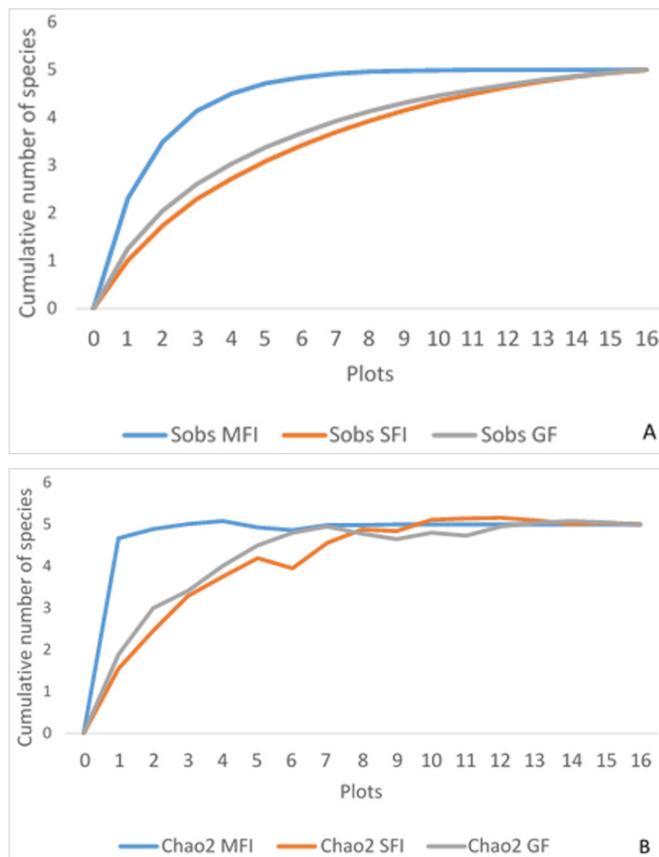


Fig 1. Accumulation curves of the observed (A) and estimated species richness (B) in the visited habitats. Abbreviations: FI = mature forest island; SFI = secondary forest island, GF = Gallery Forest.

Species richness and species diversity of the recorded bees

Five bee species (*H. gribodoi*, *M. ferruginea*, *A. mellifera*, *M. bocandei* and *M. togoensis*) were all collected in each of the surveyed habitats. However, different values of Simpson and Evenness indexes were obtained for these habitats. The highest values of these indexes were found for the mature forest island, followed by the gallery forest and the secondary forest island. Furthermore, the Bray-Curtis index based on the species composition of habitats, showed an important similarity between the mature forest island and the secondary forest island (Fig 2).

Abundance and distribution of the beehives of arboreal social bee species exploited by chimpanzees

A total of 114 beehives were recorded within all the surveyed habitats; 95 belonging to the stingless bees and 19 to the honeybees. The highest mean beehive density was observed in stingless bees (2 beehives/ha); while only 0.4 beehives/ha was registered in the honeybees. In terms of beehives' density and abundance at the habitat level, statistical analyses revealed significant differences (Kruskal-Wallis test: $\chi^2=6.79$; $df=2$; $p=0.03$), with a decrease ranking going from the mature forest island to the gallery forest through the secondary forest island (Table 2).

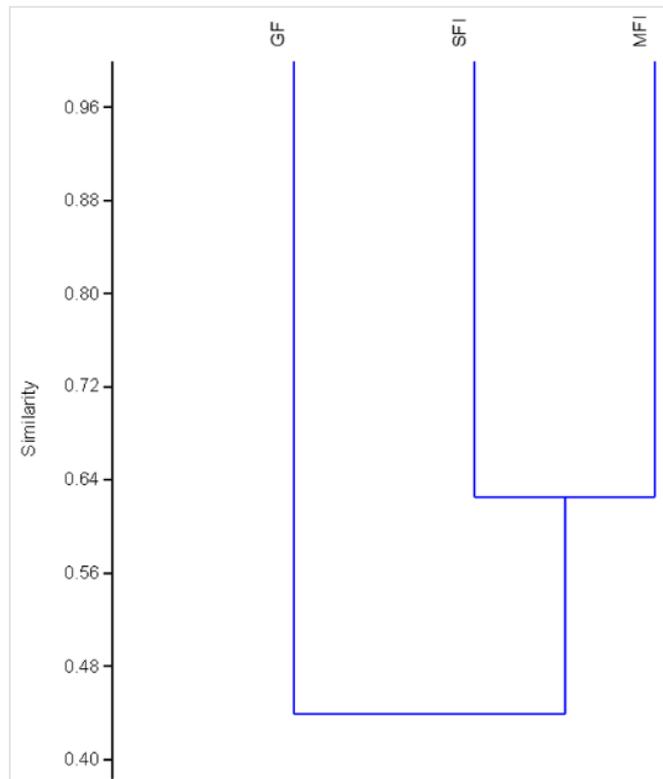


Fig 2. Similarity of species composition of the visited habitats based on Bray-Curtis index. Abbreviations: FI = mature forest island; SFI = secondary forest island, GF = Gallery Forest.

A total of 36 beehives (roughly 32 % of the total recorded ones) were found with chimpanzees' honey exploitation tools. Most of the beehives exploited by chimpanzees were found in stingless bees (i.e. 89.19 %, $n=32$). In contrast, only 11.11 % ($n=4$) of beehives exploited by chimpanzees were in honeybees. At the habitat level, 22 exploited beehives were observed in the mature forest island while 8 were found in the gallery forest and 6 in the secondary forest island. The most exploited bee species by chimpanzees was *M. ferruginea* respectively followed by *M. bocandei*, *M. togoensis*, *H. gribodoi* and *A. Mellifera*. In contrast, the highest number of non-exploited beehives were observed in *H. gribodoi*, respectively followed by *A. mellifera*, *M. togoensis*, *M. ferruginea* and *M. bocandei* (Fig 3).

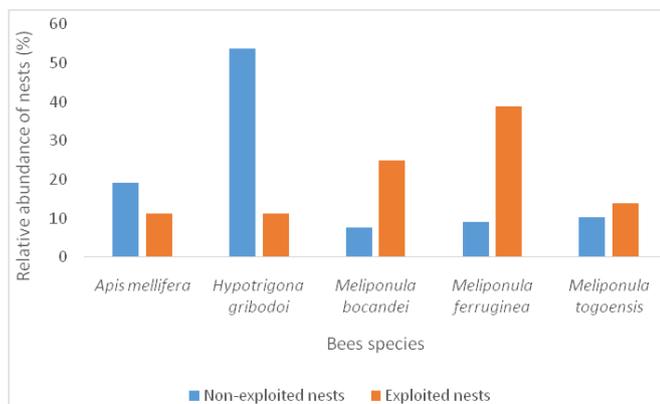


Fig 3. Bee species-specific relative abundance of nests exploited and non-exploited by chimpanzees.

Availability of the resource provided by bees to chimpanzees and the potential nesting trees

We observed six aggregations of beehives for *H. gribodoi* with a maximum of seven beehives observed in the same dead tree. On the other hand, only one case of aggregation was observed for *M. ferruginea*, with two beehives found on *Dialium guinneense*. Concerning secondary forest island, we found the highest abundance of beehives for *H. gribodoi* within the mature forest island and the secondary forest island. On the other hand, in the gallery forest, the beehives of *M. ferruginea* were the most abundant (Table 3). Moreover, in the mature forest island, *M. bocandei* had the highest number of exploited beehives ($n=7$), while *M. ferruginea* had the highest number of exploited beehives in the gallery forest ($n=6$).

Table 2. Densities of bees' beehives and potential nesting trees in the three habitats sampled.

Habitats	Densities		
	Total observed beehives	Beehives/ha	Potential nesting trees/ha
Mature Forest Island	67 ^a	4.2 ^a	98.8 ^a
Secondary Forest Island	30 ^b	1.9 ^b	58 ^b
Gallery Forest	17 ^c	1.1 ^b	94.6 ^a

The highest density of bee-nesting potential trees was found in the mature forest island (98.8 trees/ha) followed by the gallery forest (94.6 trees/ha) and the secondary forest island (58 trees/ha). These habitat-specific densities were found significantly different from a forest type to another (Kruskal-Wallis test: $\chi^2=16.72$; $df=2$; $p<0.05$). Mann-Whitney pairwise test indicated a significant difference between the density of bee-nesting potential trees of the visited habitats (Table 2).

Table 3. Values in brackets represent the number of beehives exploited by chimpanzees for each bees species in the habitats.

Bee species	Habitats			
	MFI	SFI	GF	Total and RA
<i>Apis mellifera</i>	10 (3)	5 (1)	4 (0)	19 (4)
<i>Hypotrigena gribodoi</i>	26 (3)	19 (1)	1 (1)	46 (5)
<i>Meliponula bocandei</i>	10 (7)	2 (1)	3 (1)	15 (9)
<i>Meliponula togoensis</i>	9 (4)	2 (1)	2 (0)	13 (5)
<i>Meliponula ferruginea</i>	12 (5)	2 (2)	7 (6)	21 (13)
Total	67 (22)	30 (6)	17 (8)	114 (36)

Beehives' availability on tree species and their potential exploitation by chimpanzees

Beehives of arboreal bee species were encountered on 17 tree species during this study (dead trees were not taken into account). These species belong to 9 plant families

and 15 genera. Most of the beehives were found on trees of the Leguminosae family (i.e. *Dialium guinneense*, *Albizia adianthifolia*, *A. zygia*, *Tamarindus indica* and *Tetrapleura tetraptera*, *Cynometra megalophylla*).

On the 114 observed beehives, 91 were found on living trees and 23 on dead ones. Of the 91 beehives found on living trees, 33 were exploited. On the other hand, among the 23 beehives found in cavities of the dead woods, only 3 beehives were exploited by chimpanzees. The highest abundance of beehives was found in the cavities of *Dialium guinneense* and *Manilkara multinervis*. These main plant species were respectively followed by *Celtis integrifolia*, *Albizia adianthifolia*, *Cynometra megalophylla*, *Anogeissus leiocarpus* and *Vitex* sp.. The lowest number of bee beehives were found in cavities of *Albizia zygia*, *Tetrapleura tetraptera*, Liana, *Vitellaria paradoxa*, *Antiaris toxicaria*, *Ficus ingens*, *Ficus* sp., *Diospyros mespiliformis* and *Cola gigantea* (Table S1).

The number of tree species on which beehives were encountered was higher in mature forest island (13 species, 12 genera, 7 Families) than the secondary forest island (6 species, 6 genera, 5 families) and the gallery forest (6 species, 6 genera, 4 families). *Dialium guinneense* was identified as the main nesting tree species of the mature forest island. In the secondary forest island, *Manilkara multinervis* is the main plant species preferentially chosen by bee species for the establishment of their beehive (Table S1). *Cynometra megalophylla* is the most important plant species supporting the highest number of beehives within the gallery forest. Moreover, a high significant difference was found between the total number of observed trees and the number of trees on which bee nest exploited by chimpanzees were found in the different habitats (Mann-Whitney test: mature forest island: $\chi^2=35$, $df=1$, $p<0.05$; secondary forest island: $\chi^2=45.5$, $df=1$, $p<0.05$; gallery forest: $\chi^2=48.5$; $df=1$; $p<0.05$) (Table S1).

Beehives of the sampled bee species were respectively found established on a plant species diversity ranging from 4 to 8 species. *Meliponula ferruginea* was identified as the bee species establishing beehives on the highest diversity of plant species (i.e. 8 species), followed by *M. togoensis* and *M. bocandei* with 7 species each one. Beehives of *H. gribodoi* were encountered on 6 plant species while those of *A. mellifera* were generally found established on trees of 4 plant species. However, most of the beehives of *A. mellifera*, *M. togoensis*

and *M. bocandei*, were recorded in the cavities of *Dialium guinneense*'s trees. In contrast beehives of *H. gribodoi*, were registered in high quantities on trees of *Manilkara multinervis*. No beehive of this bee species was observed on *Dialium guinneense* while the highest number of beehives of *M. ferruginea* was found on trees of *Cynometra megalophylla*.

Relationship between the diameter at breast height of trees, the nesting choice of bees and the honey exploitation by chimpanzees

Bee species recorded in this study were found nesting in cavities of trees with a DBH ranging from 15 to 87.3 cm. *Meliponula bocandei* was found nesting in trees with a high DBH (mean DBH: 52.5 cm \pm 3.6, $n=15$) while *H. gribodoi* nested in trees with the lowest DBH (mean DBH: 39.6 cm \pm 3.7, $n=46$). However, no significant difference was found between the mean DBH of nesting trees of all bee species (Kruskal-Wallis test: $\chi^2=6.41$, $df=4$, $p>0.05$). Nevertheless, Mann-Whitney pairwise test showed a significant difference in the DBH of nesting trees between *A. mellifera* and *M. bocandei* ($U=37$, $p<0.05$), between *M. bocandei* and *H. gribodoi* ($U=54$, $p<0.05$) and between *M. togoensis* and *M. bocandei* ($U=90.5$, $p<0.05$) (Table S2). Finally, no significant difference was found in the DBH of nesting trees with beehives identified as exploited or not by chimpanzees (Mann-Whitney test: $\chi^2=894.5$, $df=1$, $p>0.05$) (Table S3).

The highest value of beehive's height was observed in *A. mellifera* (6.3 m \pm 1; $n=19$) followed by *M. bocandei* (5.9 m \pm 0.7; $n=15$), *M. ferruginea* (5.3 m \pm 0.7; $n=21$), *M. togoensis* (4.9 m \pm 0.8; $n=13$) and *H. gribodoi* (3.8 m \pm 0.3; $n=46$) (Table S2). Results also showed that chimpanzees have an exploitation preference of *A. mellifera* low height's beehives. Indeed, it is only in this species that a significant difference was found between the height of exploited beehives and non-exploited beehives (Mann-Whitney test: $\chi^2=2$, $df=1$, $p<0.05$) (Table S4).

Status of nesting trees (dead or living) and nesting place on trees

All the beehives of *A. mellifera* and *M. ferruginea* were found in cavities of living trees trunks, while only those of *H. gribodoi* beehives were observed in all the considered parts of trees. *Meliponula bocandei* and *M. togoensis* were both found in only two parts of trees (i.e. trunks of living trees and dead trees) (Table 4).

Table 4. Relative abundance of bee species' beehives found on living trees and dead trees.

Bee species	Relative abundance of beehives on parts of trees in brackets (%)			
	Trunks of living trees	Dead parts of living trees trunks	Dead branches of living trees	Dead trees
<i>Apis mellifera</i>	19 (100)	0	0	0
<i>Hypotrigona gribodoi</i>	4 (8.89)	9 (20)	14 (30.43)	19 (42.22)
<i>Meliponula bocandei</i>	14 (93.33)	0	0	1 (6.67)
<i>Meliponula ferruginea</i>	21 (100)	0	0	0
<i>Meliponula togoensis</i>	11 (84.62)	0	0	2 (15.38)

Discussion

In this study, we found that chimpanzees of the Comoé National Park exploited all the five species of arboreal social bees which were recorded in three forest types surveyed during the present study. However, there was some evidence the stingless bees (*H. gribodoi*, *M. ferruginea*, *M. bocandei*, *M. togoensis*) are more exploited than the honeybees (*A. mellifera*). This observation could probably be explained by the aggressive defense strategy adopted by the honeybees to secure their beehives and honey. Indeed, African honeybees are notorious for defending their beehive through aggressive stinging – the stings are too painful for many animals that they can't withstand for long time (Hodgson et al., 2010). In contrast, stingless bees are recognized to mainly build passive defenses for their beehives such as thick walls of mud and wax. The main strategy they use to make their beehives inaccessible is to build them up to one meter underground (Tornyie & Kwapong, 2015). However, none of these passive defense systems were found in the stingless bees of the CNP. Indeed, they only build thin wax wall or used thin cracks as entrance to their arboreal beehives on one hand or build their beehives on high height branches (personal observation). In the stingless bees of the CNP, only *H. gribodoi* was seen with an aggressive behavior against the disturbance of their beehives. This species was not found stinging but workers invade the attacking by targeting all his orifices such as ears, eyes, mouth, nostrils (case of a disturbance caused by human) in order to destabilize him (personal observation).

A mean density of 2.4 beehives/ha was found within the surveyed habitats. This density was found higher than those reported before in Brazil (Siqueira et al., 2012) and Ghana (Tornyie & Kwapong, 2015). However, we can assume that the observed range of densities (i.e 1.4 - 2.4 beehives/ha) was underestimated, due to human error in detecting beehives. Indeed, the detection of bee beehives in natural ecosystems, especially in forests is difficult and may affect the assessment of their abundance as suggested by Dorazio and Connor (2014). Moreover, the bee beehives' density within habitat seems to depend on the habitat type, the availability and diversity of potential nesting trees. In fact, high beehives densities were found in forests with a high plant specific richness (e.g. high floral resource for bees) and large DBH trees (i.e. the forest island). In contrast, a relatively low density of beehives was observed in the gallery forest which was found mainly dominated by one plant species (*Cynometra megalophylla*). These results are in line with those of Eltz et al. (2002) and Roubik (2006), who showed that the uneven distribution of bee species across habitats may be explained by various factors including food resources for bee foraging and the availability of suitable nesting places. In the present study, this is well demonstrated by the highest beehive density and the important number of chimpanzees' honey exploitation tools found in the mature forest island in comparison to the other habitats. Finally, one of the important

reasons of this observed density can be the adaptability of bee species to habitat types. Indeed, *Hypotrigona gribodoi* and *M. ferruginea* had the highest number beehives in the surveyed habitats, with *M. ferruginea* as the most exploited bee species by the CNP's chimpanzees. These observations can be explained by the fact that this species build beehive types adapted to various type of habitats including disturbed ones (Hamisi, 2016). In addition, the high number of tools found under the beehives of *M. ferruginea* can also be explained by wide distribution of this species (e.g. high abundance within habitats). Moreover, *H. gribodoi* was identified as the species with the highest monospecific nesting aggregation on the same tree, suggesting (i) the absence of an intra-specific nesting competition in this species (Nkoba et al., 2012), (ii) the poor ability of this species in locating new nesting places by its scout bees (Eltz et al., 2003) or (iii) its short flight ability and dispersion across fragmented habitats (Araújo et al., 2004).

As reported by Cortopassi-Laurino et al. (2009), the present study revealed that the most used trees used by the bees to beehive in CNP belong to the Leguminosae's family. In contrast, Nkoba et al. (2012) identified the family Euphorbiaceae as the mostly nested plant species by stingless bee species in Kakamega forest. At the plant species level, *Dialium guinneense*, *Manilkara multinervis* and *Cynometra megalophylla* were found with the highest number of beehives in their cavities. The highest beehive number was found on *Dialium guinneense* probably due to the structure of this tree. The suitability of this species as nesting substrate may be related to relatively medium size of their trunks which very often have cavities. Similar tendency was reported by Kajobe (2007) where *M. ferruginea* seemed to have some selectivity preferences for *Parinari excelsa*. In fact, as suggested by Hubbell and Johnson (1977), bee species are opportunistic in selecting nesting place and generally use tree species presenting cavities with correct dimensions and purpose. However, our result contrasts with Nkoba et al. (2012), who observed a little selectivity within four Meliponini species in the Kakamega forest in Kenya for a nesting trees preference.

Arboreal bee species, in the present study, were found nesting in cavities of trees with a DBH range from 15 to 87.3 cm, in agreement with the results of several authors (Darchen, 1972; Eltz et al., 2003; Venturieri, 2009; Tornyie & Kwapong, 2015). Bee species were found choosing nesting trees based on the presence of cavities in the trunk and the size of the DBH of the plant species. Furthermore, the size of these cavities and their respective location on trees were found determinant in the establishment of beehives. However, the exploitation of beehives by chimpanzees was not plant species DBH size dependent. Some bee species (*A. mellifera* and *M. bocandei*) were found nesting very high on trees. On the other hand, *H. gribodoi* had the lowest mean height of beehives and also a lowest number of honey exploitation tools found under its beehives. This is probably due to the small size of this species on one hand and the difficulty in locating the small cavities of its beehives.

Most of the encountered bee species (*M. bocandei*, *M. ferruginea*, *M. togoensis* and *A. mellifera*) were found nesting preferentially in trunks of living trees; while the beehives of *H. gribodoi* were mostly found in dead parts of trees. However, beehives located in the cavities trees trunks were found more exploited by chimpanzees than those found on branches, probably due to the important quantities of honey generally found in trunks (Michener, 2000). The choice of living or dead trees to beehive is may be a defense strategy of the colony. Indeed, according to Roubik (1989) and Martins et al. (2004), a strategy of defense against predators and parasites, guarantee of a longevity of colonies, in some Meliponini is the establishment of beehives on living trees.

In conclusion, beehives density within habitats was found depending on the habitat type, the availability and diversity of the nesting trees. Arboreal bee species were found choosing their nesting trees based on the presence of cavities in the trunk and the size of the DBH of the plant species. Frequent exploitation of stingless bee's honey by chimpanzees was observed, except for *H. gribodoi*. *Meliponula ferruginea* was the most exploited species by chimpanzees in the Comoé National Park. These primates don't have a particular choice for beehives when we consider the DBH of trees nesting but they tend to exploit *A. mellifera* nests with low height. Complementary researches are needed to assess the influence of the quantity and quality of honey on one hand and the beehive's structure on the other hand, in their exploitation choice by chimpanzees. Data should also be collected on the involvement of the five bee species in the pollination of trees (e.g. production of fruits consumed by chimpanzees), through the melissopalynology.

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Authors' Contributions

Nicodénin Angèle SORO: Investigation, Data collection, Data curation and Writing the original draft.

Juan LAPUENTE: Investigation, Data collection, Methodology, conceptualization, writing, review and editing.

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Supplementary Material

Table S1: Relative abundance of plant species on which arboreal social bees' beehives were observed.

Family	Tree species	MFI	SFI	GF	Total	Relative abundance (%)
Leguminosae	<i>Dialium guineense</i> Willd., 1796	69/15/10	21/7/3	41/2/1	131/24/14	26.37
	<i>Albizia adianthifolia</i> (Schumach.) W. Wight, 1909	75/7/1	4/0/0	11/0/0	90/7/1	7.69
	<i>Albizia zygia</i> J.F. Macbr., 1919	19/1/0	1/0/0	5/0/0	25/1/0	1.1
	<i>Tamarindus indica</i> L., 1753	7/3/3	1/1/1	0	8/4/4	4.4
	<i>Tetrapleura tetraptera</i> (Schumach. & Thonn.) Taub., 1891	11/0/0	22/0/0	4/1/1	37/1/1	1.1
	<i>Cynometra megalophylla</i> L., 1753	5/1/1	0	973/5/5	978/6/6	6.59
Ulmaceae	<i>Celtis integrifolia</i> Lam., 1983	119/10/0	28/0/0	36/2/1	183/12/1	13.19
	Liana	0	1	0	1	1.1
Sapotaceae	<i>Manilkara multinervis</i> (Baker) Dubard, 1915	19/8/3	20/11/2	4/2/0	43/21/5	23.08
	<i>Vitellaria paradoxa</i> C.F. Gaertn., 1807	1/1/0	0	0	1/1/0	1.1
Combretaceae	<i>Anogeissus leiocarpa</i> (DC.) Guill. & Perr., 1832	105/4/0	40/0/0	9/0/0	154/4/0	4.4
	<i>Antiaris toxicaria</i> Lesch., 1810	10/1/0	3/0/0	3/0/0	16/1/0	1.1
Moraceae	<i>Ficus ingens</i> (Miq.) Miq., 1867	6/0/0	6/1/0	0	12/1/0	1.1
	<i>Ficus</i> sp.	17/1/0	9/0/0	0	26/1/0	1.1
Verbenaceae	<i>Vitex</i> sp.	5/2/1	0	4/2/0	9/4/1	4.4
Ebenaceae	<i>Diospyros mespiliformis</i> Hochst. ex A.DC., 1844	42/1/0	61/0/0	14/0/0	117/1/0	1.1
Sterculiaceae	<i>Cola gigantea</i> A. Chev., 1908	7/0/0	36/1/0	9/0/0	52/1/0	1.1
Total		516/55/19	252/22/6	1113/14/8	1881/91/33	100
	p values	0.0005	0.001	0.002		

Abbreviations: MFI = mature forest island; SFI = secondary forest island, GF = Gallery Forest

Data in cells are reported as follows: total individual species-specific observed trees/ number trees on which bee nests were found/ number of trees on which bee nest exploited by chimpanzees were found.

PS: The lianas were not taken into account in the total of individual species-specific observed trees and in the number of trees on which bee nest exploited by chimpanzees were found. The p values compare the total number of observed trees and the number of trees on which bee nest exploited by chimpanzees were found.

Table S2: Characteristics of beehives and the nesting trees of the encountered bee species.

Bees species	DBH range (cm)	Mean DBH (cm)	Range of beehives' height (m)	Mean height of beehives (m)
<i>Apis mellifera</i>	31.2 - 51.6	39.9 ± 1.9	1 - 15	6.3 ± 1
<i>Meliponula togoensis</i>	28.7 - 67.8	47.1 ± 5.4	2 - 11	4.9 ± 0.8
<i>Meliponula bocandei</i>	32.2 - 87.3	52.5 ± 3.6	1.2 - 15	5.9 ± 0.7
<i>Meliponula ferruginea</i>	15 - 75.5	45.9 ± 4.1	2.3 - 9	5.3 ± 0.7
<i>Hypotrigona gribodoi</i>	19.7 - 60.5	40.1 ± 2	0.6 - 7	3.8 ± 0.3

Table S3: Range and mean of DBH of the exploited and non-exploited beehives in the recorded bee species.

Bees species	DBH range (cm)		Mean DBH (cm)	
	Exploited beehives' trees	Non-exploited beehives' trees	Exploited beehives' trees	Non-exploited beehives' trees
<i>Apis mellifera</i>	39.5 - 51.6	31.2 - 49	45.6 ± 3.5	38.3 ± 2.2
<i>Meliponula togoensis</i>	22.3 - 54.1	28.7 - 67.8	39.4 ± 0.8	51.95 ± 7.7
<i>Meliponula bocandei</i>	32.2 - 87.3	41.4 - 65.3	52.2 ± 5.5	53.1 ± 4.1
<i>Meliponula ferruginea</i>	28.7 - 68.8	15 - 75.5	47.2 ± 4.7	43.3 ± 8.6
<i>Hypotrigona gribodoi</i>	19.7 - 47.8	21.7 - 60.5	33.8 ± 8.1	40.7 ± 2.1

Table S4: Height of exploited beehives or not by chimpanzees.

Bees species	Range of beehives heights (m)		Beehives meanheights (m)	
	Exploited beehives	Non-exploited beehives	Exploited beehives	Non-exploited beehives
<i>Apis mellifera</i>	1 - 5	2.5 - 15	2.1 ± 1	7.7 ± 0.9
<i>Meliponula togoensis</i>	2.5 - 11	2 - 7	5 ± 1.7	4.8 ± 6.1
<i>Meliponula bocandei</i>	3.5 - 7	1.2 - 15	6.8 ± 0.9	4.4 ± 1
<i>Meliponula ferruginea</i>	2.7 - 14	2.3 - 9	5.9 ± 0.9	4 ± 0.9
<i>Hypotrigona gribodoi</i>	2.5 - 5	0.6 - 7	4.8 ± 1.3	3.8 ± 0.3

