Prey spectra of two swarm-raiding army ant species in East Africa

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Dorylus molestus; Dorylus wilverthi; earthworms; Kibale; montane forest; Mount Kenya; polyphagy; predation.

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Abstract
Although swarm-raiding army ants are considered keystone predators in tropical forest ecosystems, information on the prey spectra of most species is based on anecdotal reports and not on systematic studies with extensive sampling. We analysed prey samples of 18 colonies of the two afrotropical species Dorylus (Anomma) molestus and Dorylus (Anomma) wilverthi (4289 prey items in total) to examine the prey composition variation within and between species and to determine the best methodology to obtain reliable prey spectrum estimates for a given species, site and season. Variation in prey composition was substantial for D. molestus even within a single site and season, with the biomass proportion of the most important prey type differing by a factor of 12. Conclusions from studies using small samples sizes may thus be misleading. We demonstrate that the method of assessing prey spectra in terms of relative prey item numbers often produces biased results, and therefore recommend relative prey biomass as the more useful parameter. The near absence of earthworms, which always constituted a substantial part of the D. molestus prey, in the diet of D. wilverthi is interpreted to result from subtle differences in swarm-raiding behaviour between these two species, but could alternatively also be due to low availability. Similar studies recording prey composition as biomass proportions and analysing large samples sizes from many colonies are needed to understand the effect of army ant swarm raids on invertebrate communities in afrotropical forests.

Introduction
Army ants are nomadic social predators that are considered keystone species in tropical forest ecosystems (Gotwald, 1995; Boswell, Britton & Franks, 1998). The raids of certain species can have a strong impact on prey populations (Otis et al., 1986; Vieira & Höfer, 1994) and are believed to contribute to the maintenance of arthropod diversity in tropical forests by creating a mosaic of patches in different stages of recovery (Franks & Bossert, 1983). Predation by army ants may constitute an important factor in the evolution of nesting behaviour (Longino, 2005) and other life-history traits of leaf-litter ants (Kaspari & O’Donnell, 2003).

While the majority of army ant species hunt in narrow columns, a few raid in broad conspicuous aboveground swarms (Gotwald, 1995). Swarm raiding is one of the most impressive examples of coordinated group activity shown by animals, with hundreds of thousands or even a few million ant workers forming a dense carpet that sweeps through areas of 1000 m² or more in a single day (Leroux, 1982; Franks et al., 1991). Any animal that is incapable of escaping the approaching swarm and lacks effective defensive mechanisms is captured, killed, dismembered (if necessary) and carried back to the nest. This type of foraging behaviour is also displayed by species not usually considered to be army ants (defined by the combination of the three traits obligate collective foraging, nomadism and highly specialized, i.e. ‘dichtadiiform’ queens; Brady, 2003). It has been reported for at least one Leptogenys species (subfamily Ponerinae; Maschwitz et al., 1989) as well as for Pheidologeton diversus and Pheidologeton silenus (subfamily Myrmicinae; Moffett, 1984, 1988). Swarm raids appear to be an efficient strategy to find and harvest abundant and evenly distributed small prey (such as solitary insects) as well as rare and very patchily distributed large prey (such as carcasses). As a consequence, swarm-raiding ants have highly diverse food spectra (Rettenmeyer et al., 1983; Moffett, 1987; Maschwitz et al., 1989; Gotwald, 1995).

What then determines the exact composition of food retrieved in swarm raids? The assemblages of available prey animals can differ between habitats and even on smaller spatial scales between patches visited during a single day’s raid due to habitat heterogeneity (Janzen & Schoener, 1968) and perhaps also due to differences in the time elapsed since the last army ant raid (Franks & Bossert, 1983). Moreover, the composition (as well as the biomass) of tropical forest
arthropod communities can vary between rainy and dry seasons (Denlinger, 1980; Franks, 1980; Frith & Frith, 1990; Burgess, Ponder & Goddard, 1999). This spatial and temporal variation in prey availability is likely to affect the prey spectra of swarm-raiding ants and, indeed, Franks (1980) found differences in the prey composition of Eciton burchellii on Barro Colorado Island (Panama) between the dry and rainy seasons. However, the actual prey composition could, on the other hand, also reflect differences in swarm-raiding behaviour between species, which may have evolved to allow some degree of prey specialization and thus reduce interspecific competition. Finally, the prey spectrum of a given species could also be influenced by seasonal differences in hunting behaviour resulting from environmental constraints such as low humidity and high temperatures (e.g. Meisel, 2006).

In view of the presumed ecological importance of the epigaeic swarm-raiding army ants in the African subgenus Dorylus (Anomma) (i.e. the fierce and famous ‘driver ants’, Savage, 1847) and the relevance of an animal’s diet as a significant life-history trait, it is surprising to note that our knowledge of the prey spectra of these ants is generally still very sparse. Several authors presented lists of prey types found to be retrieved during casual and unsystematic observations (Savage, 1847; Vosseler, 1905; Cohic, 1948). In the few systematic studies conducted, prey spectra were – like in most other studies on army ant food habits (e.g. Rettenmeyer et al., 1983; Powell & Franks, 2006) – recorded only in terms of relative prey numbers. If the mass of prey items retrieved by swarm-raiding ants varies widely, the results may be confounded by differences in item mass between prey types. Moreover, the sample sizes were low even in the most thorough analysis of Dorylus (Anomma) food habits (1357 prey items from 19 colonies at six sites in two countries; Gotwald, 1974a), making some of its conclusions doubtful. For example, the two species Dorylus nigricans and Dorylus gersteckeri were found to prey exclusively on earthworms in Ghanaian rainforest (Gotwald, 1974a), although D. gersteckeri is known to search for prey only in the leaf-litter whereas D. nigricans also climbs vegetation in search of prey (Gotwald, 1974b). It is hard to conceive that this fundamental difference in hunting behaviour would not result in substantial differences in their food spectra.

In the present study, we used prey samples that had been collected primarily for the purpose of examining food transport behaviour. The results concerning food transport will be presented elsewhere. Our aim here was to record the variation in item mass within prey samples and the variation in prey composition within and between sites, seasons and species so as to evaluate which sampling method can provide representative data on the prey composition of driver ant species. We found extensive within-species variation even within a single site and make suggestions for the most suitable sampling strategy. Our data also provide the first tentative evidence for subtle differences in hunting behaviour between the two study species.

### Study sites and methods

Observations and collections of Dorylus molestus Gerstäcker, 1858 (species status: Gotwald, 1974a) were made at two sites at the eastern slope of Mount Kenya, Kenya, between September 2001 and March 2002 and between January and March 2003. The first study site (0°14’S, 37°34’E, altitude 1850 m a.s.l., henceforth MtK1) is identical to the one used by Schöning, Njagi & Franks (2005). The vegetation is montane Ocotyle asamabarenensis (Lauraceae) forest. This area receives c. 2250 mm of rainfall mostly in the two rainy seasons from the end of March–May and from the end of October–December (Map 1 in Bussmann, 1994). Study site 2 (henceforth MtK2) was the area around the Meru Mount Kenya Lodge (0°09’S, 37°26’E, altitude 2950 m a.s.l.) and represents a mosaic of Hagenia abyssinica (Rosaceae)/Podocarpus spp. (Podocarpaceae) forest patches, bamboo Simarundaria alpina (Poaceae) patches and grassland. Rainfall at this altitude is lower (about 1500 mm, Bussmann, 1994) but also shows the same seasonality. The D. molestus colonies at this site literally exist at the distributional limit of the species as we found no colonies at higher altitudes at this side of the mountain.

Dorylus wilverthi Emery 1899 was studied in the Kibale Forest National Park at Kanyawara, Uganda (0°34’N 30°22’E, 1500 m a.s.l.). The vegetation is categorized as a moist evergreen forest, transitional between lowland rain forest and montane forest. The rainfall pattern is also bimodal; the two rainy seasons are from March to May and from September to November. The total annual rainfall averaged 1750 mm. A more detailed site description can be found in Chapman, Chapman & Gillespie (2002).

Food items were collected from open sections of foraging trails over the horizontal surface at a distance of 10–20 m away from the nest. The transporting ant worker or worker group and the transported food item passing a predetermined point were collected using forceps and placed in 0.5 or 1.5 mL vials filled with 70% ethanol depending on their sizes. Then, the next laden worker or group passing the collection point was taken and so forth until the sample size reached about 100 for the less abundant category.

Depending on prey item traffic flow and the relative numbers of singles and groups, these collections took between 3 and 6 h to complete. The area from which food items were retrieved during the sample-collection period may therefore have varied between 220 and 450 m² (assuming a swarm raid width of 10.3 m and a swarm raid speed of 7.2 m h⁻¹; Schöning et al., 2005) for D. molestus. The approximate area covered by D. wilverthi swarm raids during the collection periods could not be calculated due to insufficient data on swarm raid width but preliminary data suggest that it was larger than for D. molestus (C. Schöning, pers. obs.). The movements of all colonies were carefully monitored during the study periods and a given colony was only used once for the collection of a food sample.

For D. wilverthi, three samples (n_{total} = 729 items) were taken at Kibale during the dry season (July 2002). For D. molestus, nine food samples (n_{total} = 2148 items) were collected at MtK1 during the dry season (February–March 2002).
2002, March 2003) and three food samples (n_{total} = 616 items) were collected there during the rainy season season (April 2003). At MtK2, three samples (n_{total} = 796 items) were taken during the dry season (February 2002).

Later, in the laboratory, these prey items were identified, oven-dried for 48 h at 60 °C and then weighed using an R 200 D balance (Sartorius GmbH, Göttingen, Germany). The dry mass of the food item was considered to represent its biomass (see ‘Discussion’). Food items were only identified to high taxonomic levels (phylum, subphylum and, where appropriate, class, order and family), because identifying prey items that usually only constitute pieces of animals to the species level is extremely difficult and because distinguishing between lower taxa did not allow meaningful comparisons of the various sample categories. For comparisons of prey spectra, we included all those prey categories that accounted for at least 5% of the prey items or the biomass in any food sample. These categories were Annelida (earthworms), Arachnida (spider, mites, pseudoscorpions, ticks, etc.), CollemboLae, Crustacea (almost exclusively isopods), Insecta, Gastropoda (snails, slugs), Myriapoda (centipedes, millipedes) and seeds. All the remaining prey types were subsumed under ‘Others’. Some prey items could not be identified at all, because they constituted only small animal tissue fragments. These items were classified as ‘Unknown’. In order to allow comparisons with published data on food habits of other swarm-raiding ants, the prey items of insect origin were classified further into the four categories (1) Lepidoptera + Coleoptera; (2) other non-social insects; (3) ants; (4) other social insects.

We did not consider the retrieval of liquid prey by ant workers in their crops (Gotwald, 1974a) in this study, but this should not introduce any bias because the amount of nutrients gained from liquid prey is likely to be small in comparison with the amount of nutrients retrieved in the form of solid prey carried slung underneath the body and because the liquid prey originates from the same animals whose parts were sampled by collecting solid prey.

Prey item mass data were LN-transformed before statistical analysis to obtain normal distributions. We used Nested ANOVAs with colony nested within sample category to compare between prey mass between species, sites and seasons. The two-sided Student’s t-test was used to compare prey mass between items carried by groups and singles within samples. Because of unequal variances, the Mann–Whitney U-test was used to compare the proportions of prey types between sites, seasons and species. These statistical tests were performed using STATISTICA 6.0 (StatSoft Inc.). The relative numbers and biomass of different food types as well as the relative numbers and biomass of food items carried by singles and groups were calculated. For each sample, we compared the food item numbers actually recorded for each food category (observed frequency) with the numbers predicted from the biomass proportion of that particular food type (expected frequency) using the G-test. In order to ascertain that the lowest observed frequency was always ≥5 (Sokal & Rohlf, 1995, pp. 698 ff.), we had to pool the least frequent category with the next larger one in some cases (and sometimes repeat this procedure).

### Results

#### Prey item mass

Food item mass varied over more than three orders of magnitude, and this was also true within some samples (e.g. by a factor of 1802 in D. molestus colony C at MtK2, range 0.03–54.07 mg, Table 1). The range of prey item mass overlapped widely between those carried by groups and single porters (Table 1) and in two colonies the heaviest items were carried by singles. The items carried by groups were on average heavier than those carried by single workers in all colonies (t-test, t ≥ −3.42, P always < 0.01).

When between-colony variation was taken into account, dry season prey item mass did not differ between D. wilverthi and D. molestus at MtK1, but between D. wilverthi and D. molestus at MtK2 with D. wilverthi items being heavier (Nested ANOVA, P < 0.01). Moreover, prey item mass was lower in D. molestus samples collected at MtK2 than in D. molestus samples collected at MtK1 (P < 0.0001). However, when this last comparison was restricted to earthworm items, only colony but not site (P = 0.21) had a significant influence. Prey items recovered by D. molestus at MtK1 during the dry season were heavier than those retrieved during the rainy season (P < 0.01). When this comparison was again restricted to items of annelid origin, only colony but not season (P = 0.53) had a significant effect on annelid prey item mass.

#### Prey composition

The variation in prey composition within a given species, site and season was very pronounced. The largest number of samples had been collected at MtK1 during the dry season. Here, earthworms were the most important food type in terms of biomass, but their proportion ranged from 7.5 to 93.8%.

The dry season prey spectra of D. wilverthi and D. molestus at MtK1 differed significantly in their proportions (Mann–Whitney U-test; Annelida: U = 0, P = 0.013; Insecta: U = 0, P = 0.013; Gastropoda: U = 0, P = 0.013; Unknown: U = 2, P = 0.33). For D. wilverthi, insects constituted the most important prey type, while centipedes, millipedes and isopods were not found to be retrieved. There were only two earthworm pieces among the D. wilverthi prey. In contrast, earthworms were much more important for D. molestus at both sites and in both the dry and the rainy season (Table 2, Fig. 1). The dry season prey spectra of D. wilverthi and D. molestus at MtK2 differed significantly in their proportions (Mann–Whitney U-test; Annelida: U = 0, P = 0.0495; CollemboLae: U = 0, P = 0.0495; Crustacea: U = 0, P = 0.0495; Insecta: U = 0, P = 0.0495; Gastropoda: U = 0, P = 0.0495; Myriapoda: U = 0, P = 0.0495). Only the proportions of Arachnida differed significantly between the dry season D. molestus prey spectra at the two Mount Kenya sites (Mann–Whitney U-test; U = 1, P = 0.021). Only the proportions of CollemboLae differed significantly between the dry and rainy season prey spectra.
at the lower site (Mann–Whitney U-Test; $U = 0.0$, $P = 0.013$).

Workers and brood of social insects constituted a surprisingly low proportion (always <5%) of prey biomass in all samples (Table 3). Ants were rare, while social wasps or bees were not present in any food sample. *Odontotermes montanus* termite colonies are abundant at MtK1, but nests were never seen to be attacked and only two termite workers were found among the samples. A single direct observation of *D. molestus* workers attacking and retrieving foraging termite workers was made at this site during a separate study in October 2005 (D. Kronauer & C. Schöning, pers. obs.). The three *D. molestus* samples collected in the rainy season contained between 0.9 and 24.7% social insect biomass. Whole or pieces of *O. montanus* termite alates made up the bulk of this prey mass (mean dry mass of termite alate prey = 19.28 ± 12.36 mg, $n = 8$, range 1.32–36.17 mg). During the rainy season and especially in the first weeks after its start, *D. molestus* colonies at the lower study site have often been observed to transport many of these alates.

Measuring prey composition as percentage of item numbers versus percentage biomass

There were significant differences between the proportions of food types measured in relative numbers and in relative biomass in all but two of the 18 food samples (Table 2).

### Discussion

The key results of this study are the high variability in prey item mass, the high variability in prey composition even within a given study site and season, and the actual differences in the prey spectra of *D. wilverthi* and *D. molestus*. In the following, we first discuss possible explanations for these results and then highlight general implications for assessing the prey composition of swarm-raiding army ants.

The high variation in prey item mass found here is consistent with the results from an analysis of *D. wilverthi* food transport behaviour (Franks et al., 1999) and has to be considered when devising a sound sampling strategy.

We found significantly lower prey item masses during the rainy season as well as at MtK2. These results are unlikely to be linked to differences in worker size frequency distributions in the swarm but rather to prey density and the prey animal size frequency distributions. The reason is that earthworms were never carried whole but always disassembled and the earthworm pieces retrieved during the rainy season as well as those retrieved at MtK2 were not significantly lighter than those recovered by *D. molestus* colonies at MtK1 during the dry season. It is interesting to speculate that *D. molestus* colonies at the high-altitude study site have much less prey available per unit area because invertebrate abundance generally decreases with altitude (e.g. Tattersfield et al., 2001) and that these
colonies thus preyed to a larger extent on Collembola and other small animals because larger and more profitable prey was scarce.

The largest sample basis was available for *D. molestus* at the lower Mount Kenya site in the dry season. The variation in prey composition in these samples was surprisingly high even at the high taxonomic levels under consideration. This pronounced variation is even more remarkable when one takes into account that the samples apparently came from relatively large areas (see ‘Methods’), which should have reduced the effect of small-scale spatial variation. The observed variation might be due to larger scale habitat heterogeneity. Another intriguing possibility that also deserves further study is that the differences in prey composition reflect different stages of recovery of the invertebrate communities since the last army ant swarm raid. At MtK1, where nest stays even of non-reproductive colonies can last rather long (>3 weeks) and colony density is high relative to foraging range (Schönig *et al.*, 2005), areas of different stages of recovery are likely to form a complex mosaic and

### Table 2

| Prey group | Annelida | Arachnida | Collembola | Crustacea | Insecta | Gastropoda | Myriapoda | Seeds | Others | Unknown | G
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<tbody>
<tr>
<td><strong>D. wilverthi</strong> 1500 m a.s.l. dry season</td>
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<td>0</td>
<td>3.79</td>
<td>1.1NS</td>
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| **D. molestus** 1850 m a.s.l. dry season |
| B'         | 92.12    | 0.33      | 0          | 0.66      | 0.08    | 0          | 0.65      | 0     | 7.4    | 22.6*** | 49.3*** |
| F          | 87.72    | 0.35      | 0.35       | 0         | 5.61    | 3.86       | 0.35      | 0     | 2.1    | 1.33    |    |
| GA         | 31.98    | 2.85      | 1.24       | 0         | 34.31   | 6.16       | 18.93     | 0     | 4.7    | 22.6*** |    |
| KA         | 30.77    | 4.07      | 1.81       | 0.08      | 36.20   | 9.50       | 9.50      | 0     | 8.14   | 1.23    |    |
| L'         | 25.60    | 0.65      | 0          | 0         | 52.09   | 13.73      | 1.55      | 0     | 6.41   | 10.2*   | 63* |
| 28.92      | 1.61     | 0.46      | 0          | 0         | 42.57   | 16.87      | 1.61      | 0     | 8.04   |        |    |
| 79.00      | 0.46     | 0.46      | 0          | 0         | 7.31    | 9.13       | 0         | 0     | 4.11   |        |    |
| LA         | 74.80    | 0.13      | 1.10       | 0         | 11.89   | 1.52       | 10.36     | 0     | 0.27   | 13.3*** |    |
| OA         | 84.07    | 0.44      | 0.44       | 0         | 5.31    | 6.19       | 2.21      | 0     | 1.33   |        |    |
| QA         | 7.52     | 1.15      | 0.98       | 0         | 61.43   | 5.67       | 22.13     | 0     | 1.11   | 60.4*** |    |
| B          | 16.39    | 5.04      | 1.26       | 0.08      | 55.88   | 9.66       | 9.66      | 0     | 2.10   |        |    |
| C          | 39.82    | 0.69      | 0          | 0         | 3.31    | 1.30       | 0         | 0     | 0.89   | 3.36NS  |    |
| 91.56      | 0.42     | 0.42      | 0          | 0         | 3.38    | 2.53       | 0         | 0     | 2.17   |        |    |
| V          | 29.55    | 0.70      | 0          | 0         | 58.29   | 3.87       | 3.40      | 0.77  | 3.42   | 28.2*** |    |
| 40.20      | 1.31     | 0.46      | 0          | 0         | 42.36   | 3.06       | 5.24      | 0.87  | 6.99   |        |    |
| **D. molestus** 1850 m a.s.l. rainy season |
| E          | 38.24    | 8.24      | 0.10       | 0.12      | 48.17   | 0.11       | 1.22      | 0     | 0.55   | 23.4*** |    |
| 45.14      | 7.28     | 2.43      | 3.40       | 0         | 35.44   | 0.49       | 1.94      | 0     | 3.88   |        |    |
| G'         | 67.49    | 3.43      | 0.24       | 0.64      | 21.85   | 4.31       | 0.63      | 0     | 1.40   | 54.6*** |    |
| 54.33      | 3.37     | 7.21      | 1.92       | 0         | 23.07   | 4.81       | 0.96      | 0     | 4.33   |        |    |
| X          | 43.00    | 0.12      | 0.04       | 0.17      | 36.53   | 18.57      | 0.06      | 0     | 1.51   | 36.3*** |    |
| 53.96      | 0.50     | 0.50      | 0.99       | 0.99      | 17.33   | 24.26      | 0.50      | 0     | 1.98   |        |    |
| **D. molestus** 2950 m a.s.l. dry season |
| A          | 20.90    | 4.04      | 0.82       | 0.98      | 52.93   | 1.47       | 6.83      | 5.63  | 3.20   | 86.8*** |    |
| 12.36      | 7.11     | 13.11     | 0.37       | 0.47      | 48.69   | 0.75       | 4.87      | 3.37  | 1.87   | 7.49    |    |
| B          | 7.08     | 1.60      | 0.28       | 4.33      | 82.44   | 0.98       | 2.60      | 0     | 0.68   | 48.1*** |    |
| 8.87       | 4.44     | 5.24      | 5.24       | 0.40      | 70.16   | 0.40       | 2.02      | 0     | 0.36   |        |    |
| C          | 31.97    | 6.50      | 1.80       | 5.11      | 40.07   | 5.88       | 3.01      | 0     | 0.19   | 5.47   | 189.6*** |

Proportion of different prey groups as percentage of biomass (upper value) and percentage of item numbers (lower value).

G-test, NS, not significant.

*P < 0.05, ***P < 0.001.
colonies might therefore encounter very different communities of available prey animals even in the course of a single raid.

Given the large variation in prey spectra within the MtK1 site during the dry season, we feel that caution is warranted in the interpretation of the statistically significant differences found between the two Mount Kenya sites and the dry and the rainy seasons at MtK1. The prey item sample sizes examined for each of these sites and seasons are substantially larger than those of any previous study on *Dorylus* (*Anomma*) prey spectra, and yet it seems likely that these differences might not hold when samples are collected from more colonies and raids. On the other hand, other real differences might have gone unnoticed due to the small number of colonies examined.

The conspicuously low proportion of earthworms, which always represented a substantial amount of the *D. molestus* prey, in the food spectrum of *D. wilverthi* may result from a real difference in the hunting behaviour between the two species. Because earthworms are nearly ubiquitously present in afrotropical forest ecosystems (Fragoso & Lavelle, 1992; Edwards & Bohlen, 1996) and colonies of the coexisting species *Dorylus kohli* colonies were found to prey on them at Kibale (C. Schöning, pers. obs.), earthworms should in general be available as prey to *D. wilverthi*. It has been proposed that differences in the prey spectrum of army ant species reflect the use of different foraging strata (Rettenmeyer et al., 1983; Rościszewski & Maschwitz, 1994) and this could apply also to *D. wilverthi* and *D. molestus*. During *D. molestus* swarm raids, clusters of workers often stay behind when the main swarm has passed over an area and start digging. In many cases, earthworms later emerge from these tunnels trying to escape or are carried out of them in pieces. This behaviour has never been observed in *D. wilverthi* swarm raids. These direct observations of foraging behaviour together with the differences in food spectra indicate that *D. molestus* searches in the vegetation, on the ground surface and also intensely in the leaf-litter and top-soil layers, whereas *D. wilverthi* appears to restrict its hunting efforts to the ground surface and the vegetation where it encounters and captures mostly lepidopteran and coleopteran larvae. The higher advance speed of *D. wilverthi* swarm raids (25 m h\(^{-1}\); Raignier & van Boven, 1955) compared with that of *D. molestus* (mean 7.2 m h\(^{-1}\); Schöning et al., 2005) could be an important functional correlate of these differences in prey spectra. Faster swarms will probably be better at capturing larger and more agile prey, while they might be less able to search for and extract hidden prey from substrates like leaf-litter, soil or dead wood. However, because the *D. wilverthi* and *D. molestus* samples were collected at different sites, the hypothesis that the near absence of earthworms in the *D. wilverthi* diet is linked to differences in swarm raiding behaviour needs to be tested in future studies in which availability is determined.

![Figure 1](image_url) The relative biomass of different prey types for *Dorylus wilverthi* at Kibale (Uganda) and for *Dorylus molestus* at two sites at Mount Kenya (Kenya). The bars represent the mean, while the whiskers indicate the standard deviation.
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Table 3 Composition of insect prey for *Dorylus wilverthi* (Dw) at Kibale, Uganda and for *Dorylus molestus* (Dm) at two sites at Mount Kenya, Kenya

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<thead>
<tr>
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The upper value represents the percentage of a particular insect group among all insect prey (in % dry mass), while the lower value represents the percentage among all prey (also in % dry mass).

Compared with the neotropical swarm-raiding army ants *E. burchelli*, the afrotropical *D. wilverthi* and *D. molestus* retrieve much less social insect prey (Franks, 1980; see also Franks et al., 1999). The only exceptions are termite alates, which become seasonally important. The extremely low proportion of termite workers and soldiers in the diet of *D. wilverthi* and *D. molestus* supports the contention that this prey type is generally very rare in prey spectra of swarm-raiding *Dorylus* (Anomma) species (Schöning & Moffett, in press). Because *D. wilverthi* and *D. molestus* do not avoid raids on ants as the swarm-raiding *P. diversus* does (Moffett, 1987), the low percentage of ant prey may reflect the relatively lower abundance of ant colonies at our high-elevation study sites (≥1500 m a.s.l.) compared with those found in lowland rainforest in Central and South America from where prey composition data are available for *E. burchelli*.

Assessing the prey spectra of these species of swarm-raiding army ants by calculating the relative prey item numbers gave results different from those obtained when calculating the relative biomass proportions. Which method is preferable? It has to be emphasized that a food item’s dry mass as measured here is also not directly equivalent to its nutritional (i.e. energetic) value, because dry mass also includes for example, exoskeleton parts that are not consumed but later discarded onto a colony’s refuse pile. The accuracy of employing dry mass as an indicator of nutrient amount will probably vary with prey type. Dry mass is likely to be a very good indicator in animals consisting only of soft tissues such as Annelida, but be less suitable for heavily armoured invertebrates like isopods and some beetles. In spite of these possible discrepancies, the use of dry mass is to be preferred over item numbers when recording prey spectra. The reason is that prey item dry mass varies over three orders of magnitude. The bias resulting from potential differences in the proportion of exploitable dry mass between prey types is therefore much smaller than the bias introduced by giving items of vastly differing dry mass the same weight in the analysis. It is immediately obvious that a collembolan (dry mass about 0.09 mg) is of minimal nutritional value to a colony compared with an *O. montanus* alate (>30 mg dry mass). Recording prey spectra by using dry mass is a straightforward and quick method, if prey items are pooled for each category and not weighed individually as in this study.

Since our sampling strategy was devised with the primary aim of examining food transport behaviour, our data do not allow precise recommendations for determining prey composition, but it is clear that the number of prey items and colonies should be as high as possible for a given species, site and season and that a sample size as that gathered during the dry season at MtK1 would be highly desirable. Even larger sample sizes are likely to be necessary when prey composition is examined at lower taxonomic levels. More detailed insights into the diet of driver ant species, the influence of swarm raids on prey population dynamics and the link between swarm raiding behaviour and diet will only become possible when a large-scale sampling approach is also followed at other sites.

### Acknowledgements

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References


