Army ant defensive behaviour and chimpanzee predation success: field experiments in Nigeria

O. Allon1, A. Pascual-Garrido2,3 & V. Sommer1,3

1 Department of Anthropology, University College London, London, UK
2 Grupo UCM para el Estudio del Comportamiento Animal y Humano, Departamento de Psicobiología, Facultad de Psicología, Universidad Complutense de Madrid, Madrid, España
3 Gashaka Primate Project, Serti, Taraba State, Nigeria

Abstract

Across Africa, chimpanzees prey on army ants, typically using stick tools. Population differences in predation patterns reflect environmental as well as sociocultural factors. However, as for ecological constraints, we lack information about how the ants’ defensive response unfolds over the course of a predatory attempt and how this influences chimpanzee reward. We studied these aspects of insectivory in the habitat of Nigerian chimpanzees through field experiments with previously used tools. The speed with which ants run up a tool decreased continuously during experimental dips into nests. This suggests that soldiers with long legs run up the tools first, before fanning out to deter the intruder. Workers attacking later on were increasingly smaller, thus running less fast. Yet, because more and more insects join the defence, harvesting yield (g dry weight) steadily increased for the first 17 min, to then drop markedly. We hypothesize that the length of dipping sessions by wild chimpanzees is limited by either diminishing return or discomfort caused by being continually bitten. Actual harvesting success cannot be reconstructed from ant remains in chimpanzee faeces without knowing what proportion of consumed insects is detectable in excreta. Through human self-experiments, we found that only 10% of ingested ants are found in an excretion. Based on counts of ant heads in chimpanzee faeces, this translates into 12.9 g dry weight ingested per dipping session, which is far more than elsewhere. Although prey availability and harvesting technique varies across sites, our data still suggest a much greater yield for Nigeria. One reason for this may be a particular aggressiveness of Dorylus rubellus. While this is the only army ant species preyed upon in Nigeria, it is not regularly eaten elsewhere. Standardized experiments and faecal analyses across study sites will be necessary to better understand how ecological constraints influence chimpanzee myrmecophagy.

Introduction

Army ants live in colonies with millions of workers (Leroux, 1982; Kronauer, 2008) and are therefore a profitable prey item for many animals. Chimpanzees at various sites across Africa also feed on army ants. Population differences in predation techniques seem to reflect both social traditions and ecological factors (review in Schöning et al., 2008) and are thus a focus of the emerging paradigm of ‘cultural primatology’ (McGrew, 2004).

Depending on species, ants can differentiate between threats (non-nestmate conspecifics, competing species, social parasites) and tailor attack strategies accordingly (Scharf, Pamminger & Foitzik, 2011). For example, they may drag food competitors out of their nest, while killing scouts of slave-making ants that could inflict dramatic losses to the colony (Scharf et al., 2011). Army ants respond to predatory chimpanzees in a particular way by streaming to the surface to defend their colony through painful bites (Schöning, Kinuthia & Franks, 2005). In response, chimpanzees typically harvest army ants with stick tools, thereby minimizing the bites they receive. Ant dipping involves inserting a wand into an ant trail or nest entrance. Once a number of insects have run up the tool, chimpanzees transfer them into the mouth (see descriptions in Goodall, 1986). In some populations such as Taï/Ivory Coast and Bossou/Guinea, chimpanzees open ant nests to feed on workers and brood directly with their hands (Boesch & Boesch, 1990; Humle & Matsuzawa, 2002). Variations in tool length are largely explained by characteristics of the ant species targeted (Humle & Matsuzawa, 2002; Schöning et al., 2005). So-called intermediate species foraging within leaf litter tend to retreat upon disturbance and are often
Army ant defence during simulated chimpanzee predation

O. Allon, A. Pascual-Garrido and V. Sommer

harnessed by relatively short tools. Epigaeic foragers who hunt on the forest floor and up in vegetation possess longer legs and faster speed. They respond aggressively upon disturbance, quickly attacking a foreign object. Tools used to harvest these species therefore tend to be much longer.

The function of myrmecophagy in chimpanzees is still poorly understood. Thus, it is unclear why certain chimpanzee populations do not consume army ants, despite them being readily available. Certainly, absence of ant eating is not simply explained by the presence of meat or other animal matter (e.g. bees, termites, other ants) in the diet (Schöning et al., 2008). Moreover, nutritional analyses indicate that army ants contribute only minimally to chimpanzee diet (Deblauwe & Janssens, 2008). Straightforward nutritional explanations are therefore difficult to maintain.

Functions could be better assessed if we knew more about the constraints imposed by the prey itself. For example, we lack published data about how the ants’ defence unfolds during a predatory attempt by chimpanzees, and how this influences harvesting success. The actual intake of ants has also rarely been quantified. Harvesting success could theoretically be reconstructed from inspection of faecal samples, but there are no data on the correlation of ingested ants and remains in faeces. Alternatively, indirect experimental data can mimic chimpanzee predation techniques (Hummle & Matsuzawa, 2002; Möbius et al., 2008).

Within this framework, we conducted experiments and faecal sample analyses that focus on the least known chimpanzee taxon, the Nigeria-Cameroonian subspecies (Sommer & Ross, 2011). We aim to address the following questions: Does speed and/or mean weight of workers attacking a tool change over a dipping session? How does dip-length influence yield? How does intake in ant dry mass develop over a dipping session? What is the optimal duration of targeting a nest given the dynamics of diminishing return? What might cause chimpanzees to terminate a dipping session? What proportion of consumed ants is detectable in subsequent excreta?

We hope our research will clarify mechanisms of army ant consumption and the relative importance of this prey in the feeding ecology of chimpanzees across study sites (McGrew, 1992). This may ultimately allow us to better understand the potential functions of ant eating, which are likely to involve arbitrary social conventions that characterize site-specific cultures of particular chimpanzee communities (McGrew, 2004).

Material and methods

Study area and study animals

Research took place in Nigeria’s Gashaka Gumti National Park (6670 km²; 06°55′ – 08°13′ N, 11°13′ – 12°11′ E). Climate is highly seasonal. Mean annual rainfall is 1973 mm, of which 96.3% fall from May to October, followed by 5 dry months (Sommer & Ross, 2011). Research is concentrated on chimpanzees (Pan troglodytes vellerosus aka elliotti; Oates, Groves & Jenkins, 2008) in the surroundings of Kwano, a field station maintained by the Gashaka Primate Project (583 m asl; 07°19′ N – 11°35′ E). This Gashaka-Kwano community is estimated to have about 35 members that range over about 26 km² (Sommer et al., 2004). Chimpanzees are regularly seen, but not habituated to such degree that individual follow would be possible. The apes use tools to prey upon honeybees, stingless bees, arboreal ants and army ants – but do not eat termites. Here, we focus on the consumption of army ants (Schönig et al., 2007). The dominant species is the epigaeic form Dorylus rubellus, found in 98.4% of 513 ant samples obtained from colony nests, ant trails, chimpanzee faeces and at light sources (males) (taxonomic identification: Caspar Schönig). All data of the current study refer to this species. While we cannot exclude the possibility, there is little evidence that chimpanzees harvest army ants from trails at this site. Instead, they use relatively long dipping wands (n = 360, average length 83.8 cm, average diameter 5.1 mm; Fowler et al., 2011) to extract their prey from nest cavities.

Measurements of defensive behaviour of army ants

Simulated chimpanzee attacks

We mimicked the predatory behaviour of tool-using chimpanzees at army ant nests to study the insects’ response (design modified after Möbius et al., 2008). Each experiment was conducted at a previously undisturbed colony (n = 16) by O. A., local field assistants – in particular Bobbo Buba – and volunteers (June to September 2008). For each nest, we used a different tool of similar dimensions that had been abandoned by chimpanzees more than 2 months before. Its tip was inserted at a 45° angle about 5 cm deep into the entrance (without enlarging it), prompting the ants through slight back and forth movements to attack. Our experiments lasted considerably longer than the 13 min reported in Möbius et al. (2008) because we aimed to infer why chimpanzees dip only for certain durations.

It was not possible to manufacture standardized new tools because source plants used by Gashaka chimpanzees (Pascual-Garrido et al., 2012) had not been identified at the time. Using old tools might have affected results as they may have been less pliable or otherwise lacked the surface characteristics of newly made implements (McGrew, 1974). In addition, old tools might, theoretically, have born olfactory traces from conspecific ant colonies or chimpanzees. However, insect alarm pheromones are composed of highly volatile compounds and dissipate quickly (e.g. Napper & Pickett, 2008). The lack of scent of chimpanzee hands or saliva on newly manufactured tools is actually an argument in favour of experimenting with discarded tools, given the intention to mimic ape attacks. In any case, army ants get quickly agitated upon disturbance, and the sudden release of large amounts of pheromones will likely override any pre-existing stimuli. Moreover, wild chimpanzees also employ previously used tools during repeat visits to ant colonies (McGrew, 1974) – something also observed at Gashaka.
Ant speed

How fast ants run up a dipping tool is a proxy for the readiness to attack intruders. To measure speed, two markings were carved into the tool, 10 and 30 cm from the end inserted into the nest. The first mark was left visible while tool movements alerted the ants. One experimenter was dipping, while a second monitored ant speed. Times were recorded from when the first ant passed the 10-cm mark until the first passed the 30-cm mark. These were not necessarily the same individual ants. The tool was then withdrawn and the ants shaken off. Measurements were taken at 1-min intervals for 20 min at eight different nests.

Ant yield

The number of insects caught was measured via experimental sessions that included eight sequences of four dips. These lasted for 2, 4, 6 and 8 s in a randomized order, thus simulating variability in dipping. A single session of 32 consecutive dips was conducted at a given nest (n = 8). One experimenter was dipping, while a second called out dip durations. Ants were collected after each dip. For this, the first experimenter swept harvested ants into a bucket with 50 mL of 70% ethanol. The bucket was swirled, causing the ants to clump. This allowed a third experimenter to transfer them into a sealable plastic bag for later processing, while the first experimenter continued. Intervals between dips lasted for 60 s. A session therefore consisted of 20 s for the four dip durations combined, plus 240 s for the four intervals between dips. The resulting total of (8 ¥ 260 s = 2080 s) = 34.7 min translates to 0.9 dips min⁻¹. Between-dip intervals allowed the experimenters to adjust positions to minimize exposure to the biting ants.

Ant weight

Dorylus ants lack distinct castes as workers vary substantially in size, with individuals allocating themselves to specialized tasks (Schöning et al., 2005). The largest workers are heavily involved in colony defence. We calculated mean weights across dip sequences to assess if and how worker size varies over a session. Samples were processed and dried at 110 °C for 1 h before weighing (Ecology Laboratory, Roehampton University/UK).

Ant remains in chimpanzee faeces and self-experiments

Faecal samples from Gashaka-Kwano chimpanzees (n = 59) were macroscopically inspected between January and April 2005 by Darren Ellis and field assistant Maigari Ahmadu (Ellis, 2005). Counts of broken ant heads (usually only those of large workers could still be identified as such) were divided by two and added to the number of complete heads. To obtain relative head numbers, overall numbers were divided by faecal dry mass recorded with a balance (KERN CM 320-1, Balingen, Germany). Correlations between numbers of ingested ants and remains detectable in faeces were assessed via self-experiments by V. S. (8 February 2011, 12 January 2012, 19 January 2012). For each of these, 100 large Dorylus workers were immobilized in whiskey, ingested, masticated with 12 chewing motions and swallowed. Remains detectable in subsequent excreta were counted.

Results

Findings are reported as t (total), a (average), m (median), r (range min–max), SD (standard deviation).

Ant speed

Over the course of experimental sessions, attack speed decreased markedly (r = 0.63, P = 0.01) (Fig. 1). Ants showed the greatest readiness to attack at the start (5.5 s) and became steadily slower by up to 40% towards the end (7.7 s).

Ant yield

The numbers of caught ants averaged 383 ants per dip (m 257, r 6–1334, s 330.1; n = 256) and clearly increased with dip length: 2 s (a 132, m 104, r 6–307, s 96.5); 4 s (a 335, m 253, r 61–1.022, s 258.8); 6 s (a 430, m 376, r 55–292.1); 8 s (a 634, m 512, r 178–1.334, s 396.3) (r = 0.9820; Fig. 2). Yield (g dry weight) increased likewise with dip length: 2 s (a 0.5, m 0.4, r 0–1.4, s 0.3); 4 s (a 0.8, m 0.7, r 0–2.5, s 0.6); 6 s (a 0.9, m 0.8, r 0.1–3.3); 8 s (a 1.1, m 0.8, r 0.1–4.7, s 0.8) (r = 0.9627).
Yield (g dry weight) at different nests varied substantially. Average figures and totals for the eight dipping sequences at individual colonies were as follows: [nest 1 (a 6.5, m 6.5, r 3.3–8.9, s 1.7; t 52.4); nest 2 (a 5.4, m 5.5, 4.5–6.7, s 0.7; t 43.2); nest 3 (a 3.3, m 4.0, r 0.7–5.2, s 1.8; t 26.4); nest 4 (a 2.8, m 2.8, r 1.9–3.4, s 0.5; t 22.0); nest 5 (a 2.6, m 2.7, r 1.7–3.4, s 0.7; t 21.0); nest 6 (a 2.0, m 2.0, r 0.7–5.7, s 1.6; t 16.3); nest 7 (a 1.6, m 1.5, r 0.7–2.5, s 0.7; t 12.8); nest 8 (a 1.5, m 1.4, r 0.6–2.7, s 0.7; t 12.1)]. Overall average yield for whole sessions was thus 25.8 g (a 3.2, m 3.3, r 1.7–4.8, s 1.0).

A fixed-effect regression model was used to assess the effects of dipping sequence within a session (DSeq) while controlling for the correlated measurements within each nest. It was found that yield varied significantly between different nests ($F_{(7,55)} = 19.402, P < 0.001$).

The linear fixed-effect model with DSeq as a predictor was not significantly different from the null model ($F_{(1,55)} = 0.10, P = 0.76$, adj $R^2 = 0.67$). DSeq was non-significant at $P = 0.76$ ($B = 0.02, t = 0.31$). However, the quadratic fixed-effect model with the inclusion of $DSeq^2$ was significantly different from the null model ($F_{(2,54)} = 3.52, P = 0.04$, adj $R^2 = 0.70$). $DSeq$ was now significant at $P = 0.011$ ($B = 0.74, t = 2.64$), and $DSeq^2$ was significant at $P = 0.011$ ($B = -0.08, t = -2.63$). The quadratic model was a significantly better fit compared with the linear model (likelihood ratio test: $X^2(1) = 7.72, P = 0.005$). Thus, the distribution of yield across the succession of eight dipping sequences followed a reversed U-shaped trajectory (Fig. 3).

**Ant weight**

The average dry weight of an individual worker across all eight nests was 2.3 mg (m 2.3, r 1.6–2.9, s 0.6). Figures for individual colonies were as follows: nest 1 (a 2.9, r 0.6–4.2); nest 2 (a 2.9, r 1.5–6.7); nest 3 (a 1.8, r 1.3–3.1); nest 4 (a 2.4, r 1.8–3.1); nest 5 (a 1.6, r 1.3–2.2); nest 6 (a 1.7, r 1.0–2.6); nest 7 (a 2.1, r 0.4–3.0); nest 8 (a 2.9, r 1.7–4.1). Average worker weights across nests thus varied only by a factor 1.8. This contrasts with weights for successive dipping sequences at the same nest (range 0.4–6.7 mg), which corresponds to a factor of 16.8. The latter finding reflects the marked change in mean worker mass over a session (Fig. 4), with the largest soldiers attacking first before giving way to smaller workers.

The mean number of ant heads in 59 chimpanzee faeces was 576 (m 636, r 3–4, s 907.1). More than a third of the samples (35.6%) contained fewer than 100 ants (counts: 3, 5, 8, 12, 17, 28, 32, 34, 38, 40, 52, 63, 65, 67, 68, 70, 73, 75, 87, 90), and

---

**Figure 2** Number of ants caught and yield as a function of dip length.

**Figure 3** Total average yield as a function of dipping sequence order within an experimental session. Curve based on fixed-effect regression analysis. Average values are shown for illustrative purposes only.

**Figure 4** Mean weight of individual ants harvested during eight successive dipping sequences.
three quarters not more than 700. Only 10 samples (16.9%) contained more than 1000 ants (counts: 1344, 1360, 1485, 1530, 1559, 1592, 2509, 3063, 3348, 4636). Relative numbers averaged 12.9 heads g⁻¹ dry faeces mass (m 5.4, r 0.2–120.6, s 22.0).

Using these head counts and mean individual worker weight (2.3 mg), the average dry mass of ants excreted during a single defaecation was calculated as 1.3 g, with enormous variation (r 0.01–10.7, s 2.2). Two-thirds of faeces (64.4%) contained less than 1 g of ants, and the vast majority (93.2%) less than 4 g (Fig. 5).

### Number of ingested and excreted ants

The correlation between ingested ants and those detectable in faeces was assessed through self-experiments, in which a human volunteer chewed and swallowed batches of 100 large Dorylus workers. The number of detectable heads (H) and other fragments (O) and intervals (in hours) between ingestion and excretion was as follows: experiment 1 (11 H/14 O/17 h; 10 H/2 O/23 h); experiment 2 (11 H/9 O/15 h; 7 H/6 O/27 h; 23 H/18 O/39 h; 3 H/4 O/51 h; 5 H/1 O/67 h); experiment 3 (8 H/2 O/16 h; 31 H/10 O/38 h; 2 H/1 O/45 h; 0 H/0 O/68 h).

Thus, of 100 ingested insects, only a fraction was detectable in a given subsequent defaecation (heads: a 10.1, m 8, r 0–31, s 9.3; other body parts: a 6.1, m 4, r 0–18, s 6.0). Values vary slightly for the number of heads, whether we consider the first two defaecations after ingestion (a 13.0, m 10.5, r 7–31, s 9.0), defaecations during only the first subsequent morning (a 16.8, m 11, r 8–11, s 1.7), defaecations during the first and second subsequent mornings (a 16.8, m 11, r 8–31, s 9.8) or defaecations during the first, second and third subsequent mornings (a 12.7, m 11, r 6–31, s 10.7).

Given that we do not know when the chimpanzees ingested the ants before we collected the sample from under their night nest, it seems most appropriate to assume that 10.1% of ingested insects are detectable in excreta produced during the subsequent 3 days.

### Discussion

Our experiments in the home range of Nigerian chimpanzees assessed the response of army ant colonies to attacks by predatory apes, and estimates numbers and dry weight of ants the apes are likely to consume.

### Ant speed

Tool insertion provokes the ants to defend their nest entrance. They can bite the chimpanzee’s hand sooner if they run up a tool with greater speed. Theoretically, this should force the apes to use longer tools or dip for shorter (Möbius et al., 2008). Nevertheless, the pace of defending ants virtually halved over the course of a 20-min dipping session (cf. Fig. 1). One possible explanation is that ants may react more aggressively at first contact with a substrate still devoid of alarm pheromones (Hölldobler & Wilson, 1990), and that speed decreases as the tool becomes saturated with these olfactory signals. However, decreasing speed more likely reflects that average worker size decreased steadily over the course of the session (cf. Fig. 4). Thus, the first ants to come out are ‘soldiers’ that occupy a nest’s top portion (Schöning et al., 2005). These then seem to fan out to deter the intruder. This assumption is compatible with observations that defenders ‘move up the tool without biting it’, suggesting that the insects can ‘differentiate the inanimate object from the predator’ (McGrew, 1974: 504). Such explanation for a decreasing speed is consistent with inferences made from morphology, in that larger workers have longer legs and therefore run faster (Schöning et al., 2008). It would be interesting to know if chimpanzees adjust dipping duration over a session in response to decreasing speed.

### Harvesting yield

On average, longer insertions of the tool resulted in a higher reward (cf. Fig. 2). However, yield varied markedly throughout sessions. The ants seemed to need some time to respond after the initial disruption, with relatively few workers attacking the tool early on. Yield then increased rapidly, peaking half way through, before tailing off (cf. Fig. 3). Yield perhaps diminished in later stages because ants retreat deeper into the nest cavity. This could coincide with the most vulnerable colony members, for example, brood and queen, having been moved to relative safety. Alternatively, diminishing yield may again result from workers – especially larger individuals – not concentrating on the tool anymore, but spreading outwards in attempts to deter the source of the disturbance.

Yield also varied substantially across different nests, perhaps reflecting different colony sizes or reproductive stages.
What determines dipping session length?

Unlike in termite eating, when chimpanzees may fish for several hours (e.g. Goodall, 1986), individual apes spend comparatively shorter periods dipping for army ants (Gombe/Tanzania: 15.0 min, range = 3–48, n = 27, McGrew, 1974; Bossou/Guinea: 11.4 min, range 0.0–51.5, n = 34, Yamakoshi & Myowa-Yamakoshi, 2004). Average dip rate, that is, frequency of tool insertion/withdrawal/ingestion of ants varies considerably between 2.6 min⁻¹ at Gombe/Tanzania (McGrew, 1974), 1.4 min⁻¹ respectively 2.4 min⁻¹ at Bossou/Guinea (Yamakoshi & Myowa-Yamakoshi, 2004 respectively Humle, 2006) and 12 min⁻¹ at Tai/Ivory Coast (Boesch & Boesch, 1990).

The causes for this variation are unknown. One possibility is that session length may be based on an optimal foraging strategy that takes decreasing yield into account. In our experiments (cf. Fig. 3), yield peaked at 17 min, half way through a session (note that this assessment is likely to be true for any frequency of dips). Corresponding data for other chimpanzee study sites have not been published.

Alternatively, discomfort caused by being continually bitten might lead the apes to quit. Indeed, for the human experimenter (O. A.), bites became increasingly frequent as the session progressed. Chimpanzees, including those at Gashaka, cope with this by shifting position and perching on saplings or overhanging branches (e.g. McGrew, 1974; Humle & Matsuzawa, 2002). The human experimenter also tried this, but found that the ants would soon be up in the vegetation as well. The problem is made worse, as chimpanzee foraging parties tend to harvest the insects together. At Bossou/Guinea, individual dipping sessions of 11 min are embedded in episodes that average 27 min and 2.8 chimpanzees (range 1–9, n = 12 episodes; Yamakoshi & Myowa-Yamakoshi, 2004). Accordingly, even if a chimpanzee dips only briefly, he or she will face irate ants stirred up by others. Session length might therefore reflect a trade-off between yield and pain.

The hypotheses could be tested at sites with habituated chimpanzees by measuring the apes’ average dipping time and then conducting experiments that last longer. If diminishing return is the cause, yield should decrease markedly once average session length has been reached. The discomfort hypothesis would be supported if the apes quit before yield peaks.

Reconstructing consumption from faecal samples

In the absence of direct observational data, ant remains in chimpanzee faeces may offer some clues to actual harvesting success. On average, 576 insects were recovered from single faeces, which translates into 1.3 g dry weight. However, ant fragments in a single faecal dropping do not necessarily represent the intake from an entire feeding session. Chimpanzees may chew so thoroughly that many exoskeletons are crushed beyond recognition, leading to faecal head counts that seriously underestimate actual consumption. Moreover, fragments might be distributed across several excretions as the pointed exoskeletons get caught in the digestive tract. This would explain extremely small faecal head counts (e.g. 3, 5, 8) unlikely to represent all that was eaten. The human self-experiments support these assumptions. Of 100 chewed and ingested large Dorylus workers, heads on average of only 10.1% were detectable in the first subsequent excreta. The correlation between ingested ants and faecal remains therefore suggests that 89.9% of all ingested ants will not show up in a given individual faeces. If we assume the validity of the self-experiment, actual harvesting success for chimpanzees at Gashaka-Kwano averages (1.3 × 100/10.1 =) 12.9 g dry weight per session.

The self-experiments are likely to be valid at least in principle, because digestive processes of Homo and Pan are similar in that chitin cannot easily be processed (Jollès & Muzzarelli, 1999) and with respect to digestive kinetics (Milton & Denmment, 1988). While chimpanzee gut and colon are larger than those of (Western) humans, mean transit time in both Pan and Homo reveals a relatively slow turnover of ingesta. Thus, increased consumption of animal source foods such as meat in the human lineage (Milton, 2003) did not change basic gut kinetics, which is a conservative trait.

Controlled experiments in which captive chimpanzees are fed known numbers of army ants followed by faecal inspections could clarify this issue further. At sites with habituated chimpanzees, harvested dry weight could be calculated from experiments that mimic the average dip frequency and session length observed in the apes.

Inter-site comparisons

Harvesting success of army ants cannot readily be compared across chimpanzee study sites because different species might occur (e.g. faster running epigaeic vs. slower intermediary form) and these might be exploited with different techniques (e.g. dipping at trails or nests, with the ants then nibbled or swiped off the tool) (Schönung et al., 2008).

For example, an experimental dip at Gombe caught 292 ants (McGrew, 1974), whereas dips at Tai procured only 15 ants (Boesch & Boesch, 1990). Even if these would belong to the same species, such numbers say very little, as army ants display continuous polymorphism (Schönung et al., 2005). In our study, mean weights between the smallest and largest ants differed by a factor of 17 (0.4–6.7 mg). Unless mean ant size is measured, weight is the obvious alternative unit of comparison. The average army ant dipping session of 15 min at Gombe/Tanzania yielded an estimated 17.6 g fresh weight (McGrew, 1974), while experimental 13-min sessions at Tai/Ivory Coast yielded 20.0 g (range 2.9–39.9 g, n = 15; Möbius et al., 2008). Our experiments produced average weights of 25.8 g dry mass per nest, with a corresponding figure for fresh weight that ought to be considerably higher. However, session length was much longer at Gashaka.

Nevertheless, a rough comparison can still be made between Gashaka-Kwano and dipping experiments at Bossou/Guinea and Tai/Ivory Coast, given the same number of dips (n = 32) and similar methodology. These experiments produced average yields of about 3400 ants (range c. 500–7500)
for Taï, but probably half of that for Bossou (estimated from Möbius et al., 2008: Fig. 3). At Gashaka-Kwano, average yield was easily three to six times higher with 11217 harvested ants (range 5260–22 782). Admittedly, experiments in Nigeria lasted about three times longer, but if 32 dips had been executed over just 13 min (as in Möbius et al., 2008), yield would only have been about 15% lower (cf. Fig. 3). Earlier experiments at Bossou with 102-cm long tools and dips of 2–120 s collected an average of 77 ants (median 60, range 13–544; Humle & Matsuzawa, 2002). This compares with a mean of 383 ants collected with slightly shorter tools at Gashaka in experimental dips that averaged a mere 5 s.

We are therefore left with the possibility that harvesting success of Gashaka-Kwano chimpanzees is much higher than elsewhere. This might be due to a particular aggressiveness of D. rubellus. This species is either not harvested at other known chimpanzee study sites or not occurring – with the exception of Goualougo/Congo, where it is only one of several species preyed upon (Schöning et al., 2008; Sanz, Schöning & Morgan, 2010). We currently lack direct observations of chimpanzee dipping sessions that could support or refute this assumption.

Our data suggest that, while the function of myrmecophagy is still poorly understood, harvesting success is likely constrained by the prey’s defensive responses as they unfold over a dipping session. Information from other sites similar to that elsewhere. This might be due to a particular aggressiveness of D. rubellus. This species is either not harvested at other known chimpanzee study sites or not occurring – with the exception of Goualougo/Congo, where it is only one of several species preyed upon (Schöning et al., 2008; Sanz, Schöning & Morgan, 2010). We currently lack direct observations of chimpanzee dipping sessions that could support or refute this assumption.

Our data suggest that, while the function of myrmecophagy is still poorly understood, harvesting success is likely constrained by the prey’s defensive responses as they unfold over a dipping session. Information from other sites similar to that collected during the present research could clarify this issue further.

Acknowledgements

The Nigeria National Park Service granted a research permit to the Gashaka Primate Project (GPP). Gashaka Gumti National Park provided logistical support. The work would have been impossible without local field assistants, in particular Bobbo Buba and Buba Bello. O.A. thanks volunteers James Vernon and Anna Meris for assistance in the field, and especially Emily Emmott for statistical advice. Dry weight measurement was enabled by Claire Ozanne, Centre for Research in Ecology, Roehampton University London. Caspar Schöning, Länderinstitut für Bienenkunde, Hohen Neuendorf, Germany, provided valuable advice and identified all army ant samples. O.A.’s fieldwork was partly supported by a veterinary studentship from the North of England Zoological Society/Chester Zoo, who also provide GPP’s core funding.

References


