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Influence of the hypogaecic army ant *Dorylus (Dichthadia) laevigatus* on tropical arthropod communities

Received: 18 September 2002 / Accepted: 16 December 2002 / Published online: 11 February 2003
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Abstract The majority of army ant species forage hypogaecally. Due to the difficulties in observing these ants, their potential influence on hypogaecic and epigaecic arthropod communities has not yet been investigated. As the first hypogaecally foraging army ant studied in detail, we attracted *Dorylus laevigatus* to areas monitored for their arthropod diversity. Here, for the first time, the same sites were sampled before and after an army ant raid. Furthermore, interactions between *D. laevigatus* and the five most common ground-nesting ant species were noted and their life-history traits compared, allowing first inferences on possible mechanisms of their coexistence. The occurrence of *D. laevigatus* within a study plot had no evident effect on the number of arthropod taxa or individuals collected with epigaecic and hypogaecic pitfall traps. Likewise, juvenile arthropods, which are less mobile and thus are potentially easier prey for *D. laevigatus*, showed no differences in their collected numbers before and after the army ant had visited a plot. However, significantly fewer ant species were collected with hypogaecic traps after *D. laevigatus* had been within the study plots, indicating a possible predation of *D. laevigatus* especially on two *Pseudolasius* and one *Pheidole* species. The five most common ground-foraging ant species demonstrated their ability to avoid, kill, and even prey on the army ant. The reaction of *Lophomyrmex bedoti* towards *D. laevigatus* indicated the former to be a potential prey species, while *Pachycondyla* sp. 2 showed signs of “enemy specification.” *Odontoponera diversus* and *O. transversa* actively preyed on *D. laevigatus*, while *Pheidologeton affinis* fought with *D. laevigatus* over resources. All ant species could co-occur with *D.*

laevigatus at palm oil baits. Adding to the differences detected in previous studies between *D. laevigatus* and epigaecally foraging army ant species, the occurrence of this hypogaecic army ant seems to have less devastating effects on arthropod community compositions than those of epigaecically mass raiding species.

Keywords Interspecific interactions · Foraging · Arthropod community · Borneo

Introduction

The ability to conduct highly organized mass raids, which can take the form of a column or swarm (Schneirla 1934), is one of the most characteristic traits of army ants (Gotwald 1982). Within a day's raid, an army ant colony can remove large amounts of booty, e.g., 40 g of dry animal matter may be harvested by an *Eciton burchelli* colony (Franks 1982a) or 90,000 insects by an *E. hamatum* colony (Rettenmeyer et al. 1980). Because they can remove such large amounts of animal matter, army ants represent the top predators of leaf litter arthropods and even of small vertebrates in some areas (Brosset 1988; Roberts et al. 2000). A raid can temporarily reduce the overall arthropod abundance and the diversity of taxa in the leaf litter (Otis et al. 1986). Areas raided by *E. burchelli* were found to contain a substantial number of patches in different states of recovery (Franks and Bossert 1983). In this way, army ants are presumed to prevent the establishment of climax communities and thus to enhance arthropod diversity (Gotwald 1995).

Due to their easier accessibility, most studies have concentrated on epigaecally active army ant species. However, the majority of species forage hypogaecally (Gotwald 1982). These species prey at least to some extent on soil-structuring animals such as termites, ants, and earthworms (e.g., Gotwald 1974a, 1974b, 1978; Darlington 1985; Berghoff et al. 2002a). Despite their potential importance for soil communities, the influence of hypogaecic army ant species on soil faunas has not yet

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been investigated. This lack of studies is due to their foraging being concealed and, at least partially, to the hard-to-predict foraging movements of hypogaeic ants. Epigaeically active army ants continuously alter the direction of their raids and eventually move to new foraging areas (Gotwald 1995). Although the direction of a swarm can be influenced over short distances by offering food (Witte and Maschwitz 2000), it seemed improbable to draw these ants to a certain area other than by chance. Being the first hypogaeic army ant studied in detail, *Dorylus (Dichthadia) laevigatus* was shown to recruit to palm oil baits in large numbers, locating the majority of baits within short periods of time (Berghoff et al. 2002a). This difference in bait utilization from epigaeically active species was linked to differences in foraging and raiding strategies, which included the long-term exploitation of bulky food sources and the establishment of stable trail systems (Berghoff et al. 2002a). The foraging peculiarities enabled us to draw *D. laevigatus* to census areas and thus to study the impact of a hypogaeic army ant on the soil and ground arthropod fauna. The arthropod diversity was monitored in census areas before and after *D. laevigatus*, which has a broad diet (Weissflog et al. 2000; Berghoff et al. 2002a), was attracted to the areas. The effects of army ant raids are often especially visible in ground ant communities, exhibiting reduced species and colony numbers in raided areas (Franks 1982a; Perfecto 1992; Hirosawa et al. 2000). Because of this, we analyzed the recorded ant communities in more detail, comparing species and individual numbers before and after *D. laevigatus* had visited the areas. Furthermore, we report on the interactions between *D. laevigatus* and the five most common ground-foraging ant species, indicating possible mechanisms of coexistence.

Materials and methods

Study sites

The study was conducted in the Kinabalu National Park and surrounding areas at Poring Hot Springs (Sabah, Malaysia, Borneo; 6°5' N 116°3' E). Data were collected between March and August 2000, March and May 2001, and March and May 2002. Study plots ($n=7$) were established in different habitats to evaluate the occurrence and abundance of *Dorylus (Dichthadia) laevigatus* and other ground-foraging ant species. Habitats included a meadow, young and old secondary forests, primary lowland, and lower montane rainforest (for details on study plot data, see Berghoff et al. 2002a). Long-term study plots were established during the first study period and were reactivated during the following two years. Studies on short-term study plots were restricted to a single study period.

Baits

On all study plots, ants were baited using sieve buckets buried in the ground. Each bucket held one liter of soil and was baited with 50 ml palm oil (for a detailed description of the method, see Berghoff et al. 2002a). Ants were able to access the baits either from the soil surface or through the surrounding soil. In this way,

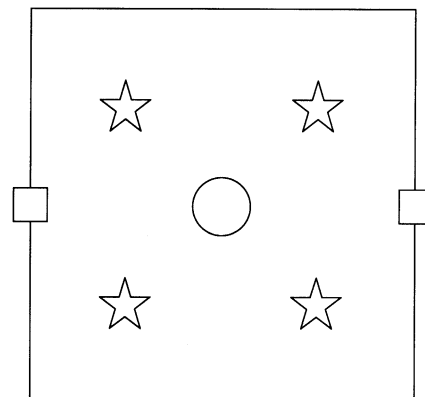


Fig. 1 Trap arrangement in each of twelve 1-m² census areas (squares) to which *Dorylus (Dichthadia) laevigatus* was attracted. Circles Sieve bucket, stars epigaeic pitfall traps, squares hypogaeic pitfall traps

epigaeically as well as hypogaeically foraging ants could be recorded during the regular bait checks. During each bait check, the sieve buckets were removed from the ground and the occurrence, abundance, and location of all ant species were recorded. Abundance was visually estimated and assigned to one of five classes: (1) 1–10; (2) 11–100; (3) 100–1,000; (4) 1,000–5,000; and (5) >5,000 ants. Samples of occurring ant species were collected, preserved in 75% ethanol, and later identified with the key of Bolton (1994). Species were compared to the reference collection of the University of Würzburg, and unidentified species were assigned morphospecies numbers. Voucher specimens were included in the reference collections at the University of Würzburg, Germany, and the Sabah Parks Headquarter, Malaysia.

Census areas

After monitoring the occurrence of *D. laevigatus* in two long-term study plots (one in primary rainforest and one in old secondary forest) during two study periods, we selected these plots to investigate the possible influence of *D. laevigatus* on ground communities during the third study period. On each of the two plots, six sieve buckets were selected at random. Around each of these 12 sieve buckets, a 1-m² area (“squares”) was established, containing the sieve bucket in its center (Fig. 1). The minimum distance between two squares was 8 m. To monitor the diversity and abundance of potential prey of *D. laevigatus*, four pitfall traps (6.5 cm diameter) were established in each square (Fig. 1). Each trap was covered with a leaf to prevent water accumulation and to collect predominately species that stayed close to the soil surface. Since *D. laevigatus* forages predominately hypogaeically, two hypogaeic pitfall traps were burrowed in the soil of each square (Fig. 1). A hypogaeic pitfall trap consisted of a rectangular container (16 cm high, 5 cm wide) with three opening slits (0.5 cm high, 4 cm wide, 2.5 cm apart) on each side. Each container was tightly fitted into a dug hole, binging the surrounding soil close to the opening slits. Afterwards, containers were completely covered with soil, making them accessible only to animals that dug through at least some soil. After epigaeic traps were allowed to settle for 4 days, hypogaeic traps were inserted and all traps within a study area were opened, filled with 2% formalin, and left to collect for 3 consecutive days. After removing the collected animals, epigaeic traps were closed and hypogaeic traps were extracted from the soil. For data analysis, the four epigaeic as well as the two hypogaeic traps were pooled for each square. On the day following trap collection, all sieve buckets of a study plot were baited with palm oil. Sieve buckets were checked daily and occurrence of *D. laevigatus* and other ant species was noted. Since *D. laevigatus* can be observed occasionally at the soil surface at night (Berghoff et al.

2002a), a plot was checked an additional time during the night once the army ant had entered a square. To investigate potential changes in the arthropod communities due to the presence of *D. laevigatus*, epigaeic pitfall traps were opened and hypogaeic traps were inserted in the same holes as before on each square whose sieve bucket was occupied for 3 days by *D. laevigatus*. All traps were left to collect for 3 days. Collected arthropods were sorted by order and ants by species.

Interactions

To further analyze the interactions between *D. laevigatus* and ground-foraging ant species, we focused on the five most common species, i.e., *Pheidologeton affinis*, *Lophomyrmex bedoti*, *Odontoponera transversa*, *O. denticulata*, and *Pachycondyla* sp. 2. Except for *O. denticulata*, which was restricted to non-forested study plots, data were collected for all species on all seven study plots. All species recruited to palm oil baits, where they were observed alone as well as co-occurring with *D. laevigatus* during innumerable bait checks. In the case of these species co-occurring with *D. laevigatus*, a bait check was regularly extended to observe interactions. Besides noting the behavior at baits, foraging habits of each species were observed and food samples were taken. Nest structure was analyzed by excavating five nests for each species, except for *Pachycondyla* sp. 2. To test the species' reaction toward the army ant, 20 *D. laevigatus* were released in the field close to the entrances of 10 different nests of each species. Since no nest was found for *Pachycondyla* sp. 2, it was confronted with *D. laevigatus* in the laboratory. In separate experiments, two *Pachycondyla* sp. 2 were united in a petri dish with two individuals of *D. laevigatus*, *O. transversa*, *P. affinis*, and *Dolichoderus* sp., respectively ($n=6$ repetitions for each species). Respective behavior was noted during the course of 10 min.

To analyze the interactions between *D. laevigatus* and its strongest competitor at baits, i.e., *P. affinis*, we kept, in a separate laboratory experiment, large worker samples (>2,000 ants) of both species in separate soil-filled containers. After 24 h, the containers were connected via plastic tubes to opposite sides of an arena (20×20 cm) covered with a thin layer of soil. Respective behavior and interactions were observed continuously for the first 3 h and, afterwards, every hour for the next 3 days.

Results

Arthropod communities

Overall, epigaeic and hypogaeic pitfall traps collected 12,660 individuals. Of these, 7,509 individuals (59.3%) were ants and 578 individuals (4.6%) represented juvenile arthropod stages (Table 1). Since ants will be treated separately, they are not included in the following analyses.

Epigaeic traps of a square yielded on average 10 ± 1.89 SD arthropod orders and 166 ± 81.86 SD individuals. Hypogaeic traps, of which there were only half as many per square, collected significantly fewer orders (average = 6 ± 1.95 SD) and individuals (average = 53 ± 27.39 SD) (Wilcoxon test, orders: $Z=-3.071$, $P=0.002$; individuals: $Z=-2.824$, $P=0.005$). However, looking at juvenile stages of arthropods, both trap types yielded similar numbers of individuals (Wilcoxon test $Z=-1.897$, $P=0.058$). Ensifera and Caelifera were the only taxa exclusively found in epigaeic pitfall traps. Species of all hypogaeically collected orders were recorded also in epigaeic traps.

Table 1 Collected individuals of the most common taxa in epigaeic and hypogaeic pitfall traps before and after *Dorylus (Dichthadia) laevigatus* recruited to the squares. Included are only the 10 squares in which *D. laevigatus* was recorded; 1,338 individuals, including 658 Formicidae and 46 juveniles, were collected on the two excluded “control” squares

	Epigaeic pitfall traps		Hypogaeic pitfall traps	
	Before	After	Before	After
Acarina	203	322	85	116
Araneida	45	35	4	6
Chilopoda	4	7	31	8
Coleoptera	173	112	84*	19*
Collembola	700	985	109*	228*
Formicidae	1,050	2,002	717	3,082
Hemiptera	49	61	8	6
Isopoda	55	65	1	15
Isoptera	30	8	139	16
Juveniles	135	248	83	66
Others ^a	41	78	54	37
Sum	2,485	3,923	1,315	3,599

* Significant differences (Wilcoxon-Test) Coleoptera: $Z=-2.2552$, $P=0.011$; Collembola: $Z=-2.668$, $P=0.008$

^a Contains 14 taxa, none of which contributed 50 or more specimens to any trap category

After baiting the sieve buckets with oil, they were located by *Dorylus (Dichthadia) laevigatus* on average 11.67 ± 2.24 SD days later. The sieve buckets of two squares in the old secondary forest were not located by *D. laevigatus* within the study period (approximately 3 weeks). To minimize potential environmental variations due to long study periods, the traps of these two “control” squares were opened following the schedule of the last occupied square (22 days after completing the first trapping period). Due to the low number of these controls, they will be excluded from the following analyses.

No significant differences were detected in the overall number of collected orders or individuals before and after *D. laevigatus* had recruited to the squares (Wilcoxon-Test, orders – epigaeic traps: $Z=-1.723$, $P=0.085$; hypogaeic traps: $Z=-7.680$, $P=0.442$; individuals – epigaeic traps: $Z=-1.376$, $P=0.169$; hypogaeic traps: $Z=-0.530$, $P=0.078$). Due to their limited mobility, juvenile arthropods are thought to be more vulnerable than adults to fall prey to army ants (Gotwald 1974b). However, neither the number of juveniles nor the number of termites, another likely prey of *D. laevigatus* (Berghoff et al. 2002a), differed significantly between the collections before and after *D. laevigatus* visited the squares (Table 1). Earthworms, also commonly preyed on by *D. laevigatus*, were collected in too low numbers (i.e., 47 within all squares and collections) to evaluate any potential changes in their abundance. Comparing the collections of the main taxa for an effect of *D. laevigatus*, only the numbers of Coleoptera and Collembola collected in hypogaeic traps before and after *D. laevigatus* had recruited to the squares differed significantly (Table 1). However, the number of Coleoptera showed a similar decline from eight to one collected specimen in the hypogaeic traps of the two control squares. The number of Collembola, on the other

Table 2 Ant individuals collected with epigaeic ($n=40$) and hypogaeic ($n=20$) pitfall traps before (BD) and after (AD) *D. laevigatus* was attracted to the study plots (squares, $n=10$). The two excluded control squares collected 6 additional species and overall 658 ant individuals

	Epigaeic pitfall traps		Hypogaeic pitfall traps		No. occupied squares
	BD	AD	BD	AD	
Aenictinae					
<i>Aenictus</i> sp. 8	3				1
<i>Aenictus</i> sp. 9			37		1
Cerapachyinae					
<i>Cerapachys</i> sp. 4	1				1
Dolichoderinae					
<i>Dolichoderus</i> sp. 2	1				1
<i>Dolichoderus</i> sp. 3		2			1
<i>Tapinoma</i> sp. 1	1				1
<i>Technomyrmex</i> sp. 1		1			1
<i>Technomyrmex</i> sp. 2	1				1
Dorylinae					
<i>Dorylus laevigatus</i>				970	6
<i>Dorylus cf. vishnui</i>	17				1
Formicinae					
<i>Acropyga</i> sp. 1			20	1	2
<i>Camponotus</i> sp. 2		2			1
<i>Camponotus</i> sp. 3	1				1
<i>Camponotus</i> sp. 4	1				1
<i>Camponotus</i> sp. 5			1		1
<i>Paratrechina</i> sp. 7	2	3			1
<i>Paratrechina</i> sp. 8	3	4	1		5
<i>Pseudolasius</i> sp. 2			1		1
<i>Pseudolasius</i> sp. 5			31		1
<i>Pseudolasius</i> sp. 6		1	7	5	3
<i>Pseudolasius</i> sp. 7		10	54		2
Leptanillinae					
<i>Leptanilla</i> sp. 1			3		1
Myrmicinae					
<i>Crematogaster</i> sp. 5	1				1
<i>Lophomyrmex bedoti</i>	493	849	117	338	10
<i>Monomorium</i> sp. 3	1				1
<i>Myrmecina</i> sp. 1	2	1			3
<i>Myrmecina</i> sp. 2			1		1
<i>Myrmecaria</i> sp. 3	3	6			3
<i>Oligomyrmex</i> sp. 1			4	15	3
<i>Oligomyrmex</i> sp. 2	2	14	5		2
<i>Oligomyrmex</i> sp. 6		1			1
<i>Oligomyrmex</i> sp. 7	2		1	1	1
<i>Oligomyrmex</i> sp. 8	36	1	17	6	3
<i>Oligomyrmex</i> sp. 9			93	4	6
<i>Pheidole cariniceps</i>	1	2			2
<i>Pheidole clypeocornis</i>				2	1
<i>Pheidole plagiaria</i>	1	1			1
<i>Pheidole sabahna</i>		2			1
<i>Pheidole spinicornis</i>		1			1
<i>Pheidole</i> sp. 1		4	1		1
<i>Pheidole</i> sp. 17	2				1
<i>Pheidole</i> sp. 18			13		4
<i>Pheidole</i> sp. 19	3	3	19	52	5
<i>Pheidole</i> sp. 20	1				1
<i>Pheidole</i> sp. 21	3	1			3
<i>Pheidologeton affinis</i>	168	458	145	1609	10
<i>Pheidologeton pygmaeus</i>	1	2	5		4
<i>Pheidologeton</i> sp. 1	217	505		55	3
<i>Proatta butelli</i>	1	2			3
<i>Recurvidris</i> sp. 1		3			1
<i>Smithistruma</i> sp. 1				3	1
<i>Smithistruma</i> sp. 2		1			1
<i>Solenopsis</i> sp. 1	4	1	16	6	3
<i>Strumigenys</i> sp. 2		2			2
<i>Strumigenys</i> sp. 3	2				2
<i>Strumigenys</i> sp. 4		1			1

Table 2 (continued)

	Epigaeic pitfall traps		Hypogaeic pitfall traps		No. occupied squares
	BD	AD	BD	AD	
<i>Tetramorium</i> sp. 5				1	1
<i>Tetramorium</i> sp. 7		1			1
<i>Tetramorium</i> sp. 8		3			1
<i>Tetramorium</i> sp. 9	2	1			2
<i>Tetramorium</i> sp. 10	1				1
<i>Trichoscapa</i> sp. 1				1	1
Ponerinae					
<i>Anochetus</i> sp. 2	2				2
<i>Diacamma intricatum</i>	1	1			2
<i>Gnamptogenys</i> sp. 2	1				1
<i>Gnamptogenys</i> sp. 3			1		1
<i>Hypoponera</i> sp. 1	1	1			2
<i>Hypoponera</i> sp. 2	3	2	8	1	3
<i>Hypoponera</i> sp. 8			2		1
<i>Hypoponera</i> sp. 9	1				1
<i>Leptogenys mutabilis</i>		19	11	4	4
<i>Leptogenys</i> sp. 2		45			1
<i>Leptogenys</i> sp. 4	5	5			6
<i>Leptogenys</i> sp. 5	2	4		1	4
<i>Leptogenys</i> sp. 6	2				1
<i>Odontomachus rixosus</i>	1	1			1
<i>Odontomachus</i> sp. 1	14	3			1
<i>Odontoponera transversa</i>	20	13		2	9
<i>Pachycondyla sharpi</i>	1	2	7		4
<i>Pachycondyla tridentata</i>	2	4			4
<i>Pachycondyla</i> sp. 1	11	12		1	2
<i>Pachycondyla</i> sp. 2			95	4	7
<i>Pachycondyla</i> sp. 4	3				1
<i>Pachycondyla</i> sp. 12	1				1
<i>Pachycondyla</i> sp. 13		1			1
<i>Ponera</i> sp. 1			1		1
Unidentified genus	1				1
Individuals	1,050	2,002	717	3,082	
Species	50	46	29	22	

hand, stayed much the same in hypogaeic traps of control squares between the first (19 specimens collected) and the second (22 specimens collected) trapping period.

Ant communities

Summarizing the yield of epigaeic and hypogaeic pitfall traps, 93 ant species from 37 genera were collected (Table 2). As before, the two plots to which *D. laevigatus* did not recruit during the study period will not be included in the following calculations. Of the remaining 87 species, 45 were recorded with at least three individuals (Table 2). Of these, 16 species (36%) were collected exclusively with epigaeic and 22 exclusively with hypogaeic traps; 42% of the species were collected with both traps (Table 2). As for the overall arthropod diversity, epigaeic traps collected more ant species per square (average 8.57 ± 2.82 SD) than hypogaeic traps (average 5.57 ± 2.31 SD).

D. laevigatus was found in none of the traps prior to baiting the sieve buckets (Table 2). After baiting with palm oil, *D. laevigatus* recruited to the sieve buckets of 10 squares, which it visited for 3 days, when the traps were opened. During the 3-day trapping period, *D. laevigatus*

deserted 8 of the 10 occupied sieve buckets. The army ant was found in 8 hypogaeic traps on 6 of the 10 occupied squares.

Comparing the number of species collected by epigaeic traps before and after *D. laevigatus* had recruited to the squares, no significant differences were found (Wilcoxon-Test, $Z = -0.535$, $P = 0.593$). However, hypogaeic traps collected significantly fewer species after *D. laevigatus* had recruited to the squares than before (Wilcoxon-Test, $Z = -2.673$, $P = 0.008$). Night checks around baits occupied by *D. laevigatus* revealed no increased epigaeic ant activity or nest evacuations.

During the after-*Dorylus* trapping period, five squares were raided by mass-raiding ants. These raids were indicated by traps of a square with more than 100 individuals of such species, i.e., *Pheidologeton* sp. 1 (one occasion, 505 ants), *P. affinis* (two occasions, 1,181 and 184 ants), and *D. laevigatus* (three occasions, 102, 121, and 612 ants). Since the high numbers of raiding individuals may conceal abundance changes of other ant species, the above individual numbers were not included in the comparison of collected individuals. Epigaeic as well as hypogaeic traps collected similar numbers of individuals before and after *D. laevigatus* had visited the

squares (Wilcoxon test, epigaecic traps: $Z=-0.969$, $P=0.333$; hypogaecic traps: $Z=-1.274$, $P=0.203$).

Interactions between *D. laevigatus* and selected ground ant species

Some life-history traits of the five focus species are summarized in Table 3. All species were active independent of time of day.

Lophomyrmex bedoti nests belonged to two types: satellite nests with up to five entrances housing workers, brood, and Hemiptera, and main nests consisting of several soil nests interconnected via hypogaecic tunnels. *D. laevigatus* workers released around entrances of satellite nests were generally avoided. Twice, the release of *D. laevigatus* resulted in the temporary evacuation of a satellite nest. In contrast, when *D. laevigatus* was released at main nest entrances, *L. bedoti* workers accumulated at the entrances and occasionally attacked the army ant.

The abundance of *L. bedoti* at baits did not differ significantly between baits with and without *D. laevigatus* (Mann-Whitney $U=306.00$, $P=0.537$). Co-occurring with *D. laevigatus*, *L. bedoti* restricted its bait access mainly to the top of the bait and retreated upon contact. Regularly, *L. bedoti* collected dead *D. laevigatus* workers from baits (e.g., left after fights with *P. affinis*; see below).

Odontoponera denticulata and *O. transversa* exhibited very similar life-history traits (Table 3). The nests of both species were connected to neighboring nests via hypogaecic tunnels. Probably due to these tunnels, all nests were evacuated when the experimental excavations reached the nesting chambers. Without other species present at a bait, both *Odontoponera* species removed pieces of soil soaked with oil. However, when *D. laevigatus* joined at a bait, both *Odontoponera* species switched to hunting the army ant. While the abundance of *O. transversa* did not differ significantly between baits with and without *D. laevigatus* (Mann-Whitney $U=3,282.00$, $P=0.665$), abundance of *O. denticulata* increased in the presence of *D. laevigatus* (Mann-Whitney $U=231.00$, $P=0.002$). When releasing *D. laevigatus* close to nest entrances of both *Odontoponera* species, workers of the latter species effectively guarded their nest entrances, preventing the army ants' descent into the nest tunnel. Incoming foragers started to hunt dispersed *D. laevigatus* and carried them into the nest.

Pachycondyla sp. 2 nests could not be detected, as the species quickly retreated into the soil when encountered during a bait check. On 14 occasions, *Pachycondyla* sp. 2 shared a bait with *D. laevigatus*, where its abundance did not differ significantly from its mean abundance (Mann-Whitney $U=412.00$, $P=0.899$). Twice, five to six *Pachycondyla* sp. 2 were observed to successfully maintain a small bait area, although co-occurring with more than 1,000 *D. laevigatus*. When the species were mixed during the bait check, a few interspecific fights could be observed, after which *Pachycondyla* sp. 2 retreated into

Table 3 Life-history traits of five common ground-foraging ant species

	<i>Lophomyrmex bedoti</i>	<i>Odontoponera denticulata</i>	<i>Odontoponera transversa</i>	<i>Pachycondyla</i> sp. 2	<i>Pheidologeton affinis</i>
Habitat ^a	U, SF, PF	U	PF	U, SF, PF	U, SF, PF
Height [m] ^b	1060	500	880	680	1470
Colony size	>100	>100	>100	>100?	>10,000
Nest type	Polydomous soil nests	Polydomous soil nests	Polydomous soil nests	Unknown	Multi-chambered soil nest
Nest/square ^c	0.92±0.79	Unknown	0.58±0.67	Unknown	0.92±0.67
Foraging stratum	Hypogaecic and epigaecic	Predominately epigaecic	Predominately epigaecic	Hypogaecic	Hypogaecic and epigaecic
Foraging strategy ^d	Single foragers, TT	Single foragers	Single foragers	Single foragers	Single foragers, TT
Observed food	Oil, tuna, honey, cookies, Homoptera, arthropods	Oil, tuna, honey, cookies, arthropods	Oil, tuna, honey, cookies, arthropods	Oil, tuna, honey, cookies, arthropods	Oil, tuna, honey, cookies, arthropods, annelids, seeds
Class/baits ^e	2: 11–100 ants	1: 1–10 ants	1: 1–10 ants	1: 1–10 ants	4: 1,000–5,000 ants

^a U urban vegetation, SF secondary forest, PF primary rain forest

^b Height up to which the species was recorded at oil baits along an altitudinal transect reaching 1,470 m

^c Average number of nests (±SD) found by baiting twelve 1-m² study areas (squares)

^d TT trunk trails

^e Mean abundance class on the second day of bait occupation

Table 4 Interspecific fights between *Pheidologeton affinis* and *D. laevigatus* at baits. The percentage in which *D. laevigatus* won and lost the bait ownership depending on the order of arrival is given.

1st species at the bait	Bait ownership by <i>D. laevigatus</i>			
	Won (%)	Lost (%)	Draw (%)	<i>n</i>
<i>P. affinis</i>	14	21	64	14
<i>D. laevigatus</i>	58	25	17	12
Both species	71	14	14	7

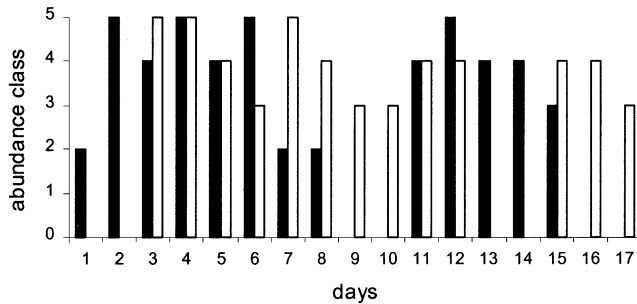


Fig. 2 Abundance of *Pheidologeton affinis* (black bars) and *D. laevigatus* (white bars) co-occupying a single bait. Interspecific fights could be observed on days with co-occurring species. For abundance classes, refer to text

the ground. On the following days, no *Pachycondyla* sp. 2 were found at these baits. Mixing *Pachycondyla* sp. 2 with *O. transversa*, *P. affinis*, and *Dolichoderus* sp., respectively, in the laboratory, the species quickly retreated whenever they met. However, when mixed with *D. laevigatus*, *Pachycondyla* sp. 2 immediately attacked the army ant. Each *D. laevigatus* worker was repeatedly stung by one or both *Pachycondyla* sp. 2. All *D. laevigatus* were paralyzed within the first minute of the experiments.

Pheidologeton affinis immediately recruited large numbers of nest mates and attacked and killed *D. laevigatus*, when it was released close to *P. affinis*' nest entrances. At baits, the abundance of *P. affinis* did not differ significantly between baits with and without *D. laevigatus* (Mann-Whitney $U=8799.00$, $P=0.622$). However, at least some fighting activity could always be observed when both species co-occurred at a bait (Fig. 2). A fight ($n=33$) was judged as won when one species maintained the lone bait ownership for 3 consecutive days. The outcome of a fight seemed to be related to the order in which the species arrived at a bait (Table 4). When worker samples were connected to an arena in the laboratory, both species dispersed onto the arena within 1 h. Upon contact, *D. laevigatus* assumed an aggressive posture but caught *P. affinis* only rarely. On the other hand, single *D. laevigatus* workers were overwhelmed by groups of *P. affinis* workers, pinning *D. laevigatus* to the ground. After 3 h of the experiment, *D. laevigatus* used two trails across the arena. These trails were lined with medium and major workers, shielding the trails from surrounding *P. affinis*. After 24 h, *D. laevigatus* had

The outcome was called a draw when both species left the bait on the same day

moved across the arena and into the container of *P. affinis*, which accumulated at the soil surface. This situation was maintained until the end of the experiment.

Discussion

A variety of methods have been developed to sample ground and litter arthropod communities. Litter techniques (e.g., Winkler sifting or Berlese funnel) represent methods enabling the effective collection of litter fauna, while direct and intensive sampling methods are well suited to gain an inventory of ant species richness (Bestelmeyer et al. 2000). However, all these methods cause major disturbances to the soil and litter fauna, preventing the possibility of re-sampling the same area after a short while. Although pitfall traps will not catch all species (Greenslade 1973; Bestelmeyer et al. 2000), the combination of epigeic and hypogaeic traps should provide a reasonable collection of potential *Dorylus (Dichthadia) laevigatus* prey species. The high numbers of juveniles in hypogaeic traps indicated the soil stratum to be rich in this potential prey. Ants comprised 59% of all collected specimens, and they dominated in all traps (Table 1). Most ant species with more than two collected specimens were restricted either to epigeic (36%) or hypogaeic (22%) traps. Similar species restrictions to epigeic and hypogaeic traps were also found by Quiroz-Robledo and Valenzuela-González (1995).

The possibility of attracting *D. laevigatus* predictably and within short periods of time to a bait enabled the first study of the potential influence of a hypogaeic army ant on soil fauna. However, the presence of the bait could also influence the species' foraging behavior. Although oil is probably fed to some extent to the larvae (Berghoff et al. 2002b), other food, in particular proteins, is needed to rear the larvae (Weissflog et al. 2000). Because of this, *D. laevigatus* would need to extend its foraging beyond baits. When army ants locate a food source during a mass raid, foragers are recruited from the swarm to that site (Witte and Maschwitz 2000). Not all arriving foragers stop at the prey but proceed a little further into the surrounding area (Witte and Maschwitz 2000). This "recruitment overrun," which is closely linked to the spatial development and extension of raids, has been described for mass-raiding species such as *Neivamyrmex*, *Pheidologeton*, and *Leptogenys* (Topoff et al. 1980; Moffett 1988; Witte and Maschwitz 2000). With initial

abundances of more than 5,000 ants per sieve bucket (Berghoff et al. 2002a), a bait literally flows over with *D. laevigatus* workers, some of which disperse due to recruitment overrun into the surrounding area. If prey is discovered, nest mates will be recruited further into the area, as was observed for *D. laevigatus*, extending its foraging into the soil surrounding a recently located bait, where they preyed on *Paratrechina* sp. (Berghoff et al. 2002a). As indicated by the presence of *D. laevigatus* in hypogaeic pitfall traps, the squares thus should have been subject to at least some raiding activity. Most sieve buckets were deserted by *D. laevigatus* after 3–5 days, indicating that the oil was not sufficient to keep the ants within the area. This should further increase the likelihood of raids into the surrounding area.

When comparing areas recently raided by epigaeically foraging *Eciton burchelli* or *Aenictus* species to control areas, a strong influence of the army ants on litter arthropods was shown (Franks 1982b; Otis et al. 1986; Hirosawa et al. 2000). While prey ants took about 100 days to recover to half their original abundance, populations of crickets and roaches quickly recovered due to individual migration to the site (Franks 1982a). Migration of succession species to empty patches also increased the ant diversity after a raid (Franks and Bossert 1983). Because of this, effects of an army ant raid are most likely to be seen a few days after a raid. Arthropods were trapped 3 days after *D. laevigatus*, which preys on earthworms and a wide variety of arthropods including termites and broods of ground-nesting ants (Weissflog et al. 2000; Berghoff et al. 2002a, 2002b), had entered a square. No significant differences were found in the number of arthropod orders, individuals, or juveniles collected with epigaeic or hypogaeic traps. A decrease in Coleoptera numbers in hypogaeic traps was also seen in control squares and thus was probably linked to some external factor. The significant increase in Collembola collected in hypogaeic traps after *D. laevigatus* was recorded in the squares may be linked to the epigaeic and hypogaeic mass raids, which probably flushed Collembola from the leaf litter during this trapping period. Similar to overall arthropod numbers, ants showed no effects in the number of collected individuals. However, hypogaeic traps, collecting in the preferred foraging stratum of *D. laevigatus*, collected significantly fewer ant species after *D. laevigatus* had visited the squares. In particular, the disappearance of two *Pseudolasius* and one *Pheidole* species, which were numerous in the first collection (Table 2), could indicate predation by *D. laevigatus*. The effect of the only reported hypogaeic raid of an army ant species, i.e., *Labidus coecus*, on an ant community resulted in one dead colony out of 23 colonies attacked (Perfecto 1992). A similar impact of *D. laevigatus* would hardly be detectable by the methods applied here. However, the lower species numbers in traps after *D. laevigatus* had visited the squares could also be related to the mass raids of three other ant species in the same time frame. Most prey ant species seem to flee into the vegetation (Hirosawa et al. 2000; Berghoff et al. 2002a)

or to related nests (LaMon and Topoff 1981; Droual 1984) during a raid, which can temporarily reduce ant abundance in a raided area. The use of satellite nests, also recorded for three of the five most common ant species in this study (Table 3), can thus provide refuges during army ant attacks (Droual 1984; Perfecto 1992). The five focus species were able to coexist with *D. laevigatus* despite conformities in habitat, foraging strata, and food preferences (Table 2, Berghoff et al. 2002a), showing different strategies to cope with the army ant. All species were able to maintain exclusive bait sections when co-occurring with *D. laevigatus*. The induced nest evacuations and defensive behavior observed for *L. bedoti* in the presence of *D. laevigatus* were recorded in similar experiments for prey species of *Neivamyrmex* (LaMon and Topoff 1981; Droual 1984). The reaction of *L. bedoti* thus identifies it as a possible prey species of *D. laevigatus*. However, due to their high density of associated nests (Table 3), mature colonies will probably be able to survive an attack (Hirosawa et al. 2000). The high aggressiveness of *Pachycondyla* sp. 2 towards *D. laevigatus* in arena tests indicates a possible “enemy specification” of *D. laevigatus*, signifying it to be a serious enemy of *Pachycondyla* sp. 2 (Wilson 1975; Hölldobler 1979). Since hypogaeic *D. laevigatus* raids are conducted by minor workers (Berghoff et al. 2002a), a strong defensive reaction by *Pachycondyla* sp. 2 could probably ward off an attack. In contrast to *Pachycondyla* sp. 2, the two *Odontoponera* species not only killed but also actively preyed on *D. laevigatus*. Such behavior was until now reported only for *Oecophylla* species (Gotwald 1995). The predatory efficiency and the use of interconnected nests probably enable these fast-moving *Odontoponera* species to restrain raiding *D. laevigatus* digging through to their nest cavity and to evacuate their nests before too many army ants arrive on the scene. A low predation pressure is further supported by the mild reaction towards *D. laevigatus* workers released at *Odontoponera* nests (compare to LaMon and Topoff 1981). On the other hand, when releasing *D. laevigatus* close to *Pheidolegton affinis* nests, or when the species met at a bait, interspecific fights would always develop. Fights at baits could continue for several days (Fig. 2). However, *D. laevigatus* was more likely to gain the bait ownership when it arrived prior to or at the same time as *P. affinis* (Table 4). In a laboratory experiment, *D. laevigatus* was shown to shield its columns from attacking *P. affinis* and thus to maintain its position or slowly advance. A similar strategy could also be demonstrated for fights between the sympatric *D. laevigatus* and *D. cf. vishnui* (Berghoff et al. 2003). Combining the observations at baits and in the laboratory, *D. laevigatus* was shown to gain and maintain new terrain by slowly advancing in tight formation and defending the gained areas at strategic points. Compensating for its lower ability to defend and retain a bait, *P. affinis* had high nest (Table 3) and forager densities, enabling it to localize most baits within 24 h (Berghoff, unpublished data). *D. laevigatus*, on the other hand,

needed on average 8.6 days to locate a bait (Berghoff et al. 2002a).

Although known to conduct hypogaecic column and occasionally epigaecic swarm raids and to prey on a wide variety of arthropods (Berghoff et al. 2002a), *D. laevigatus* showed only little effect on hypogaecic and no effect on epigaecic arthropod communities. Even when *D. laevigatus* recruited to a sieve bucket, it could occur in none or only one of the squares' hypogaecic pitfall traps. Concentrating its foraging onto a few stable trails, from which single raids originate, *D. laevigatus* can exploit larger resources over long periods of time (Berghoff et al. 2002a). In this way, only occasionally should single ant colonies fall prey to a *D. laevigatus* raid. The possible effects of *D. laevigatus* on earthworms and termites, a seemingly preferred prey (Berghoff et al., 2002a), might have been underestimated due to their low individual numbers in traps (Table 1). The five most common ground-nesting ant species were able co-occur even with more than 1,000 *D. laevigatus* at a bait by employing different strategies. Adding to the differences separating *D. laevigatus* from epigaecically raiding army ant species (Berghoff et al. 2002a, 2002b), this hypogaecic ant seems by far not as fierce a predator as, e.g., the epigaecically swarm-raiding army ant *D. nigricans*.

Acknowledgements We wish to thank the Economic Planning Unit, Sabah Parks, Maryati Mohamed of the University Malaysia Sabah, and Rosli Hashim of the University Malaya for their cooperation enabling the conduction of this study. Furthermore, we thank Marc Schäfer for his assistance in the field and two anonymous referees for their comments on the manuscript. Financial support was provided by the Deutsche Forschungsgemeinschaft (DFG Ma373/17-7).

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