

**Food spectrum and food transport by army ants:
a comparison of *Dorylus (Anomma) molestus*
and *D. (A.) wilverthi***



Fig. 1 *Dorylus (Anomma) molestus* workers retrieve food items on foraging trail.

Abstract

The African army ants *Dorylus molestus* and *D. wilverthi* both organize conspicuous massive epigaeic swarm raids in which they attack, kill, fragment and retrieve a wide range of animals. Annelids, molluscs, myriapods, and crustaceans comprise a substantial fraction of the prey of *D. molestus* colonies but are absent or nearly so in the prey of *D. wilverthi* colonies. These differences in food spectrum and direct observations of foraging behaviour indicate that the two species show subtle differences in foraging stratum use. While *D. molestus* searches in the vegetation, on the surface and intensely in the leaf-litter and top soil layers, *D. wilverthi* appears to restrict its hunting efforts to the vegetation and surface. In both species food items are carried slung longitudinally underneath the body by single workers or groups. Because *D. wilverthi* workers have on average 10.7% longer front legs and 13.9% longer hind legs than *D. molestus* workers for a given body dry mass over the common size range, the hypothesis was investigated that *D. wilverthi* workers transport more food dry mass per unit body dry mass. When comparing the transport of all food types together, *D. molestus* workers carried more food dry mass per unit worker dry mass, regardless of whether food items were carried alone or in groups. When transporting caterpillar pieces singles and groups of *D. molestus* carried the same food dry mass as *D. wilverthi* singles and groups respectively. The results indicate that the longer legs of *D. wilverthi* do not represent an adaptation for transporting relatively larger loads. Other possible selective advantages favouring longer legs in *D. wilverthi* are being discussed.

Introduction

Army ants are generally carnivorous and show different degrees of prey specialization (Gotwald 1995). The species hunting by swarm raids such as the neotropical *E. burchellii* and *Labidus coecus* or the afrotropical *Dorylus (Anomma) wilverthi* and *D. (A.) molestus* have a generalist diet (Gotwald 1995). It has been suggested that the prey spectrum of epigaeic swarm raiding *Dorylus (Anomma)* species (= driver ants) represents the relative abundance of available prey animals rather than preferences or specialization on the side of the predators (Gotwald 1974b). But despite their presumed ecological importance as key stone predators our knowledge of the diet of driver ants is rather sparse and based on very few systematic studies.

During their swarm raids prey animals are dismembered after capture if they are large relative to the ants and subsequently transported to the nest either by single workers or by groups of cooperating workers (Gotwald 1974b, Franks et al. 1999, Franks et al. 2001). It has been argued that colony foraging efficiency of polymorphic ant species in general can be increased through matching workers with prey items of corresponding size during food retrieval (Oster & Wilson 1978). However, the extent of this size-matching between ant and load size is very variable between and even within species, and this has led to doubts as to its functional significance in colony ergonomics (reviewed by Schmid-Hempel 1992). Load-size determination is a complex process (Röschard & Roces 2003). It is on the one hand influenced by the ant worker's selectivity which in turn depends on a variety of factors (e.g. colony state, Roces & Hölldobler 1994). But on the other hand load-size determination is constrained by the physical carrying capacity of the ant worker. Kaspari (1996) pointed out that size-matching can to some extent even occur in the absence of any selectivity simply because physical carrying capacity increases with ant size and thus a weak correlation may result because larger workers will on average transport larger items. He also emphasized that leaf-cutting ants and army ants can tailor their load and are therefore in a position to match their load size better to their individual carrying capacity in contrast to e.g. harvester ants which can usually only either pick a seed or ignore it (but see Schöning et al. 2004 for an exception). In leaf-cutting ants, workers anchor their hind legs at the leaf edge and pivot around their body axis while cutting, so that their reach limits the maximum area of the leaf piece they can retrieve (Lutz 1927, Wetterer 1991). In this case, hind leg length is directly a limiting factor for the foraging performance of workers and may thus be subject to selection for efficient foraging. In *Dorylus* army ants prey as well as brood is carried slung underneath the body (fig.1). This transport mode is perhaps the relic of a hypogaeic-life style which is

considered to be the ancestral state in this group (Gotwald 1978) and enables two or more ants to carry the same item with both ants facing and pulling in the same direction (Franks et al. 2001). In *Dorylus* army ants longer legs may therefore be selected for to allow transport of bulkier, hence heavier food items for a given worker mass.

Here, I describe and compare the food spectrum of *Dorylus molestus* at Mt Kenya and of *D. wilverthi* at Kibale in western Uganda, examine and compare the leg length allometries of both species and test the hypothesis that the longer-legged *D. wilverthi* workers carry more food dry mass per unit body dry mass.

Methods

Study organisms and study sites

The study was conducted at two sites. The observations on and collections of *Dorylus* (subgenus *Anomma*) *molestus* GERSTÄCKER (species status, Gotwald 1974b) reported here were made in the Forest Reserve at the eastern slope of Mt Kenya, Chogoria, central Kenya (0°14' S, 37°34' E) at an altitude of 1850m asl between September 2001 and March 2002 and between January and March 2003. The vegetation on the study site is montane *Ocotea usambarensis* forest, although the density of this tree is quite low due to selective timber harvest in the past. This area receives a total of about 2250 mm of rainfall mostly in the two rainy seasons from March to May and from October to December (Bussmann 1994, map 1). *Dorylus* (*A.*) *wilverthi* EMERY was studied in the Kibale Forest National Park at Kanyawara, western Uganda near the base of the Ruwenzori Mountains (0° 34' N 30° 22' E, 1500m asl). The vegetation is categorized as a moist evergreen forest, transitional between lowland rain forest and montane forest. Rainfall pattern is also bimodal, the two rainy seasons are from March to May and from September to November. Total annual rainfall averaged 1670 mm between 1977 and 1994 (Chapman et al. 1997)). Mean maximum temperature was 23.3°C, and mean minimum temperature 16.4°C in the same observation period (Chapman et al. 1997).

Leg length allometries

In order to examine within and between species variation in leg length allometries for *D. molestus* and *D. wilverthi* about 100 uninjured workers of all size classes were collected in 70% ethanol from the migration trails of three colonies each. Callow workers were excluded. Measurements were taken using a MS 5 Leica stereomicroscope fitted with an ocular micrometer. The maximum possible magnification to keep a structure within the range of the ocular micrometer was used (10 – 64x). Methods recommended by Seifert (2002) were used to minimise measurement errors. Three traits were measured: front leg length (FLL) – maximum length of left front leg from trochanter to tarsal claws in dorsal view with the leg fully extended; hind leg length (HLL) – maximum length of left hind leg from trochanter to tarsal claws in dorsal view with the leg fully extended; dry mass (WDM) – specimens were dried at 60°C for 48h and then weighed to the nearest 0.01mg using a R 200 D balance (Sartorius GmbH, Göttingen, Germany). All linear measurements are in mm, while DM is given in mg. The best fit model to describe the relationship between FLL (and HLL) and the cube root of WDM for all colonies from both species together was established through

stepwise multiple regression. Higher order polynomials were included only if all coefficients were significantly different from zero (Zar 1996; Fraser et al. 2000), and if the model did not predict negative FLL (or HLL) values over the considered size range. The relative residuals (absolute residual divided by predicted value) from this common regression model were then compared using the t-test and additionally a mixed model nested ANOVA with species as fixed factor and colony as random factor nested within species to test the relative importance of inter- vs. intraspecific differences in allometries. Moreover, best fitted models of FLL (and HLL) vs. $WDM^{1/3}$ were established for the separate *D. wilverthi* and *D. molestus* data sets and the ratio of predicted wilverthi FLL vs. molestus FLL was calculated over the common size range of 0.08 to 9.13 mg.

Food spectrum

Single workers and groups of workers transporting food items were collected in a standardized fashion from sections of foraging trails of medium traffic flow over horizontal surface at a distance of 10-20 m away from the nest. On trails of high traffic flow it is impossible to ascertain that all workers picked up with the food item had actually participated in carrying or simply responded to the disturbance by biting into the item or into another worker. The transporting worker or group and her/its food item passing a predetermined point were collected using forceps and killed and stored in 0.5ml or 1.5ml vials filled with 70% ethanol depending on their sizes. Then the next worker or group passing the collection point was taken and so forth until sample size reached about 100 for the less frequent category. Thus, these food samples allow analyses concerning the relative biomass proportions of food items of different origin, the proportions of items and biomass carried by singles and groups as well as the relationship between worker front leg and prey item biomass (for singles) and between worker dry mass and prey item biomass (for both singles and groups) for the respective colony. Later in the laboratory FLL and DM were measured for single porters (WDM) and group DM for transport groups (GDM). Food items were identified and their dry mass (FDM) measured as described above.

Two such samples were taken for *D. wilverthi* and three for *D. molestus* during the dry season. Additionally for *D. wilverthi* another dry season sample was gathered with food items only and for *D. molestus* three more with food items only were taken during the wet season. Therefore, the food spectrum sample basis is three each for *D. wilverthi* during the dry season, for *D. molestus* during the dry season and for *D. molestus* during the wet season.

The relative proportions of items and item biomass carried by singles and groups were calculated as well as the relative biomass proportion of different prey categories.

Load ratio during food retrieval

The hypothesis that longer legs yield the selective advantage of being able to carry more food mass per unit body mass was examined in several ways.

(1) The best fit model to describe the relationship between FDM and WDM for single porters of all five colonies from both species together was established through stepwise multiple regression according to the rules outlined above. The relative residuals from this common regression model were then compared between *D. wilverthi* and *D. molestus* using the t-test. If longer front legs were selected for by a requirement for higher load ratio, it is predicted that *molestus* workers should have lower relative residuals.

(2) The best fit model to describe the relationship between the cube root of FDM and FLL for single porters of all five colonies from both species together was established as described above. The relative residuals from this common regression model of both species were then compared using the t-test. If front leg length is the limiting factor for maximum load mass, it is predicted that the relative residuals do not differ between the two species.

(3) A large part of food biomass is transported by groups (see results), and therefore it is important to test whether longer legs may enable *D. wilverthi* groups to carry more food by unit body mass than *D. molestus* groups. The best fit model to describe the relationship between FDM and WDM for groups of all five colonies from both species together was established through stepwise multiple regression according to the rules outlined above. The relative residuals from this common regression model were then again compared using the t-test. If front leg length is the limiting factor for maximum load mass, it is expected that the relative residuals of *D. wilverthi* groups are higher than those of *D. molestus*.

(4) As it turned out in the analysis the food spectrum differs between the two species. In order to confirm that the conclusions from 1-3 were not confounded through a bias in the useable energy density of the respective major food sources tests 1 and 3 were re-run restricting the analysis to a category which was well represented in both species – lepidopteran larvae. Even though *D. wilverthi* and *D. molestus* may not prey on caterpillars of the same species it is assumed that the larvae from Mt Kenya and Kibale will be very similar not only in their general geometry but also in their relative energy density.

(5) If longer front legs are a limiting factor for food retrieval it is predicted that *D. molestus* workers with relatively longer legs carry on average more FDM than workers with shorter

legs. A best fit model was established to describe the relationship between FLL and $WDM^{1/3}$ for all *molestus* workers singly carrying earthworm pieces (this turned out to be the major food source in this species, see results). The relative residuals from this model were used to distinguish these workers into those with relatively shorter legs (relative residual < 0) and those with longer legs (relative residual > 0). Then a best fit model was established to describe the relationship between FDM and WDM of all workers together. The relative residuals of workers with shorter and longer legs workers were compared using the t-test.

(6) Test 5 was re-run on *D. wilverthi* workers singly carrying lepidopteran larvae as food items.

(7) Test 5 was re-run on *D. molestus* workers carrying brood items during migrations in the dry season (N=160 and 146 workers from two colonies). These had been collected in the same manner as the workers transporting food items.

(8) Because a considerable proportion of food dry mass was transported by groups in both species (see results), I additionally examined the hypothesis that longer legs may enable *D. wilverthi* workers to form groups that carry relatively more food dry mass than singles while in *D. molestus* groups and singles may carry the same food dry mass per unit body mass.

The correlation between WDM (and GDM respectively) and FDM was calculated using Spearman's R.

In general I used dry food mass as a higher load ratio of workers with longer legs can only translate into a selective advantage if more energy is retrieved per unit time to feed larvae in the nest and biomass should represent a better estimate of energy content than fresh mass. Of course, not all of the dry mass is nutritionally available as e.g. the exoskeletons are usually thrown out in litter piles. In order to ensure that food category specific proportions of usable biomass do not lead to wrong conclusions in the comparison between species, test (4) was conducted. There is another possibly confounding phenomenon. As *Dorylus* (Anomma) workers can carry liquid food in their crop (Gotwald 1974b), worker dry mass might not only reflect the workers body tissue dry mass but also include the dry mass of dissolved substances. However, this phenomenon has not yet been quantified in any species and preliminary observations show that the amount of mass of dissolved substances is small compared to the worker's body tissue dry mass. It is assumed that workers of both species engage in liquid food transport and that its effect can safely be neglected for the present purpose.

All statistical tests were performed using STATISTICA '99 Edition (StatSoft, Inc.).

Further observations and data are reported at the appropriate points in the discussion.

Results

Food spectrum

Table 1 summarizes the results on food spectrum. During the dry season *D. wilverthi* retrieves mostly food of insect origin, while *D. molestus* colonies predominantly prey on earthworms. When between colony variation is taken into account, the between species differences in relative biomass proportions during the dry season in insects, annelids and molluscs are all significant (Mann-Whitney U-test, in all three cases $p < 0.05$). Moreover, *D. molestus* also hunts centipedes, millipedes and isopods, prey animal groups which were never found to be carried on *D. wilverthi* trails. The differences between dry season and wet season food spectra of *D. molestus* are not significant when one considers between colony variation (Mann-Whitney U-test, $p > 0.27$ for all groups except “unidentified”). Social insects constitute a surprisingly low proportion of prey biomass. Only 0.5 - 2.7 % of the entire biomass retrieved by either species during the dry season belongs to this category. The three wet season *D. molestus* samples contained 20.4 % (Col. X), 3.0 % (Col. B') and 0.9 % (Col. E) social insect biomass. However, in the two former cases termite alates (*Odontotermes* sp.) represented more than 96 % of the social insect biomass. Ant brood was very rare in all prey samples both in terms of numbers as well as biomass.

On other occasions I saw *D. molestus* taking food types not included in these data. *D. molestus* often attacks fresh water crabs and sometimes succeed in overwhelming and finally dismembering them. On one occasion workers killed a young mouse at the study site. In another fortuitous instance workers attacked tadpoles that were lying stranded in a dried up pond. Workers removed the flesh of *Prunus* fruits lying on the ground at the end of the dry season 2003. Finally, workers from a colony in farmland were seen to be feeding on mango peels in a litter pit.

Leg length allometries

Fig. 2 and 3 show the relationships between $DM^{1/3}$ and FLL and HLL for *D. molestus* and *D. wilverthi*. *D. wilverthi* workers have both longer front ($t=16.87$, $df=609$, $p < 0.00001$) and hind legs ($t=15.47$, $df=609$, $p < 0.00001$). Both species (FLL: $df=1$, $F=13.96$, $p=0.02$; HLL: $df=1$, $F=21.61$, $p=0.01$) and colony (FLL: $df=4$, $F=23.47$, $p < 0.00001$; HLL: $df=4$, $F=11.87$, $p < 0.00001$) had a significant effect in the nested ANOVA. *D. wilverthi* workers have on average 10.7% longer front legs (ratio range over common size range 1.083 – 1.129) and 13.9% longer hind legs (ratio range 1.113 – 1.150) than *D. molestus* workers.

Table 1 Food spectrum for *D. wilverthi* (dry season) and *D. molestus* (dry and wet season).

Species	Dw	Dw	Dw	Dm	Dm	Dm	Dm	Dm	Dm	Dw	Dm	Dm
Season	dry	dry	dry	dry	dry	dry	wet	wet	wet	dry	dry	wet
Colony	G	CC	I	L'	KA	F	E	X	B'	all	all	all
N	264	235	230	220	252	221	206	202	209	729	693	617
% Singles	45.1	51.1	43.9	47.3	54.4	54.3	52.9	48.5	49.3	46.7	52	50.2
% Groups	54.9	48.9	56.1	52.7	45.6	45.7	47.1	51.5	50.7	53.3	48	49.8
Biomass (mg)	1175.14	884.24	764.53	768.3	882.21	876.9	591.68	505.28	574.94	-	-	-
% biomass singles	27.7	30.1	30.3	26.6	37.1	36.9	41.1	23.3	25.8	29.4	33.5	30.1
% biomass groups	72.3	69.9	69.7	73.4	62.9	63.1	58.9	76.7	74.2	70.6	66.5	69.9
% biomass by prey group												
Insecta	93.2	95.9	85.7	6.7	52.1	34.3	48.1	36.3	22.1	91.6	31	35.5
Annelida	0	0.3	0	84	25.1	32	38.5	43	67.5	0.1	47	49.7
Mollusca	0.3	0	0.3	6.6	13.7	6.1	0	18.8	4.3	0.2	8.8	7.7
Myriapoda	0	0	0	0	1.5	18.9	1.8	0.1	0.6	0	6.8	0.8
Chelicerata	4.7	2.2	0	0.4	0.6	2.8	8.2	0.1	3.4	2.3	1.3	3.9
Crustacea	0	0	0	0	0	1.1	1.8	0.1	0.6	0	0.4	0.8
Plant seeds	0	0.3	0	0	0	0	0	0	0	0.1	0	0
Unidentified	1.9	1.2	14	2.2	6.4	4.7	1.5	1.5	1.4	5.7	4.4	1.5

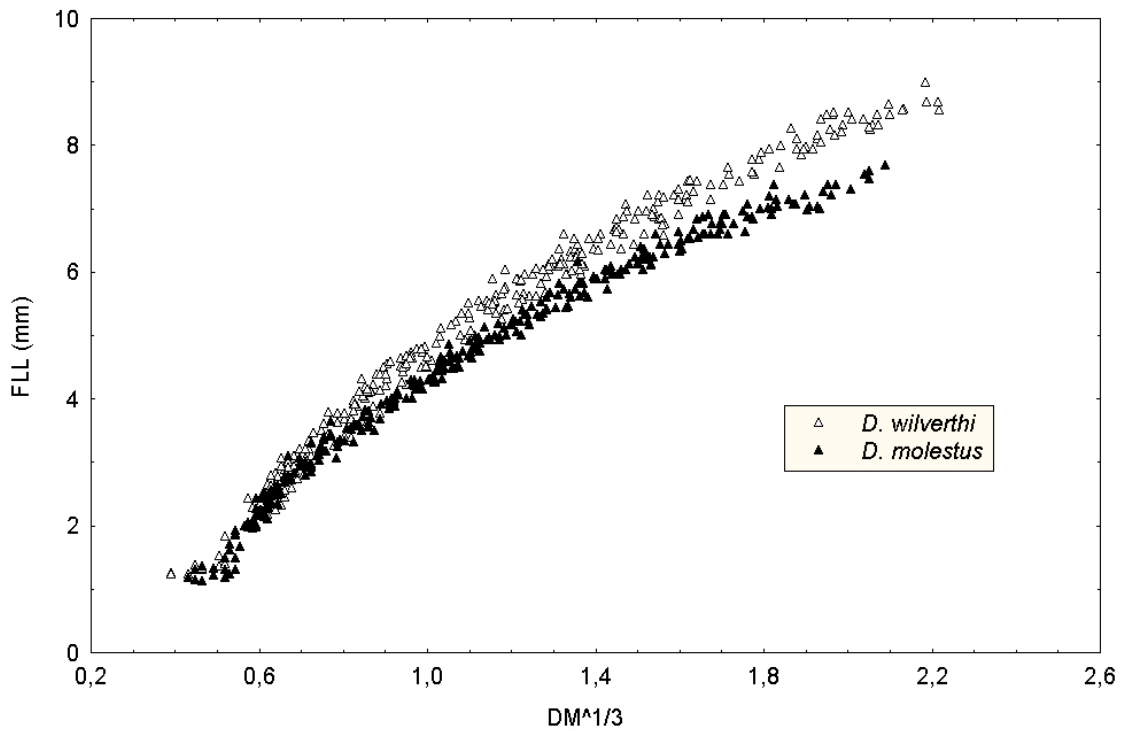


Fig. 2 Front leg length allometry of *D. wilverthi* and *D. molestus*.

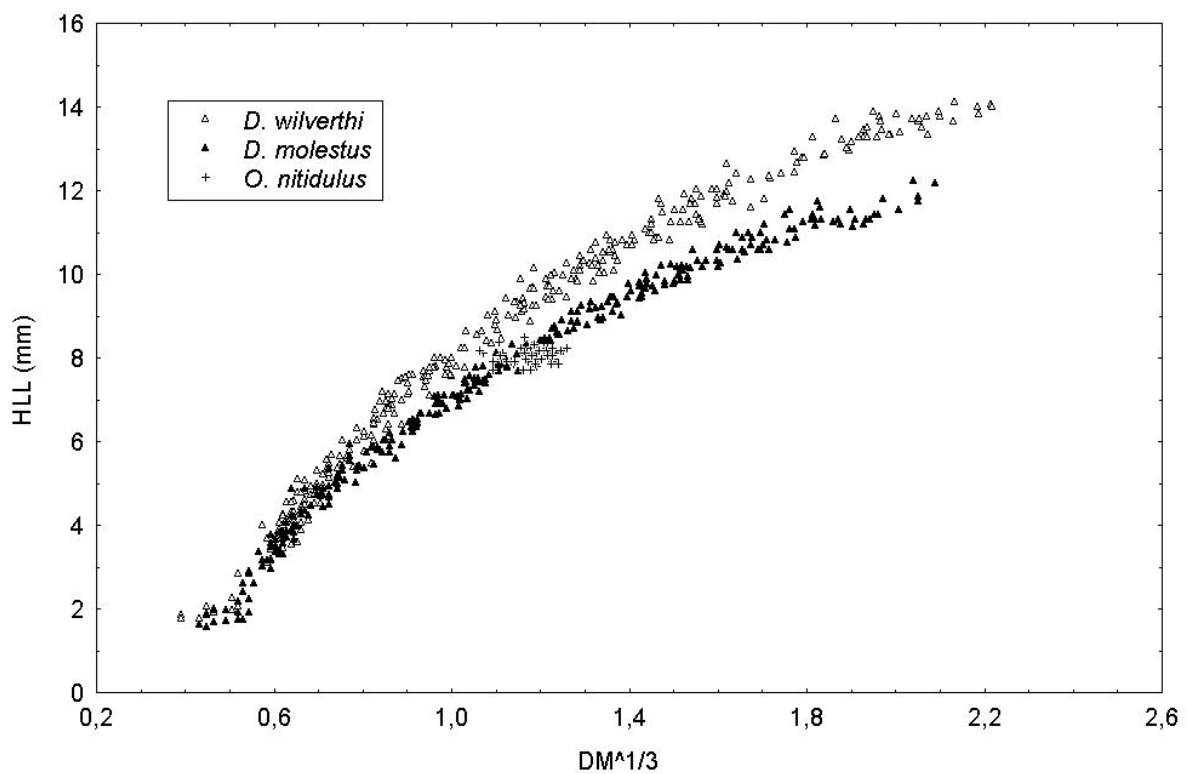


Fig. 3 Hind leg length allometry of *D. wilverthi* and *D. molestus*. For comparison data of the fast-running desert ant *Ocymyrmex nitidulus* are shown.

Load ratio during food retrieval

Single porters of *D. molestus* carry on average more FDM than *D. wilverthi* workers (test 1, $t=-3.37$, $df=576$, $p=0.0008$). Single porters of *D. molestus* carry more FDM for a given front leg length (test 2, $t=-7.37$, $df=576$, $p<0.000001$). *D. molestus* groups carry more FDM than *D. wilverthi* groups (test 3, $t=-2.35$, $df=603$, $p=0.02$). Singles of both species carry relatively the same FDM when transporting lepidopteran larvae (test 4, $t=-0.51$, $df=141$, $p=0.61$). Groups of both species carry relatively the same FDM when transporting pieces of lepidopteran larvae (test 4, $t=-1.02$, $df=221$, $p=0.31$). During transport of earthworm pieces the relatively longer legged *D. molestus* workers did not carry more FDM than the shorter legged ones (test 5, $t=0.6$, $df=121$, $p=0.96$). During transport of caterpillar pieces single *D. wilverthi* workers with longer legs did not carry more FDM than the shorter legged ones (test 5, $t=0.07$, $df=108$, $p=0.95$). Longer legged *D. molestus* workers do not carry heavier brood items during migrations than those with shorter legs (test 7, $t=-1.66$, $df=303$, $p=0.10$). In the *D. wilverthi* colonies groups did on average not carry more FDM than singles (Col. I, $t=1.669$, $df=228$, $p=0.10$; Col. G, $t=1.02$, $df=262$, $p=0.31$). In the *D. molestus* colony KA groups carried more FDM than singles ($t=3.51$, $df=247$, $p<0.001$), while groups and singles carried on average the

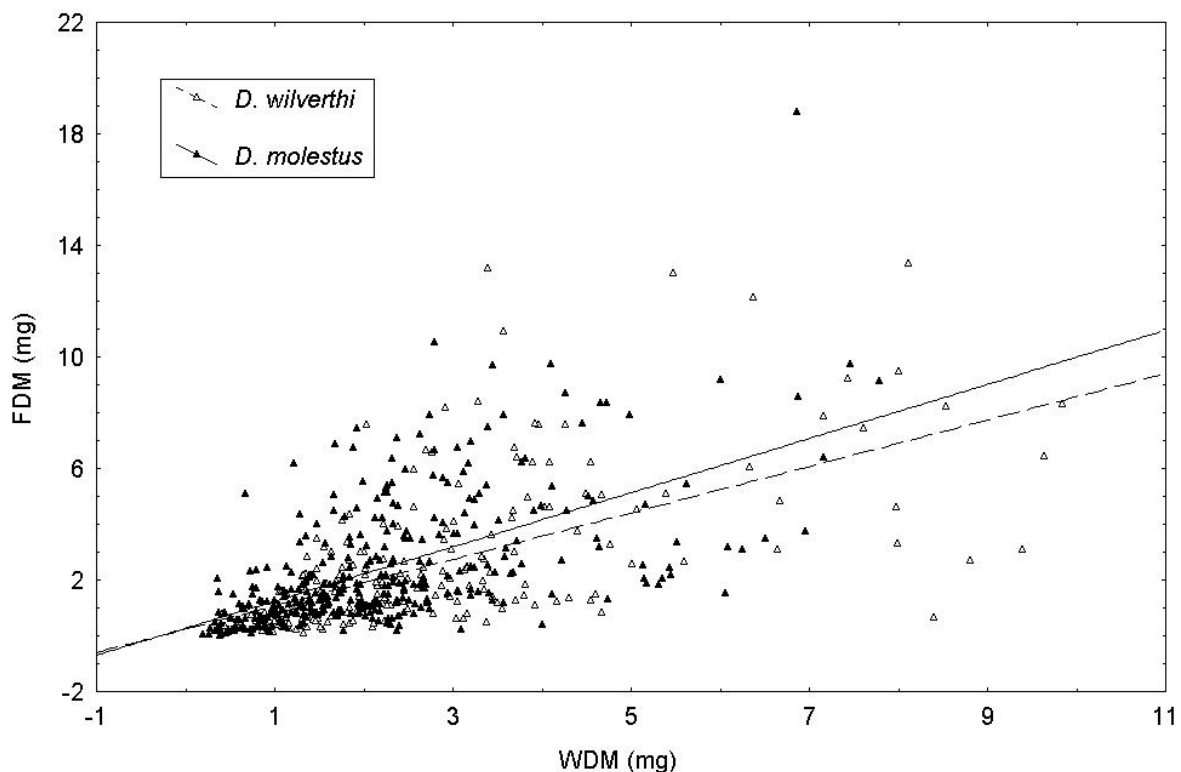


Fig. 4 Relationship between food item dry mass (FDM) and single worker dry mass (WDM) for *D. wilverthi* and *D. molestus*. Best fit least squares regression models: $FDM=0.238+0.834 \cdot WDM$ (*D. wilverthi*); $FDM=0.273+0.972 \cdot WDM$ (*D. molestus*).

same FDM in the two other *D. molestus* colonies (Col. F, $t=0.64$, $df=218$, $p=0.52$, Col. L', $t=-1.16$, $df=217$, 0.25).

The correlation between FDM and WDM (i.e. the extent of size-matching) was generally fairly low (Spearman's $R=0.67$, $p<0.000001$, $N=220$ for all single *D. wilverthi* workers combined; Spearman's $R=0.65$, $p<0.000001$, $N=358$ for all single *D. molestus* workers combined; Spearman's $R=0.70$, $p<0.000001$, $N=274$ for all *D. wilverthi* groups combined; Spearman's $R=0.64$, $p<0.000001$, $N=331$ for all *D. molestus* groups combined).

If fresh mass is the decisive factor in load size determination, a higher FDM vs. WDM correlation would be expected when restricting the analysis to single food categories which should have a more uniform water content. However, the correlation between FDM and WDM is also weak for single *D. molestus* workers carrying earthworm pieces (Spearman's $R=0.62$, $N=123$, $p<0.00001$), single *D. wilverthi* workers carrying caterpillar pieces (Spearman's $R=0.65$, $N=110$, $p<0.00001$) alone, *D. molestus* groups carrying earthworm pieces (Spearman's $R=0.71$, $p<0.000001$, $N=192$) and *D. wilverthi* groups carrying caterpillar

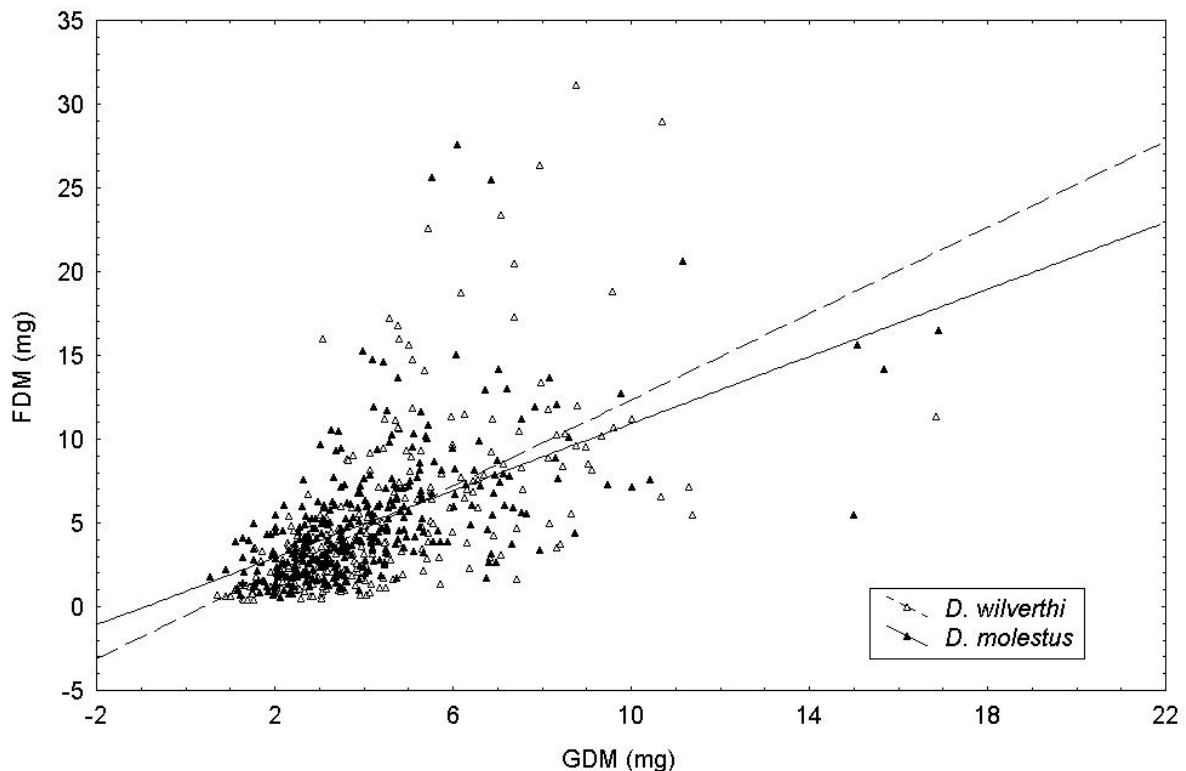


Fig. 5 Relationship between food item dry mass (FDM) and group dry mass (GDM) for *D. wilverthi* and *D. molestus*. Best fit least squares regression models: $FDM=0.536+1.287 \cdot GDM$ (*D. wilverthi*); $FDM=0.912+1.002 \cdot GDM$ (*D. molestus*).

pieces (Spearman's $R=0.67$, $p<0.000001$, $N=198$) when compared to the correlation between brood item dry mass and WDM in *D. molestus* workers transporting larvae and pupae during migrations (Spearman's $R=0.91$, $N=305$, $p<0.000001$).

Discussion

Food spectrum

In general, prey of vegetable origin represents a minute proportion in the food spectrum of both species. Although both species can certainly easily kill large animals in confinement (such as crocodiles or monkeys, Gotwald 1995, Mayr 1910), these will under normal conditions easily run off when the swarm raid approaches. However, accidental discoveries of carcasses or swarming termite alates may play a significant role in the feeding ecology of driver ants.

There are distinct differences between the dry season prey spectra of *D. wilverthi* and *D. molestus*. Gotwald (1974b) examined the prey spectra of three *Dorylus* (*Anomma*) species at several sites in Ghana, Nigeria and Kenya. Because prey spectrum varied with habitat even for a given species, he concluded that observed differences in prey spectra reflect habitat specific prey animal communities rather than preferences on the side of the predator species. *Dorylus* (*Anomma*) species are remarkably flexible in their habitat requirements. In Kenya *D. molestus* shows a distribution from 0 up to 3000m asl, thus occupying habitats as diverse as riverine woodland in semi-arid areas, home gardens, montane forest, bamboo forest and grassland (C.S. unpublished data). Thus, habitat related differences in food spectrum are certainly to be expected, but between species differences could also be caused by other factors. As earthworms also occur in Kibale Forest, their near absence in *D. wilverthi*'s prey spectrum can be better explained by species specific foraging stratum use. Within the genus *Dorylus* species certainly differ in their foraging stratum use. Species of the subgenera *Alaopone*, *Dichtadia*, *Dorylus* s.str., *Rhogmus* and *Typhlopone* hunt in the soil and only rarely if ever appear on the surface under normal circumstances ("hypogaeic"). The foraging stratum use by species of the subgenus *Anomma* is more complex. While several species such as *D. gerstäckeri*, *D. kohli* and *D. emeryi* hunt in the leaf-litter but never climb vegetation (Gotwald 1974a, Raignier & van Boven 1955, pers. observation), the typical "driver ants" such as *D. wilverthi* and *D. molestus* conspicuously forage on the surface and climb vegetation in search of prey ("epigaeic"). The findings reported here indicate that even within the epigaeic category there are subtle differences in foraging stratum use. During swarm raids workers of *D. molestus* clusters of workers stay behind here and there and start digging. In many cases earthworms later come moving out of these tunnels and try to escape but are pinned down by large workers who then proceed to fragment them. Sometimes the area over which the swarm raid proceeded looks afterwards as if the workers had ploughed through it. It is unclear which cues the workers follow when deciding to dig, yet this behaviour, which has never been seen

in *D. wilverthi* swarm raids, shows that *D. molestus* also searches intensely in the leaf litter and in the upper soil layer. *D. molestus* colonies therefore use a wider stratum than *D. wilverthi* colonies. The ultimate cause for the fact that *D. wilverthi* uses a narrower foraging stratum may be competitive exclusion by Anomma species with intermediate foraging mode from the leaf-litter and top soil layers. At Kibale *D. wilverthi* coexists with two such species, *D. emeryi* and *D. opacus*, and at Yangambi (Democratic Republic Congo) where earthworms are also lacking in its food spectrum with *D. kohli* and *D. opacus* (Raignier and van Boven 1955). In contrast, no other Anomma species were found at Mt Kenya. It would be interesting to investigate the food spectrum and foraging stratum use of *D. molestus* at sites where it coexists with intermediate species to determine how flexible foraging stratum use and food spectrum of Anomma species are.

The coarse dry and wet season food spectra of *D. molestus* do not differ in the montane forest at Mt Kenya. In general such differences could be caused by seasonal changes in the relative abundances of different prey animal groups as have been found by Burgess et al. (1999) or by humidity, temperature and soil pliability dependent foraging stratum use. On the study site at Mt Kenya there are several smaller streams and temperature as well as relative humidity remain remarkably constant throughout rainy and dry seasons in areas with closed canopy (C.S. unpublished data). On the other hand, at a finer taxonomic level seasonal differences become evident. For example, termite alates (*Odontotermes* sp.) are only available during the wet season and consequently appear only during this time in the prey spectrum.

Leg length allometries and their relationship with foraging performance

Hind and front leg length allometries differed between colonies and species as should be expected for adaptive colony traits. If longer legs are selected for due to a requirement for higher load ratio during food transport, workers with longer legs should retrieve more food dry mass in the interspecific as well as the intraspecific comparisons. To illustrate this point one can for simplicity assume that workers of both species transport items of the same material and of cylindrical form. If they carry cylinders of a given length, then the mass of these will be determined directly by their cross-sectional area. The cross-sectional area underneath a *D. wilverthi* worker will be larger than that underneath a *D. molestus* worker. If one thinks of the front legs forming a half circle with a circumference $U = 4 \cdot \text{front leg length (FLL)}$ and of the cylinder as having a radius of r , then r will scale with FLL in a linear way, because $r = \text{FLL} / \pi$. However, in contrast to r , the cross-sectional area will not scale in a linear way but quadruple when FLL is doubled. So as a *D. wilverthi* worker of a given dry

mass has 10.7% longer front legs, she can theoretically accommodate items 1.23 times as heavy as a items a *D. molestus* worker of the same dry mass can carry all else being equal. But I did not find that *D. wilverthi* workers were carrying relatively more food dry mass. In fact, the shorter legged *D. molestus* workers were carrying more food dry mass regardless of whether food items were transported alone or in groups when all prey groups were considered together. It is obvious that not all else was equal. The food spectra of the two species differed. Besides animals retrieved by both species *D. molestus* preys on animals that probably have a lower dry mass / wet mass ratio (earthworms) and also on others that probably have a higher dry mass / wet mass ratio (millipedes). When *D. molestus* and *D. wilverthi* workers carrying caterpillar pieces were compared, both carried relatively the same. Therefore it seems possible that the differences in prey spectrum may have caused the effect that *D. molestus* transported generally more. In any case, no evidence supporting the hypothesis that *D. wilverthi* workers carry relatively larger loads during food transport was found. Size-matching between food dry mass and worker dry mass during food transport was lower compared to the correlation between brood item dry mass and worker dry mass in *D. molestus* workers transporting larvae and pupae during migrations. The proportion of workers returning to the nest laden with food items is low (6-22%, mean 14% in *D. wilverthi* at Yangambi, Raignier & van Boven 1955). Together these phenomena suggest that individual workers as well as groups probably do not and should not tax their maximum transport capacity. If ample potentially assisting workers are available as on the foraging trail, then it may be more important to ensure on the one hand that items do not have to be fragmented too many times (as this increases handling time) and on the other hand that they are carried smoothly within the general traffic flow rather than to match workers with food items of tightly corresponding size. However, when the number of items to be carried is large as during migrations then workers should pick items as to make better use their transport capacity to move the entire load more efficiently and quickly. However, even during brood transport longer-legged *D. molestus* workers did not carry relatively heavier items. Therefore front leg length does not seem to be the limiting factor for the maximum dry mass of transportable food items neither in *D. wilverthi* nor in *D. molestus* workers. A requirement for transporting relatively larger loads can therefore be ruled out as the factor that has selected for longer legs in *D. wilverthi*. Food retrieval speed was not investigated in this study. It is therefore possible that longer the legged *D. wilverthi* workers achieve a higher food transport rate (as in mass times distance per unit time). But it is nevertheless clear that this would only be possible if *D. wilverthi* workers run faster.

The fact that longer legs do not yield an advantage in relation to the load ratio during food transport in the present analysis does not necessarily mean that the requirement for a higher load ratio has not at all acted as an important selection pressure in the evolution of *Dorylus* worker morphology. Species with hypogaeic and intermediate life-style have much shorter front legs (Chapter I) and in the course of the ecological niche shifts longer legs prey spectrum expansion may have necessitated the transport of more food dry mass per unit worker dry mass. Yet on the scale considered here (within epigaeic species) longer legs do not yield an advantage with respect to the load ratio.

Other possible selective advantages of longer legs

Longer legged ant species may be able to run faster (e.g. Wehner 1983). Even when compared to the extremely fast desert ant *Ocymyrmex nitidulus* (see figure 3) the two studied driver ant species have very long legs, but on the other hand run curiously slowly on the foraging trail in comparison with other army ants such as *E. burchelli* (Franks et al. 1999). So the long legs of these driver ants must certainly confer another selective advantage. Average foraging range is larger in *D. wilverthi* (C.S. unpublished data), and it is conceivable that longer legs allow more energy-efficient locomotion (Casey 1992), yet this has not been examined in any ant group so far.

Moreover, it is possible that longer legs are associated with the use of higher foraging strata. In particular, the ability to climb vegetation may be related to relative leg length. Federle et al. (1997) found that larger and longer legged species were better able to run on the slippery twigs of *Macaranga pruinosa* (Euphorbiaceae). If this is a general phenomenon not restricted to the rather special case of certain *Macaranga* species, then longer legs may represent an adaptation for climbing vegetation. More detailed studies are needed, these should also include the comparison of species with different foraging stratum use in the army ant genera *Eciton* and *Aencitus* (Rettenmeyer et. al. 1980, Rosciszewski and Maschwitz 1994, Hirose et al. 2000).