Army ant prey availability and consumption by chimpanzees (Pan troglodytes vellerosus) at Gashaka (Nigeria)

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Keywords
chimpanzee; Formicidae; Dorylinae; insectivory; myrmecophagy; food preference.

Abstract
Army ant predation by chimpanzees has been studied as an intriguing example of tool use and a possible case of cultural variation. However, the importance of army ant prey in chimpanzee diet and feeding ecology is still only poorly understood. We studied the availability and consumption of army ants in a population of the chimpanzee subspecies Pan troglodytes vellerosus in Nigeria. Army ants were collected from nests and trails (workers) and near artificial light sources (males). Three potential prey species were found: Dorylus rufescens, Dorylus gerstaeckeri and Dorylus kohli. Dorylus rufescens was by far more abundant than the other two species. Only remains from D. rufescens were present in chimpanzee faeces. This is the first report of consumption of this ant species by chimpanzees. However, because of the low availability of the other two species, it is unclear whether this pattern reflects a preference for D. rufescens. Although D. rufescens’ availability varied with weather conditions, the occurrence as well as the absolute and relative numbers of Dorylus fragments in faeces did not. This finding, together with the considerable difficulties encountered by human observers in their efforts to locate nests by following trails, suggests that the chimpanzees in this population do not harvest army ants from trails and do not use trails to locate nests. The overall occurrence of army ant fragments in 42.3% of all faecal samples is the highest ever recorded in any chimpanzee population. This indicates that in this chimpanzee population, army ant prey is not a fallback during periods of sparse availability of plant food, but quantitatively important throughout the year. Future studies will be needed to clarify which cues and strategies chimpanzees use to locate army ant nests and to assess the role of myrmecophagy with respect to macro- or micronutrient demands.

Introduction
Ants are an important food source for many African mammals, including gorillas and chimpanzees (Redford, 1987; Watts, 1989; Yamagiwa et al., 1991; Gotwald, 1995; Kingdon, 1997; Ganas & Robbins, 2004). Chimpanzees Pan troglodytes are known to feed on the weaver ant Oecophylla longinoda (e.g. at Bossou/Guinea; Sugiyama, 1995), arboreal Camponotus spp. (e.g. at Mahale/Tanzania; Nishida, 1973), Crematogaster spp. (e.g. at Lopé/Gabon; Tutin, Ham & Wrogemann, 1995), Pachycondyla analis (formerly Megaponera foetens; Bolton, 1995; at Mt Assirik/Senegal; McGrew, Baldwin & Tutin, 1988) and Dorylus (subgenus Anomma) army ants (e.g. at Gombe/Tanzania; Goodall, 1963).

Dorylus (Anomma) army ants differ from all other listed prey species by their enormous colony sizes. They form the largest single family insect societies with a worker population of up to 12 million (Leroux, 1982). The total fresh mass (including brood and workers) of an average colony with 6.5 million workers is about 40 kg (Leroux, 1982). Thus, an army ant colony potentially constitutes more lucrative prey for chimpanzees than other ant colonies. Nevertheless, their consumption is notably absent from some long-term chimpanzee study sites such as Lopé/Gabon, Mahale/Tanzania or Kibale and Budongo/Uganda (reviewed in Whiten et al., 1999).

Dorylus (Anomma) army ant nests are well defended. When an army ant nest or trail is attacked, many of the largest workers rush out of the nest entrances or from the trail to attack the source of the disturbance. Although D. (Anomma) army ants – in contrast to the Ecitoninae army ants in South America – lack a sting, they inflict painful bites with their falcate mandibles, which are suitable for piercing, for example, a human intruder’s skin. The methods used by chimpanzees to harvest army ants therefore usually involve the use of so-called dipping wands that help them to avoid the ants’ bites. The chimpanzee population at Tai/Ivory Coast represents a notable exception in that these chimpanzees often open the army ant nests and take out workers and brood directly with their hands (Boesch & Boesch, 1990).
Not only do army ants differ from all other ant prey species listed above, they also differ in one important characteristic from all other social insect prey targeted by chimpanzees. Their colonies frequently move to new nest sites because of food depletion in the vicinity of the current nest (Wilson, 1958; Schöning, Njagi & Franks, 2005a). Chimpanzees cannot therefore simply return to army ant nests after an initial discovery and harvest from them again. Instead, they need to discover active nests on a regular basis. The frequent emigrations combined with a low colony density probably necessitate an increased search effort, which may make army ant predation less efficient in terms of the food amount gained per unit time. However, little is known about chimpanzees’ strategies for locating army ants despite these constraints.

Although many studies have addressed the questions of why army ant eating behaviour is present at some sites but not at others and why the harvesting techniques show considerable variation between sites (e.g. Whiten et al., 1999; Humle & Matsuzawa, 2002), almost nothing is known about the importance of army ant prey in the diet and feeding ecology of chimpanzees. For example, it is possible that army ants are an important source of protein and/or minerals in some populations, but no data on the quantities of army ants consumed per day and their nutritional value have been reported so far. Moreover, it is unclear if ants indeed represent a ‘staple food’ (McGrew, 1992) or a ‘fall-back food’ consumed only when favoured fruit is not available (Basabose, 2002). Previous studies have not measured the abundance of army ants. It is possible that the aggressiveness of different species of army ants (Humle & Matsuzawa, 2002) leads to preferences with regard to prey species, but firm conclusions are marred by the fact that many previous studies probably did not accurately identify the army ants involved, not least because the taxonomy of this ant group is in disarray.

During a long-term study of the recently recognized fourth subspecies of chimpanzee *P. troglodytes vellerosus* at Gashaka/Nigeria (Sommer et al., 2004), ant-dipping tools were recovered from *D. (Anomma)* sp. nests and the examination of chimpanzee faecal samples confirmed the consumption of *D. (Anomma)* army ants (Fowler & Sommer, in press).

Here, we report the results from a more comprehensive follow-up study on army ant predation by chimpanzees at Gashaka. Specifically, we address the following questions. Which army ant species are available? Which army ant species are consumed? Does the availability of army ant prey vary with season, habitat or weather conditions? Does the consumption vary with season or weather conditions? How difficult is it for chimpanzees to find army ant nests?

**Materials and methods**

**Study site**

The study was conducted in Gashaka-Gumti National Park, which lies in eastern Nigeria on the border with Cameroon (583 m; 07°19’N, 11°35’E). The landscape is a mosaic of savannah and gallery forests spread along streams and rivers. The climate fluctuates half-yearly between a dry (defined as October 15–April 14) and a rainy season (defined as April 15–October 14; Fig. 1). The chimpanzee study community at Gashaka-Kwano comprises about 35 members which occupy a home range of at least 26 km². The chimpanzees are not yet fully habituated to human observers, but solid background data exist concerning variables such as foraging or nest group sizes, food availability and
tool use (Sommer et al., 2004; Fowler & Sommer, in press; Hohmann et al., in press).

Army ant availability

The occurrence and relative abundance of army ant species was measured by walking nine previously established transects (length 1675–5000 m) to discover emigration and foraging trails, swarm raids and active nests (Table 1). Habitat composition along transects (78% forest, 22% savannah) is considered representative of the area’s overall composition. Each transect was walked two–four times by D. E. for a total distance of 106.2 km between January and April 2005. The habitat type in which the trail or nest was found was recorded. Swarm raids were recorded as foraging trails. Under favourable conditions D. (Anomma) are active throughout the day and night. However, assessments of ant availability were restricted to the daytime, as chimpanzees feed almost exclusively during daylight hours. A sample of 10 large workers was taken and stored in a 1.5 mL vial filled with 70% ethanol from any ant trail found crossing a transect, from any trail or nest not more than 5 m away from a transect, and from trails or nests encountered during haphazard, random walks. In addition, army ant males (‘sausage flies’) were collected at the field station’s light sources at night in order to use another information source for recording which army ant species were present in the study area. All samples were later identified by C. S., who is currently working on a taxonomic revision of the subgenus D. (Anomma) (C. Schöning et al., unpubl. data). Voucher specimens of all species are deposited in the collection of the Zoological Museum of the University of Copenhagen, Denmark.

In order to assess whether sampling efforts were sufficient to record all army ant species present in the area, we compared the observed number of species against species richness as estimated by using three commonly used methods (Colwell & Coddington, 1994): (1) the Chao quantitative estimator (‘Chao 2’), (2) the first order jackknife procedure and (3) an asymptotic model based on Michaelis–Menten kinetics.

For the day of each transect walk, the weather conditions were scored as wet if the rainfall on the day itself was at least 3 mm or if the cumulative rainfall over the three preceding days had been at least 9 mm. All other days were scored as having dry weather conditions. These criteria were chosen post hoc as they accurately predicted the subjectively assessed ground conditions. We defined them in order to be able to predict the likely weather conditions on days with known weather data but without information on the ground conditions.

For each transect walk, the trail density was calculated as the number of ant trails or nests encountered per transect km. In addition, trail densities were also calculated separately for savannah and forest. The trail densities were later compared using the Student’s t-test or, whenever appropriate, the Mann–Whitney U-test.

The underlying assumption of assessing relative army ant abundance by recording trails and nests during transect walks was that chance encounters of both trails and nests would represent opportunities for chimpanzees to prey on army ants. Chimpanzees prey on army ants with or without tools at nests, but in some populations they also harvest army ants with tools from trails (McGrew, 1974; Humle & Matsuzawa, 2002; Hicks, Fouts & Fouts, 2005). Before this study, it was unknown whether the latter behaviour occurs at Gashaka. Moreover, observations by McGrew (1974) indicate that chimpanzees may use army ant trails to find nests; hence we assumed that if chimpanzees at Gashaka do not prey on army ants at trails, they may instead follow these trails to locate nests and feed on the ants there.

Whether or not a given army ant species is available as prey for chimpanzees depends largely on the ants’ behaviour (Schöning, Kinuthia & Franks, 2005b), (1) Species with an ‘epigaec’ lifestyle organize conspicuous swarm raids on the ground surface and up in the vegetation. These include species such as Dorylus (Anomma) molestus, Dorylus (Anomma) nigricans, Dorylus (Anomma) sjoestedti and Dorylus (Anomma) wilverthi (Raignier & van Boven, 1955; Gotwald, 1974; Leroux, 1982). Dorylus (Anomma) nigricans is preyed on by chimpanzees at Bossou/Guinea (Humle & Matsuzawa, 2002) and Taï/Ivory Coast (Boesch & Boesch, 1990).

(2) Species with an ‘intermediate’ lifestyle hunt in the leaf litter, but do not climb vegetation when foraging and inhabit less conspicuous nests. These include taxa such as Dorylus (Anomma) gerstaeckeri, which is consumed by chimpanzees at Bossou/Guinea (Humle & Matsuzawa, 2002) and Taï/Ivory Coast (Boesch & Boesch, 1990).

(3) Species with a ‘subterranean’ lifestyle hunt in the soil and their nests are not indicated by obvious cues on the surface. These species have never been reported to be consumed by chimpanzees.

We assume that epigaec, intermediate but not subterranean species are available to the Gashaka chimpanzees as prey.

To assess the difficulty for chimpanzees to actively search for and find army ant nests, we used workers carrying food (foraging trail) or brood (emigration trail) as a cue to discover nests. Trails are frequently covered by leaf litter, and emigration trails in particular may be hidden under

Table 1 Habitat composition in the chimpanzee Pan troglodytes vellerosus home range of Gashaka-Kwano/Nigeria, and transects walked during daylight surveys of army ant trails and nests

<table>
<thead>
<tr>
<th>Transect Length</th>
<th>Unit</th>
<th>Forest</th>
<th>Savannah</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>km</td>
<td>%</td>
<td>21.3</td>
<td>6.1</td>
<td>27.4</td>
</tr>
<tr>
<td>km</td>
<td></td>
<td>77.8</td>
<td>22.2</td>
<td>100.0</td>
</tr>
<tr>
<td>Distance walked</td>
<td>Dry</td>
<td>km</td>
<td>38.5</td>
<td>53.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>%</td>
<td>15.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Wet</td>
<td>km</td>
<td>37.1</td>
<td>52.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>%</td>
<td>15.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>km</td>
<td>75.6</td>
<td>106.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>%</td>
<td>30.6</td>
<td></td>
</tr>
</tbody>
</table>

Metabolic energy content of the leaves was determined using a Cahn Electrobalance 2000 system and a 7200D Infrared analyser (Fisons Instruments, UK), as described by Rose (2001). The calorific value of leaves was calculated as 393.5 ± 19.6 kcal kg–1 dry matter.

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The exact route of the trail was therefore often obscured. In such cases, we instead wandered into the general direction previously indicated by the flow of food or brood in order to locate another exposed trail section closer to the nest or eventually the nest itself.

Once located, certain nest characteristics were documented to examine whether these could be used as search cues. Thus, if the nest was located at the base of a tree, the circumference of the tree at breast height (cbh) was recorded. We checked for excavated soil piles (as described by Raignier & van Boven, 1955, for D. wilverthi, and Leroux, 1982, for D. nigricans) and whether leaf litter covered the nest entrance. We measured the maximum extension of visible nest structures. A photograph of the nest and the surrounding area was taken for visual reference, and signs of recent attack such as dipping wands or large holes were recorded. Finally, the nest’s suitability for ant-dipping by chimpanzees was established by disturbing the colony through hitting the entrance three times with a stick. After 2 min, the number of workers that emerged in the colony was established by disturbing large holes were recorded. Finally, the nest’s suitability for exploitation by chimpanzees.

Chimpanzee consumption of ants

The frequency of myrmecophagy was assessed by the analysis of chimpanzee faecal samples that were collected between March 2001 and April 2005 by or under the guidance of A. F. Chimpanzees construct a night nest each evening and the ground beneath the nesting tree was checked for faecal remains, which are typically produced in the early morning before the nest is deserted. Most samples obtained for this study were from fresh nests that had been constructed during the previous night. Faecal piles were examined in more detail by D. E. Faecal piles were brought back to the field station, dried in the sun for 3 days, and then broken up for inspection.

Samples collected between January and April 2005 were examined in more detail by D. E. Dry mass was recorded with a KERN (Balingen, Germany) CM 320-1 balance before the ant heads were counted. The number of broken heads (usually only those of very large workers could still be identified as such) was divided by two and added to the number of complete heads. The overall number of heads was divided by the dry mass of the faecal sample to obtain the relative head number. All heads were stored in vials for later identification to species level. Weather records from 2001 to 2005 produced 76 ant samples from trails and nests. The vast majority (93.4%) belonged to D. (A.) rufescens Santschi, a typical representative of the ‘epigaeic’ lifestyle. Species with an ‘intermediate’ lifestyle were represented by two samples from D. (A.) gerstaeckeri Emery and one sample from D. (A.) kohli Wasmann, whereas the two remaining samples belonged to ‘subterranean’ species in the subgenera D. (Dorylus) and D. (Typhlaphone). The species accumulation curve was satisfactorily asymptotic (Fig. 2). Species richness was estimated to be 3.50 (Chao 2), 3.99 (first-order jacknife estimate) and 3.65 (95% confidence interval 3.30–3.99, asymptotic model), respectively. Fifty-nine of the 69 D. rufescens trails found during transect and random walks were in forest habitat (86.4% foraging trails, 13.6% emigration trails) and 10 in savannah habitat (80.0% foraging trails, 20.0% emigration trails).

Among the army ant males collected at field station lights, there were D. rufescens and D. gerstaeckeri. The remaining males all belonged to subgenera other than D. (Anomma). The identification of the males does not point to a higher number of available army ant species than has been observed in the worker samples from trails and nests. Therefore, three army ant species seem to be available as prey for chimpanzees at Gashaka-Kwano.

Results

Army ant species at Gashaka-Kwano/Nigeria

Transect and haphazard walks between January and April 2005 produced 76 ant samples from trails and nests. The vast majority (93.4%) belonged to D. (A.) rufescens Santschi, a typical representative of the ‘epigaeic’ lifestyle. Species with an ‘intermediate’ lifestyle were represented by two samples from D. (A.) gerstaeckeri Emery and one sample from D. (A.) kohli Wasmann, whereas the two remaining samples belonged to ‘subterranean’ species in the subgenera D. (Dorylus) and D. (Typhlaphone). The species accumulation curve was satisfactorily asymptotic (Fig. 2). Species richness was estimated to be 3.50 (Chao 2), 3.99 (first-order jacknife estimate) and 3.65 (95% confidence interval 3.30–3.99, asymptotic model), respectively. Fifty-nine of the 69 D. rufescens trails found during transect and random walks were in forest habitat (86.4% foraging trails, 13.6% emigration trails) and 10 in savannah habitat (80.0% foraging trails, 20.0% emigration trails).

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Abundance of army ant trails during transect walks

During the 32 non-random transect walks, 47 Dorylus trails were found. A single trail – encountered during the early rainy season at the end of April – belonged to D. gerstaeckeri, whereas the remaining 97.9% were identified as D. rufescens. Because of the apparent rarity of trails of D. gerstaeckeri, a reasonably precise estimate of its trail density in the different habitats and under the different weather conditions would require a much larger sample basis than was gathered in this study. Therefore, the D. gerstaeckeri trail densities are not calculated here.

The overall D. rufescens trail density was on average 0.43 (± 0.43 sd, range 0–1.6) trails per km (Table 2). Under dry weather conditions the D. rufescens trail density was 0.21 (± 0.21 sd) trails per km and thus lower than under...
Table 2 Density of army ants in the chimpanzee Pan troglodytes vellerosus home range of Gashaka-Kwano/Nigeria (in trails per km)

<table>
<thead>
<tr>
<th></th>
<th>Total</th>
<th>Dry</th>
<th>Wet</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td>Forest</td>
<td>0.56</td>
<td>0.65</td>
<td>0.25</td>
</tr>
<tr>
<td>Savannah</td>
<td>0.06</td>
<td>0.17</td>
<td>0.00</td>
</tr>
<tr>
<td>Overall</td>
<td>0.43</td>
<td>0.43</td>
<td>0.21</td>
</tr>
</tbody>
</table>

On the basis of 46 trails of Dorylus rufescens located during 106.2 km of transect walks.

wet weather conditions (0.75 ± 0.48 SD; *t*-test, d.f. = 30, *t* = −4.32, *P* < 0.001). Dorylus rufescens trails are therefore available every 4.8 km under dry weather conditions and every 1.3 km under wet weather conditions. The mean trail density in forests was 0.25 ± 0.26 SD trails per km under dry weather conditions and thus lower than under wet weather conditions (0.99 ± 0.70 SD; *t*-test, d.f. = 50, *t* = −4.47, *P* < 0.001). In forests, D. rufescens trails are therefore available every 4.0 km under dry weather conditions and every 1.0 km under wet weather conditions. The mean D. rufescens trail density in forests was higher than in savannah areas (0.55 ± 0.61 SD trails per km vs. 0.06 ± 0.17 SD trails per km, *t*-test, d.f. = 56, *t* = 4.01, *P* < 0.001), and this is also true when dry weather conditions and wet conditions are considered separately (dry weather: 0.25 ± 0.26 SD trails per km in forests vs. 0 ± 0 SD trails per km in savannah areas, *t*-test, d.f. = 33, *t* = 3.85, *P* < 0.001; wet weather: 0.99 ± 0.70 SD trails per km in forests vs. 0.15 ± 0.26 SD trails per km in savannah areas, *t*-test, d.f. = 21, *t* = 3.61, *P* < 0.01).

Consumption of army ants by chimpanzees

Overall, 381 faecal samples were collected from 2001 to 2005, including 372 from the chimpanzee nesting sites. A subsample of 127 faeces collected between January and April 2005 was examined in greater detail.

The overall sample was used to calculate the proportion of faeces with ant fragments. Three hundred and six samples were fresh, that is they resulted from consumption during the previous day. These fresh samples were used to discern the relationship between wet and dry weather conditions during the day of consumption and ant occurrence.

Dorylus remains were found in 42.3% (161/381) of all samples. The proportion within the subsample was similar (46.5%, 59/127), and all samples with Dorylus ants contained only D. rufescens. The frequency of D. rufescens in these samples (59/59) did not differ significantly from the frequency expected from the availability during transect and random walks (71/74, with the three samples containing D. gerstaeckeri and D. kohli combined; Fisher’s exact test, *P* = 0.17).

The number of Dorylus heads in these 59 samples ranged from 3 to 4636 (median 181). The relative head number ranged from 0.2 heads per g dry mass to 120.6 heads per g dry mass (median 5.44 heads per g dry mass).

The proportion of samples with Dorylus fragments did not vary with season (dry season: 115 samples without army ants vs. 74 with army ants; rainy season: 105 without vs. 87 with; *χ^2*-test, *χ^2* = 2.87, d.f. = 1, *P* = 0.09) nor with weather condition on the feeding day (samples collected after dry weather days: 80 without vs. 57 with; samples collected after wet weather days: 97 without vs. 72 with; *χ^2*-test, *χ^2* = 0.06, d.f. = 1, *P* = 0.81). The absolute head numbers in the samples with fragments did not vary with weather conditions on the feeding day [Mann–Whitney *U*-test, *n* (dry weather) = 44, *n* (wet weather) = 15, *U* = 307.5, *Z* = 0.39, *P* = 0.70] nor did the relative head numbers in these samples [Mann–Whitney *U*-test, *n* (dry weather) = 44, *n* (wet weather) = 15, *U* = 247.5, *Z* = 1.44, *P* = 0.15]. The absolute head numbers in faecal samples with fragments did not vary with season [Mann–Whitney *U*-test, *n* (dry season) = 50, *n* (rainy season) = 9, *U* = 182.5, *Z* = 0.90, *P* = 0.37], but the relative head numbers in these samples did [Mann–Whitney *U*-test, *n* (dry season) = 50, *n* (rainy season) = 9, *U* = 101.5, *Z* = 2.60, *P* = 0.009]. In the comparisons between the dry and rainy season figures of absolute and relative head numbers, it has to be emphasized that the numbers of the samples collected during the rainy season are rather low. These results should therefore be viewed with caution.

Species other than army ants were found in 3.9% (5/127) of the more closely examined subsample. Remains of the termite-hunting P. analis were present in three samples. Two of these contained pupal cases; therefore, these ants were probably consumed intentionally from nests. Two other samples contained remains of the genus Camponotus, which may represent ground-dwelling or arboreal species. It is unclear whether they were eaten accidentally or deliberately targeted. These two species are obviously rather unimportant as food sources compared with army ant prey.

Nest searches and nest characteristics

Our nest searches (n = 65) had a success rate of 24.6%. The 16 successful searches lasted on average 29.4 ± 55.6 min (median 15 min, range 5–240 min), whereas 49 other searches were abandoned after 5–130 min without finding the nest. The vast majority of nests (87.5%) was located in forest habitat. All nests belonged to D. rufescens. The 16 located nests had little or no obligatory characteristics (Table 3). For example, a nest was equally likely to be located at the base of a tree as elsewhere. The ec of trees with nests averaged 81.3 ± 20.1 SD cm (range 50–110 cm). Therefore, they did not differ in size from the 960 trees along an 8 km straight-line transect (Mann–Whitney *U*-test; *U* = 2896.0, *Z* = −1.70, *P* = 0.09). Nests were equally likely to have conspicuously excavated soil piles as they were to have none, and they were equally likely to have a hidden nest entrance as an exposed entrance. Obvious surface cues were lacking in 18.8% of nests (3/16), whereas the average extent of those with visible nest structures (81.3%) was 141 ± 132 SD cm (range 10–510 cm).

Experimental disturbances elicited ‘no’ response in two cases, a ‘strong’ response in 10 cases, and an ‘enormous’

response in four cases. Therefore, 87.5% nests (14/16) were considered to be suitable for ant-dipping by chimpanzees.

Almost one-fifth of the nests (3/16 = 18.8%) showed signs of recent attacks by chimpanzees as ant-dipping wands were scattered in the vicinity and ants ran around frantically. One of these colonies had stayed in their nest for only 2 days, and – probably as a result of the attack – abandoned the site and emigrated to a new one.

The relative proportions of foraging and emigration trails can be used to estimate the average nest stay duration of *D. rufescens* colonies. While emigrating, *D. (Anomma)* colonies forage by up to three separate trails (Leroux, 1982; Schöning et al., 2005a). We therefore assume that every emigrating colony has at least one foraging trail. The proportion of emigrating colonies is then calculated as the ratio of emigration/foraging trails, because the number of foraging trails directly gives the number of all colonies in the population. The average nest stay duration can be calculated as the reciprocal of the proportion of colonies that emigrate. Using this method, we calculate an average nest stay duration of 4.0 days in the savannah, 6.4 days in the forest and 5.9 days overall.

**Discussion**

**Do the Gashaka chimpanzees prefer *D. rufescens* over other prey species?**

The Gashaka area was found to harbour three *Dorylus* species that are in general thought to be available as prey for chimpanzees. Our sampling efforts seem to have been sufficient, as the species accumulation curve was satisfactorily asymptotic and the maximum number of available army ant species estimated by several commonly used methods was either three or four.

The abundance of *D. gerstaeckeri* and *D. kohli* was extremely low compared with that of *D. rufescens*. Faecal sample analyses revealed the consumption of only *D. rufescens* by chimpanzees, a species not previously reported to be eaten by these apes at any other site. Because of the low availability of *D. kohli* and *D. gerstaeckeri*, it is difficult to conclude whether the Gashaka chimpanzees show a prey species preference or not. Nests of *D. gerstaeckeri* are attacked by chimpanzees at Bossou/Guinea (Humle & Matsuzawa, 2002) and Tai/Ivory Coast (Boesch & Boesch, 1990), but these sites harbour continuous rainforest. Both nest structure (and hence ease of detection) and colony density of *D. gerstaeckeri* may therefore differ substantially from the Gashaka site. Alternatively, our detailed sampling efforts did not cover the entire rainy season and might thus not have been comprehensive enough to reveal the true abundance and chimpanzee consumption of species much rarer than *D. rufescens*. Nevertheless, this study indicates that the other two potential prey species are of negligible importance as a food source for chimpanzees in this population.

**Why is *D. rufescens* prey not consumed more often when its availability is higher?**

*Dorylus rufescens* trails were by a factor of 3.6 more abundant on days with wet conditions. This reflects a response to more favourable weather as *Dorylus* workers are vulnerable to desiccation and are therefore likely to avoid venturing out into open areas under dry conditions. In fact, we never observed swarm raids in direct sunlight in open areas under dry weather conditions and a *D. rufescens* colony nesting in a savannah area close to the field station in January 2005 foraged only between dusk and about 10 AM. This may partly explain the rather low trail density in savannahs during daylight hours. A *de facto* higher colony density in forests may be the other relevant factor. *Dorylus nigricans* colonies occur at four times higher densities in gallery forests than in savannah (Leroux, 1982).

Intriguingly, *Dorylus* consumption as analysed from chimpanzee faeces did not vary with weather conditions and season. This finding suggests a two-pronged hypothesis, namely that (1) Gashaka chimpanzees do not harvest army ants from trails but mainly from nests and (2) they do not use trails to find nests.

The first part of the hypothesis is corroborated by the observation that ant-dipping tools have so far only been found directly at nests at Gashaka and never abandoned at active army ant trails (Fowler & Sommer, in press) and by the fact that chimpanzees have not been reported to collect army ants from trails without the use of tools at any study site. If the chimpanzees collected ants from trails, the *Dorylus* occurrence in faeces should be higher after days with wet weather conditions and thus higher in the rainy season. Although Hashimoto, Furuichi & Tashiro (2000) did not explicitly address seasonal patterns in army ant consumption in their study on ant-dipping by chimpanzees at Kalinzu/Uganda, their data suggest that the *Dorylus* occurrence in faeces is not higher in the rainy season there either (Hashimoto et al., 2000, fig. 1, p. 104). Hence, we expect that the Kalinzu chimpanzees do not harvest army ants from trails either, and, indeed, ant-dipping at trails has not yet been observed there (Hashimoto et al., 2000).

Conversely, we can predict that in populations where chimpanzees do harvest army ants from trails such as Bossou/Guinea (Humle & Matsuzawa, 2002) and the Ngotto Forest/Central African Republic (Hicks et al., 2005), the

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**Table 3** Nests of *Dorylus rufescens* army ants (*n* = 16), the major chimpanzee *Pan troglodytes vellerosus* insect prey species at Gashaka-Kwano/Nigeria: locations and conspicuousness

<table>
<thead>
<tr>
<th>Nest characteristic</th>
<th>% yes</th>
<th>% no</th>
<th>Fisher’s exact test, two-sided</th>
</tr>
</thead>
<tbody>
<tr>
<td>At base of tree?</td>
<td>56</td>
<td>44</td>
<td><em>P</em> = 1, NS</td>
</tr>
<tr>
<td>Indicated by conspicuous soil piles?</td>
<td>56</td>
<td>44</td>
<td><em>P</em> = 1, NS</td>
</tr>
<tr>
<td>Entrance hidden?</td>
<td>44</td>
<td>56</td>
<td><em>P</em> = 1, NS</td>
</tr>
</tbody>
</table>

NS, not significant.
occurrence of army ant prey fragments will be higher after days with wet weather conditions.

The second part of the hypothesis is supported by the finding that our attempts to follow trails as visual cues to locate ant nests turned out to be very time consuming and had a success rate of just 25%. Admittedly, chimpanzees might be better at this task, but it is unlikely that their success rates will be much higher when trails snake through dense undergrowth or under the surface of thick leaf litter. McGrew (1974) estimated that a chimpanzee can harvest 17–20 g of army ants during an average dipping session of 19 min. If locating nests takes similarly long as this dipping time – as was often the case in our searches – then the overall net energy gain would be rather low. Gashaka chimpanzees are therefore not likely to actively search for nests but to rely on chance findings. Nests are not visible from afar, but experienced foragers can detect them using soil piles resulting from nest excavation as cues. Because of the reproductive mode of colony fission (Raignier, 1972; Gotwald, 1995) and the lack of a distinct seasonal synchronization in reproduction in D. (Anomma) army ants (Raignier, van Boven & Ceusters, 1974; Leroux, 1982), the colony density is expected to stay much more constant throughout the year than diurnal trail density. Therefore, the lack of any specific chimpanzee search strategy would result in the rather constant pattern of consumption observed in this study.

Moreover, chimpanzees might rely on their spatial memory to check whether previously located nest sites are currently reused (cf. McGrew, 1974, for Gombe/Tanzania). We do not know the pattern of nest reuse of D. rufescens, but colonies resettled at previously used nest sites in half of all emigrations of D. nigricans (Leroux, 1982) and one-third of those of D. molestus (Schönning et al., 2005a). Such a search strategy would make the impractical searching for nests by following trails obsolete. It would be particularly advantageous because an active nest, once discovered by chimpanzees, cannot be exploited repeatedly over a longer nest stay duration because D. (Anomma) colonies usually emigrate to new nest sites after a predator attack (Schönning et al., 2005a; C. Boesch, pers. comm.; own obs., see above). The average stay duration of 5.9 days calculated for our site is similar to the average of 8 days for D. nigricans in a similar landscape in Ivory Coast (Leroux, 1982).

In common with many other chimpanzee research sites (e.g. Yamakoshi, 1998; Hashimoto, Furuichi & Tashiro, 2001; Basabose, 2002), seasonal variation in fruit abundance is considerable at Gashaka (Hohmann et al., in press). Army ant occurrence in faeces should therefore show a pronounced seasonal pattern if ants were a fallback food. However, there was no significant variation, demonstrating that this type of prey represents a quantitatively important food source throughout the year.

Why is the occurrence of army ant fragments in faeces so high at Gashaka?

The occurrence of army ants in faeces at Gashaka is considerably higher than at any other site for which data have been reported, including Assirik (2%; McGrew, 1992), Bwindi (1.8%; Stanford & Nkurunungi, 2003), Gombe (3%; McGrew, 1992), Kahuzi (less than 4%; Basabose, 2002) and Kalinzu (8.6%, Hashimoto et al., 2000). The nutritional content of army ant workers has not yet been examined, but it can be speculated that they may represent an important food source because of their protein content, mineral content, or vitamin B12 content (Harcourt & Harcourt, 1984), which is found only in food types of animal origin.

The frequency of mammal hunting by chimpanzees, while occurring at Gashaka (G. Hohmann et al., unpubl. data), is unknown. Termite remains have never been found in faecal samples (Fowler & Sommer, in press). The weaver ant O. longinoda, an important prey for chimpanzees at Lope/Gabon (Tutin et al., 1995), was not found at Gashaka. The termite-hunting ponerine ant P. analis – also consumed at Assirik/Senegal (McGrew et al., 1988) – seems difficult to harvest in significant quantities and was indeed rarely found in faeces at Gashaka. The fact that pupal cases were detected in two faecal samples points to the possibility that chimpanzees open nests to feed on the brood, swallowing adult workers (which can sting and have a rather obnoxious smell) only accidentally.

In any case, army ants constitute the vast majority of ant prey at Gashaka, and may thus represent a very important food source because other potential animal food types may be more difficult to get hold of at this site.

What are the implications of predation by chimpanzees for army ant nesting behaviour?

McGrew (1974) estimated that about 8775 army ant workers (equivalent to 17.6 g of army ants) are consumed by a single chimpanzee per dipping episode. Compared with an estimated average colony worker population of 6.5 million and an average colony fresh mass of 40 kg (Leroux, 1982), the numbers of workers lost through chimpanzee predation per attack seem negligible even if several chimpanzees harvest ant workers from the nest during an attack. However, attacks by predators also incur two presumably much more relevant costs. On the one hand, the queen could be damaged or killed when the nest is opened and when the dipping wands are inserted. Army ant colonies cannot replace a dead queen (Raignier, 1972), and the colony would perish in such a case. On the other hand, a chimpanzee attack often damages the structure of the nest so much that colonies emigrate to a new nest site afterwards and thus move more frequently than would be necessary because of food depletion around the nest. A higher emigration frequency may be disadvantageous because of the presumably costly excavation of a new nest and the rather high vulnerability of the queen to predation and accidents on the emigration trail. Therefore, predation by chimpanzee and other mammals may represent a significant selection pressure in the evolution of nest structure and defensive behaviour in Dorylus army ants. Future studies should examine how often individual Dorylus colonies are attacked and
whether this significantly increases their emigration frequency and mortality. Finally, one has to wonder why \textit{D. (Anomma)} colonies reuse older nests if this behaviour may give mammalian predators a cue to find them. The answer may be that colonies cannot distinguish older nests from other suitable nesting sites like mammal burrows or that avoiding laborious excavations is more important than the increase in the probability of being detected by the chimpanzee predators.

**Conclusion**

At Gashaka, chimpanzees feed on army ants more frequently than at any other chimpanzee research site. This prey type is an important food source throughout the year. It is inferred that the Gashaka chimpanzees do not collect army ants from trails and that they do not follow army ant trails to locate nests. Instead, chimpanzees may use their memory to revisit previous nest sites, which can be reoccupied by army ant colonies on a regular basis. Observations of habituated chimpanzees will be needed to clarify the exact cues used by these apes for locating army ant nests. Furthermore, detailed data on the taxonomy, abundance, behaviour and nutritional content of army ants at other sites will be needed to assess the importance of this prey type in chimpanzee feeding ecology and nutrition.

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