

# TILL THE LAST DROP: HONEY GATHERING IN NIGERIAN CHIMPANZEES

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**Abstract.** Various populations of chimpanzees attack beehives to obtain honey, often with the help of wooden tools. However, little is known about how honey abundance in tropical habitats fluctuates with season and how chimpanzees respond to this. For a woodland-savannah habitat inhabited by the Nigeria-Cameroon chimpanzee subspecies, we analyzed monthly proportions of flowering trees and vines as a proxy for honey production. We found a strict negative correlation between flowering and rainfall, probably because pollination benefits from dry conditions. Honey-gathering behavior of the Gashaka-Kwano chimpanzee community was reconstructed from tools abandoned at extraction sites. The apes use sturdy digging sticks and more slender probes, sometimes successively as a tool set, to access honey from subterranean and tree-dwelling colonies of stingless bees and honeybees. Chimpanzees exploited beehives throughout the year. However, during the dry season, when colonies had presumably hoarded more honey, hives were targeted with a greater number of tools. This was not because chimpanzee foraging party sizes had increased. Instead, individual apes used *more* probes during a given honey-gathering event – suggesting that dipping remained worthwhile for longer. In this situation, as tool tips become soft and unsuitable after prolonged dipping, the chimpanzees need to source new implements that possess hard tool points. The apes did not obtain them by breaking previously used tools into fragments, as these would be too short for successful insertions. We assume this because the average length of tools did not decrease with the increased number of apes that worked a hive. This indicates that each tool is sourced individually from raw material in the surroundings of the extraction site. Chimpanzees thus adjust the use and manufacture of tools to honey abundance, reflecting that the sugary fluid is a sought-after resource.

**Key words:** Chimpanzee, flowering, honey, honeybee, honey-gathering, insectivory, stingless bee, seasonality, tool use.

## INTRODUCTION

Humans appreciate honey for its pleasant taste. The sticky, yellowish-brown fluid sweetens and flavors foods and beverages, provides considerable energy upon ingestion, has antiseptic and antibacterial properties and also plays a role in religion (Bodenheimer 1951, Crane 1999, Wilson 2004). People harvest the vast majority of honey from the hives (Wilson 2004) of honeybees *Apini* (Winston 1987, Ruttner 1988) and stingless bees *Meliponini* (Roubik 1989, Michener 2007).

Nests of wild *Apini* may hold several kg of honey, those of *Meliponini* rarely more than 1 kg (Roubik 1989). The specific composition of honey depends on which flowers bees visit. However, in its final stage, honey is basically a mixture of carbohydrates

(near 80% sugars, including 27–44% fructose, 22–41% glucose, 4–14% maltose) and water (16–23%), plus traces of vitamins or minerals, providing about 300 kcal per 100 g (Roubik 1989).

Human practices of beekeeping encourage overproduction (Crane 1999), allowing the excess of honey to be taken from the colony. Alternatively, people may act as predators (*ibid.*), for which they need to access the hives. Wild *Apis* almost invariably construct nests in tree holes and defend them through stinging. *Meliponini* build nests in tree holes or underground in soil and fortify them with thick, hard walls made of wax, resin and other organic materials (*batumen*), leaving only a single small access hole. From this, a *cerume* tube likewise made of wax and resin often sticks out a few centimetres (Roubik 1989, Michener 2007). Stingless bees deter predators through swarming. Such counterattacks are probably not effective because of associated buzzing and bites

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but because defenders fly inside the attackers' orifices, such as eyes, ears, nose or mouth, causing considerable discomfort (APG, VS, UB, pers. obs.). To breach the bees' defenses, humans wield tools such as axes (Roubik 1989, Kajobe & Roubik 2006). Since honey is one of the few concentrated sweet substances naturally available, a whole range of non-human predators also targets it, including birds and mammals such as bears or honey badgers that rip nests apart with their claws (Wong 1984).

Apart from humans, only orangutans (van Schaik 2004) and chimpanzees (review in Sanz & Morgan 2009) access beehives aided by tools. In fact populations of all chimpanzee subspecies prey upon brood and stored honey of *Apini* and *Meliponini*. Honey gathering typically involves inserting probes ("dipping"), which tend to have frayed ends. Implements with such brush-ends can capture up to six times more honey than those with compacted ends (Tutin *et al.* 1995). Interesting geographical differences can be noted. Thus West African chimpanzees rarely use tools, but access hives sometimes by hand, perhaps because in these forests entrances are large enough (Boesch & Boesch 1990). Central African chimpanzees have developed sophisticated technical solutions, including successions of specific tools, probably because these regions are especially rich in bee species (Boesch *et al.* 2009, Sanz & Morgan 2009). Pounding or hammering hives with a large club, trying to break them, seems to be exclusive to chimpanzees of the Congo Basin (Sanz & Morgan 2009).

Chimpanzees also often use tools to harvest imago or brood of other types of social insects such as ants and termites (e.g., McGrew 1992, 2004; Schöning *et al.* 2008). Insect biology and ecology dictate to a large degree if, how, and when they can be preyed upon. Some quantitative measures of seasonality in chimpanzee insectivory are available for termites and ants, given that indigestible chitinous parts of ingested imagos can be detected in fecal samples (e.g., Schöning *et al.* 2007). At Assirik / Senegal, *Apis* wings and heads are also regularly found in fecal samples (23% over 4 years; McGrew 1983). However, elsewhere, dead bees are only occasionally detected in dung (e.g., Bulindi / Uganda; McLennan 2011). In any case, the temporal pattern of honey consumption cannot be visually discerned from dung samples. For this, we need information about the behavior of both insects and apes. Such records need to cover several seasonal cycles to account for stochastic fluctuations of parameters such as climate, habitat phenology, in-

sect colony size, chimpanzee foraging party compositions, and the apes' insectivorous behavior.

We assembled this complex portfolio of data for a tropical habitat in Nigeria via long-term records spanning eight years. Flower availability, i.e. the abundance of pollen and nectar, determines colony age structure, worker survivorship, reproductive cycles, and brood rearing in both honey- and stingless bees (Roubik 1989, Hart & Ratnieks 2002). Thus, as a proxy for honey production, we measured the flowering cycles of the major vegetation cover, i.e. trees and vines, assuming that more flowers translate into greater stores. We then tested if sympatric chimpanzees adjust their corresponding insectivorous behavior by investigating the rates at which honey-gathering tools are abandoned at extraction sites.

With this, we aim to better understand how chimpanzees cope with the constraints of a tropical environment, an ability that is so markedly expressed in humans as the closest living relatives of these apes (Lonsdorf *et al.* 2010).

## METHODS

*Study area: Northeastern Nigeria.* Our research took place in Nigeria's Gashaka Gumti National Park (GGNP; 6670 km<sup>2</sup>; 6°55'–8°13'N, 11°13'–12°11'E; Sommer & Ross 2011a). GGNP demarcates the northern edge of the Cameroon Highlands and Africa's Gulf of Guinea forests, considered a hotspot of biodiversity (Oates *et al.* 2004). The hilly southern Gashaka sector of GGNP includes lowland (<825 m), sub-montane and montane (>1650 m) strata, rising to 2419 m. Accordingly, the vegetation cover is a mosaic of savannah-woodland, riverine and lowland rain forest as well as grassland and montane forests. The Gashaka Primate Project maintains a field station at Kwano (583 m asl; 7°19'N, 11°35'E). Pronounced annual wet and dry seasons are associated with heavy downpours from mid-April to mid-November, followed by a 5-month period with very little or no rainfall. Yearly average precipitation at Kwano is 1973 mm (range 1683–2337 mm), the mean minimum temperature is 20.9°C, the mean maximum 31.9°C (Sommer & Ross 2011b).

*Study animals: Chimpanzees and bees.* The wider Gashaka region harbors the largest surviving population of the rare Nigeria-Cameroon chimpanzee subspecies (*Pan troglodytes vellerosus* aka *elliotti*; Oates *et al.* 2008). Chimpanzee studies concentrate on the Gashaka-Kwano community, with an estimated 35

members that range over about 26 km<sup>2</sup> (Sommer *et al.* 2004). Patchy food distribution causes chimpanzee communities to forage in small subgroups. Throughout the day, different members may join these parties (“fusion”) or split from them (“fission”). For Gashaka-Kwano, the mean monthly day party size was 4.1 (1–17), as calculated from 376 sightings of chimpanzees by field assistants and researchers (2001 = 70, 2005 = 76, 2006 = 68, 2007 = 69, 2008 = 93).

Chimpanzees across Africa (review in Caldecott & Miles 2005) feed mainly on ripe fruit (56–71%), leaves, and other plant parts, in particular terrestrial herbs. At some sites, faunivory is practised (0.1–4%), comprising at least 25 vertebrate prey species. Moreover, chimpanzees will often consume imagos, and brood as well as honey by exploiting colonies of eusocial insects such as termites, bees and ants. Apes at Gashaka-Kwano employ a variety of wooden tools to access colonies of social insects (Fowler & Sommer 2007, Fowler *et al.* 2011). Some taxa consumed elsewhere (McGrew 2004) are either not eaten (termites) or do not occur at Gashaka (carpenter bees *Xylocopa*). Instead, the chimpanzees regularly exploit arboreal ants (e.g., *Camponotus*), army ants (*Dorylus*) as well as hives of honeybees (*Apis*) and larger types of stingless bee (*Meliponula*, *Plebeina*).

*Data collection: Chimpanzee honey gathering.* The Gashaka-Kwano chimpanzee community is not fully habituated to human observers. Direct observations of tool use are therefore rare, but we can rely on a wealth of data on abandoned tools recovered from *ateliers*, i.e. sites where chimpanzees exploited bees. Regular surveys through the study area led to opportunistic finds of *ateliers* (2001–2008) (Fowler *et al.* 2011). In addition, between February 2006 and April 2007, field assistants and researchers numbered and marked 104 colonies of honeybees and 83 colonies of stingless bees, which were revisited at least once a month for a period of up 33 months. Details of chimpanzee attacks on hives were recorded, and discarded tools were measured by UB (February 2007–October 2008) and APG (January–June 2007, November 2007–May 2008).

The likelihood of finding abandoned tools is a corollary of search time spent in the habitat. Therefore tool finds were converted into monthly frequencies by taking into account the diurnal and annual distribution of survey time spent in the Kwano study area by field assistants and researchers (2000–2001, 2005–2008; total = 17487 hours).

*Data collection: Habitat phenology.* Main botanical features of the Gashaka-Kwano habitat were recorded from an 8-km line transect that incorporated different elevations as well as varying types of habitat, thus allowing a relatively unbiased quantification of the vegetation cover. The 4-m wide strip includes 985 trees of at least 30 cm circumference at breast height and 815 woody climbers (lianas, creepers) associated with these trees. Field assistants visited each tree twice per month at intervals of roughly two weeks and recorded absence-presence scores for parameters such as flowering, leaf-bearing, fruiting, traces left by fruit-eaters, and transect plant survivorship. Data were collected over 69 months (April 2002–June 2009) and jointly analyzed by the authors.

*Statistics.* After establishing via a Kolmogorov-Smirnov test that data are normally distributed, we tested for differences between means of two samples through a parametric one-tailed Student’s *t*-test with equal variances assumed. Linear regression with ANOVA was used to determine whether X-Y associations are statistically significant.

## RESULTS

*Rainfall and plant flowering.* Flowering of trees and vines in the mosaic forest-savannah habitat of Gashaka-Kwano follows a distinct seasonal pattern and is strongly negatively associated with rainfall (linear regression,  $R^2 = 0.781$ ; ANOVA:  $df = 1$ ,  $F = 35.567$ ,  $p < 0.000$ ; Fig. 2). Conversely, the dry months from November to March see only 3.7% of all precipitation, but more than two-thirds (68.4%) of all flowering events. Monthly proportions of flowering plants during the 5 dry months (mean 9.7%, range 6.5–13.3,  $sd$  2.8,  $N = 5$ ) are always higher than during the 7 wet months (mean 3.2%, range 0.9–6.2,  $sd$  1.8,  $N = 7$ ), which translates into a significant difference between the seasons (*t*-test:  $df = 10$ ,  $t = 4.937$ ,  $p = 0.000$ ).

*Plant flowering as a proxy for honey production.* Local park rangers and field assistants (George Karngong, Halidu Ilyasu; pers. comm. to VS) assert that beehives contain more honey during the dry season. Similarly, honey and honey beer becomes available in local villages during March and April when beehives are full of honey after the nectar- and pollen-collecting season (pers. obs.).

*Categories of honey-gathering tools.* Of 269 fecal samples of Gashaka-Kwano chimpanzees (2007–

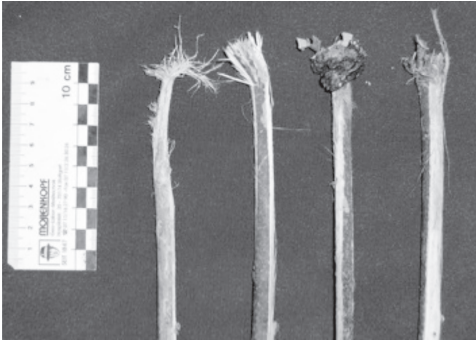


FIG. 1. Compacted frayed ends of probing sticks with which chimpanzees extracted honey from nests of stingless bees; note wax residue on third tool from left (9 January 2011). (Photo: APG).

2008), only a single one contained bee remains (an *Apis* head). Nevertheless, the apes regularly use tools to obtain honey, from both tree nests of *Apis* and tree and ground nests of *Meliponini* bees, as indicated by

abandoned stick tools, many with traces or odor of honey. Tools often had their bark partly or wholly stripped and exhibited frayed ends indicating manipulation, biting or chewing. Sometimes, comb fragments or “wads” of chewed comb enmeshed with bees were detected near honeybee hives; in rare cases, these might have been obtained with bare hands.

Over eight years of study, 707 wooden tools were recovered at or near beehives and classified as follows (cf. Fowler et al. 2011): (1) *stingless bee digging stick* (SD): relatively thick tools, employed to penetrate the defensive structures of batumen or soil that protect tree-dwelling or subterranean colonies; N = 179, mean length (ML) 38.2 cm, mean diameter (MD) 8.2 mm; (2) *stingless bee probing stick* (SP): relatively slender tools used to dip honey from perforated nests; N = 500, ML 33.1 cm, MD 6.6 mm (Fig. 1); (3) *honeybee probing stick* (HP): relatively slender tools to dip honey from *Apis* hives, invariably situated in tree cavities; N = 28, ML 44.1 cm, MD 6.0 mm.

SD and SP are often used in conjunction. The thicker SD is preferentially used to perforate hives,

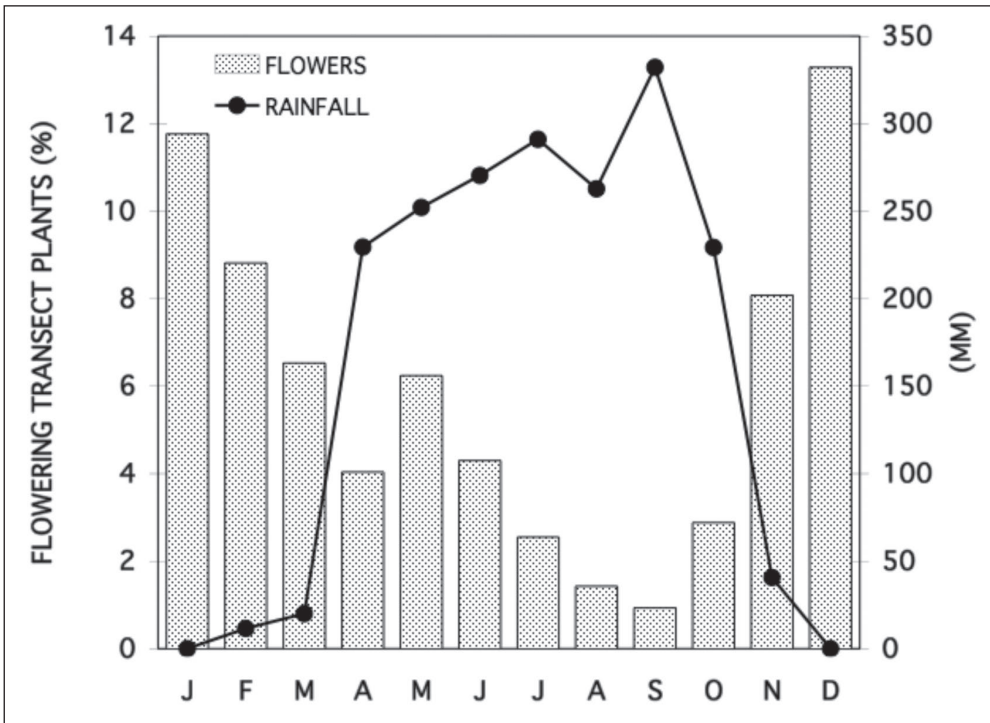


FIG. 2. Annual pattern of rainfall and flowering transect plants (trees, vines) in the mosaic forest-savannah habitat of Gashaka-Kwano.

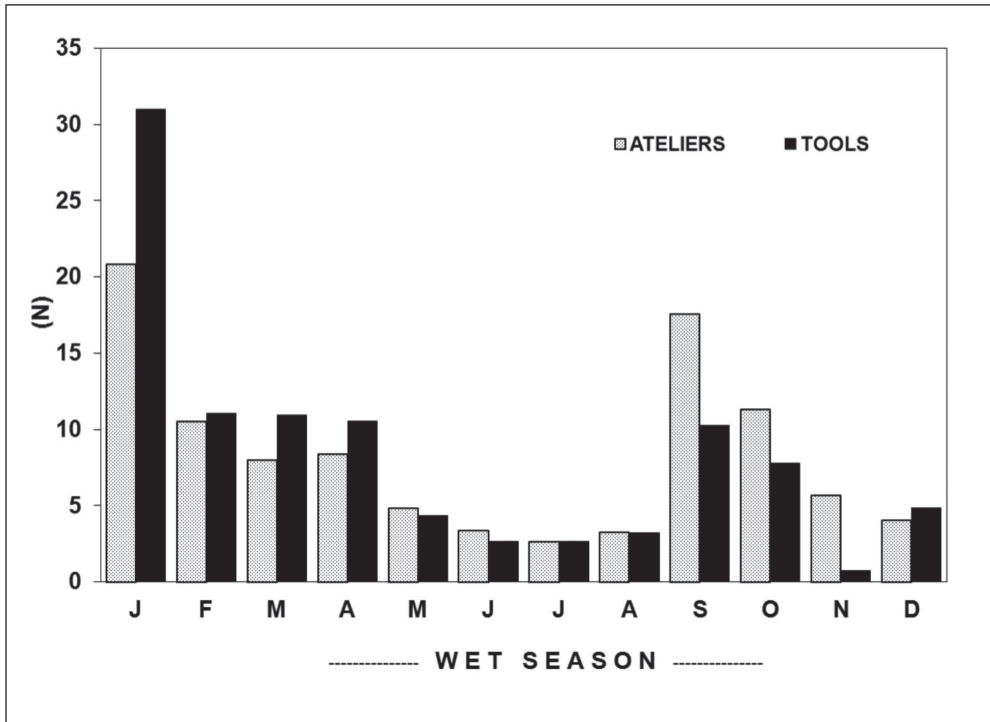


FIG. 3. Annual distribution of chimpanzee tool ateliers and individual tools recovered from exploited beehives. Monthly values are proportions of annual total. Number of ateliers vs. tools for honeybees was 12 vs. 28, for stingless bees 158 vs. 659. Monthly values are proportions of annual total corrected for search time invested by researchers.

mainly those constructed underground, whereas honey is extracted with a more slender SP. Correspondingly, implements recovered at subterranean nests are 44.2% SD and 55.8% SP, compared with tree nests with 18.8% SD and 81.2% SP.

Residues are found on more than three-quarters (77.8%) of distal tool ends, i.e. the tapering section of the stick that most often serves as a tool point, compared with less than a third (31.1%) of proximal tool ends. On 5.3% of tools, more than one type of residual is found. The most common traces on HP are residues from bark and wood, in particular “frass”, the sawdust-like powder created by wood-boring insects (40.0%), honey (33.3%), and beeswax (13.3%). Similarly, the most common traces on SP is frass, at times mixed with soil (43.6%) and honey (24.6%), followed by cerume (23.6%) and beeswax (1.4%). However, on SD, soil (sometimes with elements of frass) is by far the most common trace (90.0%), whereas cerume (7.3%) and honey (4.1%) are rare.

*Seasonal use of honey-gathering tools.* Tools are found during every month of the year (HP 9/12 months, SP 12/12 months, SD 10/12 months; Fig. 3). At first glance, there is little seasonal fluctuation, given that ateliers are recovered with similar monthly frequency during the dry season (mean 16.6, range 6.8–35.4, sd 11.3,  $N = 5$ ) than during the wet (mean 12.4, range 4.4–29.8, sd 9.4,  $N = 7$ ; t-test:  $df = 10$ ,  $t = 0.762$ ,  $p = 0.232$ ). However, twice as many tools are recovered during the dry months (mean 80.5, range 5.1–212.9, sd 79.8,  $N = 5$ ) than during the wet (mean 40.6, range 18.2–72.2, sd 24.2,  $N = 7$ ), although the difference fails to reach statistical significance (t-test:  $df = 10$ ,  $t = 1.268$ ,  $p = 0.117$ ). Moreover, counts of tools used on stingless bee colonies include both SD and SP. Interestingly, for each SD, 3.5 SP are found during wet season months, compared with 4.3 SP during the dry months.

Probes are the honey-gathering tools *sensu strictu*. Average monthly numbers of probes per atelier (Fig.

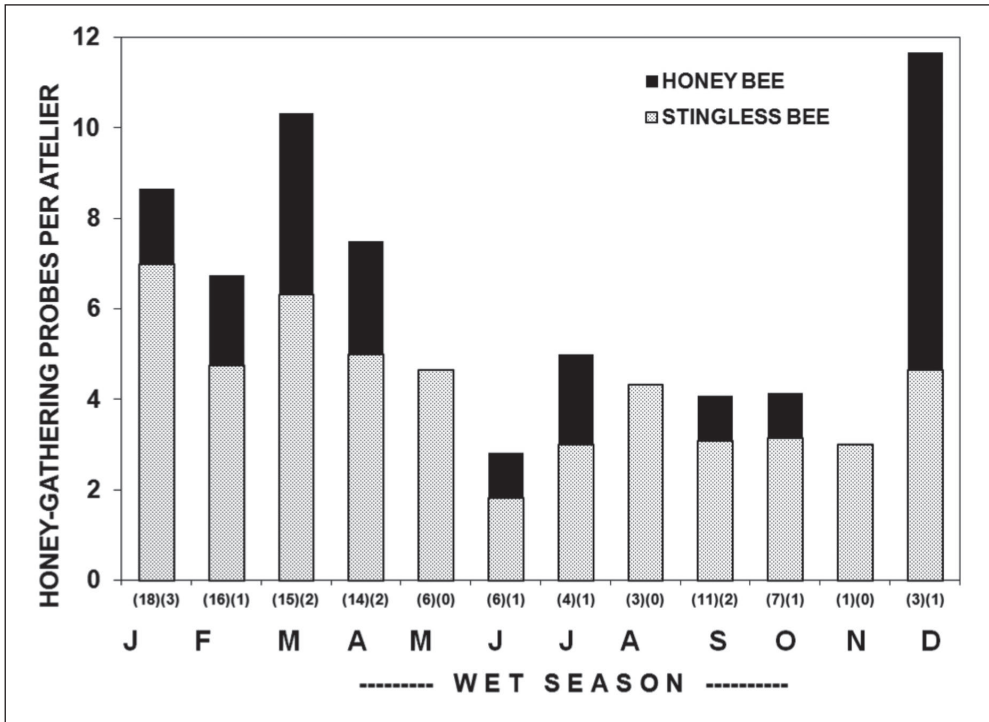


FIG. 4. Annual distribution of the mean number of bee probing sticks per atelier. Number of ateliers are given in brackets; left = stingless bees, right = honeybees.

4) confirm the impression that relatively more are used on a given extraction site during the dry (HP 2.9, SP 5.2) than during the wet months (HP 1.5, SP 3.6). Thus, overall, a single hive is worked on with almost twice as many honey-gathering tools (ratio 1:1.7) during the dry season (mean 8.1, range 3.0–11.7, sd 3.4,  $N = 5$ ) than during the wet season (mean 4.7, range 2.8–7.5, sd 1.4,  $N = 7$ ), which translates into a statistically significant difference ( $t$ -test:  $df = 10$ ,  $t = 2.386$ ,  $p = 0.019$ ).

At the same time, there exists a strongly positive and significant relationship between the monthly numbers of probes per extraction site and the proportions of flowering transect plants (linear regression,  $R^2 = 0.437$ ; ANOVA:  $df = 1$ ,  $F = 7.755$ ,  $p = 0.019$ ; Fig. 5a).

*Increased chimpanzee party sizes or frequency of tool use?*

A higher number of probes could be the result of increased chimpanzee foraging party size, with each ape, on average, using the same number of tools. Alternatively, individual chimpanzees could go

through a greater number of tools. We tested for this possibility by dividing the average monthly numbers of honey-gathering probes by the average monthly sizes of chimpanzee foraging parties (mean 4.0, median 3.9, range 3.4–5.7, sd 0.7). We plotted the resulting numbers of honey-gathering probes per individual chimpanzee (mean 1.6, median 1.3, range 0.5–3.5, sd 0.8) against the monthly proportions of flowering plants (Fig. 5b). Again, a strong positive and statistically significant relationship is found (linear regression,  $R^2 = 0.415$ ; ANOVA:  $df = 1$ ,  $F = 7.085$ ,  $p = 0.024$ ). This indicates that the greater number of tools is not linked to increased party sizes but to a greater frequency of tools used per honey-gathering chimpanzee.

*Mode of tool manufacture: Fragmentation or sourcing de novo?*

Our data indicate that chimpanzees use more tools on hives that are richer in honey. For this, chimpanzees could break existing tools into smaller fragments, in which case probes should become smaller with increasing size of ateliers. However, such

a relationship is not found (linear regression,  $R^2 = 0.000$ ; ANOVA:  $df = 1$ ,  $F = 0.002$ ,  $p = 0.962$ ; Fig. 6), suggesting that chimpanzees obtain additional tools individually from the surroundings.

## DISCUSSION

For a mosaic habitat of forest and savannah-woodland in Nigeria, we investigated the interplay between vegetation flowering, honey storing by bees, and honey-gathering behavior by chimpanzees.

Flowering of trees and vines at Gashaka-Kwano (cf. Fig. 2), as in many forests elsewhere, peaked during the dry season (reviews in Bawa & Hadley 1990, Turner 2001). On a proximate level, the plants' reduced water status is likely to trigger floral bud break. Functionally, dry season flowering facilitates pollination as humidity causes pollen to stick together and prevents insect pollinators from flying. Heavy precipitation can also damage floral structures (Turner 2001). On the other hand, fruits benefit from ripening during the wet season given increased chances of germination (cf. Wheelwright 1985).

A greater abundance of nectar-bearing flowers likely triggers increased hoarding by the bees – which is also reflected by increased availability of honey and honey-beer in local villages. Chimpanzees likewise seem to adjust their “insectivorous” behavior to annual fluctuations of honey stores, given that they employ more honey-gathering tools during honey-rich periods (Fig. 5a). We found that this is not caused by an increase in foraging party size, but by a greater number of tools employed per individual chimpanzee (Fig. 5b). For Goulougo / Congo, a similar link, albeit not quantified, has been made between “slightly higher frequencies” of honey-gathering by chimpanzees that coincide “with environmental cues such as minimum temperature in the dry season which trigger flowering events that influence honey production by bees” (Sanz & Morgan 2009: 420).

If chimpanzees succeed through repeated poking to break the inside chambers of honeybee hives apart, they may, in addition to honey, also obtain fat and protein from larvae, pupae, pollen, and imagos (McGrew 1992). However, at least at Gashaka-Kwano, such destruction is rarely seen, as hives are embedded in protective tree holes and defended through painful stings. On the other hand, the apes often succeed in breaching the defensive structures (batumen plates, soil) of stingless bee colonies.

Honey is therefore the main resource obtained through exploitation of beehives. A teaspoon represents about 20 g, equivalent to about 60 kcal. Thus if chimpanzees gather the equivalent of a couple of spoons, they ingest several hundred kcal. Whether this translates into an average net gain of energy is unknown, although doubtful. Certainly, compared to staple food such as fruit or leaves and “mainstays of animal matter in the diet” such as ants or termites, honey at best qualifies as a “treat”, i.e. “a food-stuff of high quality and much sought after even if its contribution to overall intake is minimal” (McGrew 1992: 155). Direct observation of chimpanzees in Goulougo / Congo confirm this assessment. Here, attempts to open beehives were successful in only about half of all episodes (52%) and six tool actions were required on average for each taste of honey (Sanz & Morgan 2009).

The main challenge in honey gathering is to access the bees' “relatively impregnable homes” (McGrew 1992: 154). Given that chimpanzees lack the body armor of predators such as pangolins or armadillos, they need to employ considerable cognitive abilities associated with tool production, such as causal reasoning and/or imagination (see contributions in Lonsdorf *et al.* 2010). At Gashaka-Kwano and elsewhere, this can include a “hierarchical structuring of tool use” (Sanz & Morgan 2009: 421) embodied by a “tool set” (Brewer & McGrew 1990), i.e. the use of a sturdy perforating tool followed by use of a slender dipping tool (see also McLennan 2011, for Bulindi / Uganda).

Chimpanzees adjust their behavior further if they encounter a particularly rich store of honey. The tips of probes (Fig. 1) will then be repeatedly used for dipping and constantly sucked at, licked and chewed upon. These implements will soon become soft and unsuitable for further explorative poking and perforating. Chimpanzees, in this situation, could clip or fragment the blunt tools to manufacture a fresh and functioning tool point. However, in this way, tools would become too short for further successful insertions. Therefore, as our research suggests, new tools are sourced individually from raw material in the surroundings of the extraction site (cf. Fig. 6). Seasonal adjustments in tool manufacture thus allow the chimpanzees to “scratch the bottom of the barrel”, harvesting its precious content till the last drop.

A better understanding of the relative importance of honey-gathering in the dietary regime of chimpanzees will require cross-habitat analyses of environ-

mental constraints as well as behaviors of both prey and predator. Our research provides this information for Nigerian chimpanzees as well as a study design that could be replicated elsewhere.

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