

Comparison of foraging habits between four sympatric army ant species of the genus *Aenictus* in Sarawak, Borneo

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ABSTRACT. In Lambir Hills National Park, Sarawak Borneo, we observed foraging habits of four sympatric army ant species of the genus *Aenictus*: *A. laeviceps* (F. Smith, 1857), *A. dentatus* Forel, 1911, *A. gracilis* Emery, 1893, and *A. inflatus* Yamane & Hashimoto, 1999. All of these species were demonstrated to be specialized on other ants as a food source. However, notable differences in the composition of prey ants were observed between the four species, which may reduce potential competition for the same food source and allow them to coexist. Although we consider that interspecific differences in the foraging modes, such as use of different foraging strata and prey sizes, are major factors to facilitate the prey partitioning, other factors related to difficulties in locating nests of prey, and subduing and handling of dangerous prey, also seem to affect the pattern found in the prey utilization of each *Aenictus* species. In addition, the present study presents the first prey records for *A. inflatus*, which is exceptional in the genus in having a polymorphic worker caste, with the major worker having an inflated propodeum filled with a red liquid.

Keywords: army ants, prey ants, Borneo, resource partitioning

INTRODUCTION

The two Old World subfamilies Dorylinae and Aenictinae and the New World Ecitoninae are regarded as true army ants (Wilson 1964). Army ants are characterized by group predation events, known as “raids”, in which huge numbers of ants forage simultaneously over a certain area, and usually collect various types of prey, including almost all kinds of arthropods, and also occasionally earthworms, snakes, and nestling birds (Gotwald 1995). Therefore, army ants have been described as a keystone species, which have an important effect on the abundance and composition of terrestrial communities, acting as

an intermediate disturbance factor (Franks and Bossert 1983, Berghoff *et al.* 2003). However, the single genus *Aenictus* in the subfamily Aenictinae is unusual among the army ants, because it is thought that all members of this genus are predominantly or exclusively specialized on other ants as prey (Gotwald 1995). In spite of the narrow range of prey, *Aenictus* is the most speciose army ant genus with 151 valid described species, which are mainly distributed throughout Southeast Asia (Wilson 1964, Jaitrong & Yamane 2011, Jaitrong & Hashimoto 2012).

Multiple sympatric *Aenictus* species repeatedly engage in group hunting and migration during both the day and the night, and

collect a large amount of ant prey to support their large-sized colonies (Schneirla & Reyes 1969). Therefore, competition for prey might be intense among sympatric *Aenictus* species, and they are expected to avoid competition by partitioning prey use (Rosciszewski and Maschwitz 1994). However, the mechanisms allowing the coexistence of many different, but ecologically similar species of *Aenictus* in a given habitat are poorly understood.

In Lambir Hills National Park, Sarawak Borneo, 17 species have been recorded so far (Yamane *et al.* 1996, Yamane & Hashimoto 1999, Matsumoto *et al.* 2009). In the present study, we investigated more closely the foraging habits and resource partitioning of four sympatric species of *Aenictus*: *A. laeviceps*, *A. dentatus*, *A. gracilis*, and *A. inflatus*, occurring in Lambir Hills National Park. In addition, we present the first prey records for *A. inflatus*, which is exceptional in the genus in having a polymorphic worker caste with the major having an inflated propodeum filled with a red liquid (Yamane & Hashimoto 1999).

MATERIALS AND METHODS

Study site and field census

The study was conducted in Lambir Hills National Park, Sarawak, Malaysia (4°20' N, 113°50' E; alt. 150–200 m). The park is covered by intact mixed dipterocarp forests, with an area of approximately 70 km² (Inoue *et al.* 1995). The mean annual rainfall is about 2,800 mm, without a definite dry season, although a weak seasonal change occurs in rainfall (Kato *et al.* 1995). Field censuses were conducted from July to October 1997.

We walked around in the rainforest between 0800 h and 1700 h and, whenever a raiding column of *Aenictus* was located, we sampled some adult workers for later identification and collected prey items being carried by the workers. Sampling of prey items was conducted along the column, using a vacuum insect-aspirator, during a 3–5 h period, and, at the same time, we recorded nest sites of prey ants for classification of the ants as arboreal or ground-nesting. Samples were preserved in vials filled with 80% ethanol until pin-mounted. Voucher specimens were deposited

in the insect collections of the Museum of Nature and Human Activities, Hyogo and SKY Collection at Kagoshima University.

Data analysis

The prey items carried by *Aenictus* species included both immature and adult ants. Furthermore, some prey items were fragments of body. We categorized the prey items into four types: intact (or nearly intact) adults, parts of adults, intact immatures (larvae or pupae), and parts of immatures. To determine species composition of prey ants in each *Aenictus* species, only intact or nearly intact adults were identified due to difficulties in identifying adult body parts and immatures to species-level. Dismembered adult prey were identified only to genus level. However, when pupae of prey were identifiable to species-level, we also used these records. All ants collected were identified to genus, using the keys of Hashimoto (2003), and then to species or morphospecies level, using the reference collection of Asian ants in Kagoshima university established by the International Network for the Study of Asian Ants (ANeT).

To detect differences in taxonomic composition of prey ants, Pianka's overlap index (Pianka 1973) was calculated between the four *Aenictus* species based on relative abundance of each genus of prey ants. This index ranges between 0 (no diet overlap) and 1 (complete overlap). The significance of the overlap was tested using randomization procedures in ECOSIM 7.0 (Gotelli & Entsminger 2001) with RA3 randomization algorithm. This randomization algorithm has been recommended by Winemiller & Pianka (1990), which is superior to other randomization algorithms in detecting nonrandom niche-overlap patterns.

To compare prey-size preference between the four *Aenictus* species, the head width was measured for three to five workers selected from intact adults of each prey species. prey size was compared among the four *Aenictus* species with ANOVA, and, when a significant difference was identified by the test, Steel–Dwass multiple comparison tests were used to determine statistical significance of these differences. We compared the proportion of prey types sampled

from each *Aenictus* species with chi-square tests of independence and, when a significant difference was identified, we applied a Bonferroni correction for multiple comparisons to determine the statistical significance of this difference. These statistics were performed using the SPSS ver.21 statistical package.

RESULTS

We encountered 12 raids of *A. laeviceps*, five of *A. dentatus*, three of *A. gracilis*, and three of *A. inflatus* in the investigated area. All of the four *Aenictus* species were column raiders, i.e. each of the terminal branches of a main foraging column ended in a small group of workers that search for and capture prey in a relatively small area (Fig.1). *Aenictus laeviceps* and *A. gracilis* generally performed their raids on the ground

surface, in lower vegetation, and up into trees. The raids of *A. dentatus* were conducted under the leaf litter and usually appeared on the surface for short distances. *Aenictus inflatus* had an intermediate raiding pattern between that of *A. laeviceps* and *gracilis* and that of *A. dentatus*. Its workers normally searched for prey ant nests on the lower vegetation and occasionally ramified their columns on the ground surface.

The total numbers of prey items collected from the raids were 1,260 for *A. laeviceps*, 650 for *A. dentatus*, 195 for *A. gracilis*, and 103 for *A. inflatus*. Among all the items collected (2208) only 29 (1.3%) were not ants (1 orthopteran in *A. dentatus*; 24 hymenopteran larvae and 4 scorpions in *A. laeviceps*). In all of the four *Aenictus* species, both immature and adult preys were collected. Among the prey items carried by *A. laeviceps* fragments of both immatures and adults were found.

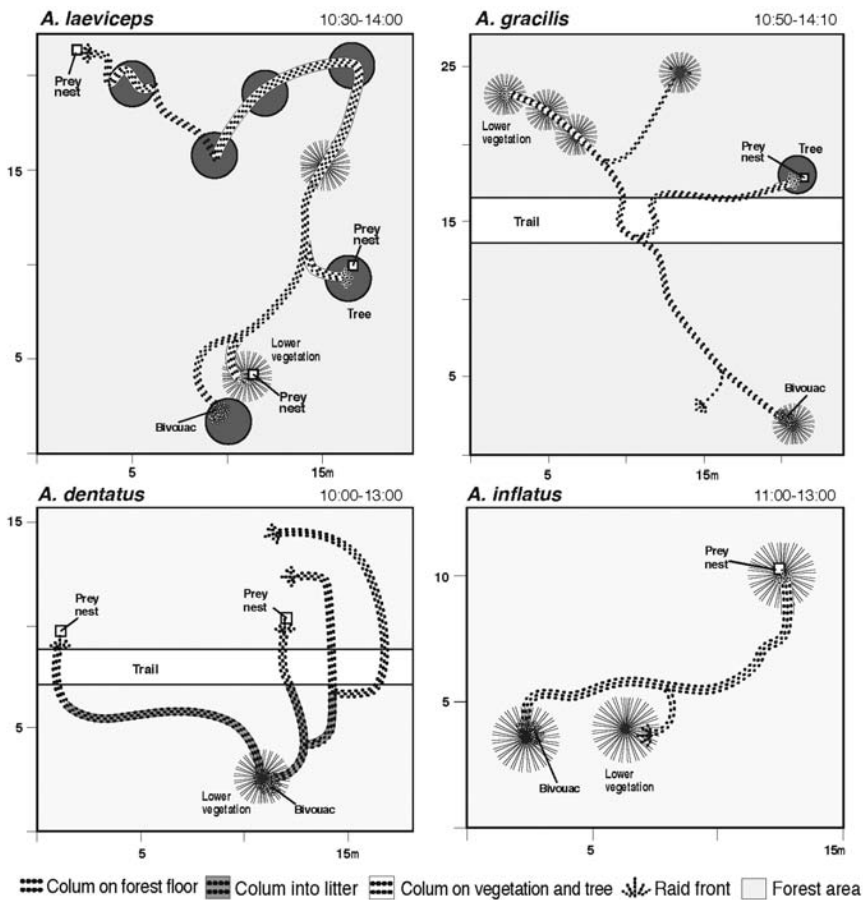


Fig. 1. Raiding patterns for the four *Aenictus* species.

Table 1. Number of prey items of the four *Aenictus* species in Lambir Hills National Park. Number of identifiable pupae prey is shown in parentheses for each taxon. A: Arboreal ant, G: Ground ant, AL: *Aenictus laeviceps* (Smith, 1857), AG: *Aenictus gracilis* Emery, 1893, AD: *Aenictus dentatus* Forel, 1911, AI: *Aenictus inflatus* Yamane & Hashimoto, 1999

Prey	Nest site	AL	AG	AD	AI
Formicinae					
<i>Camponotus (Colobosis)</i> sp. 1	A	1	0	0	0
<i>Camponotus (Myrmamblys)</i> sp. 2		2	0	0	0
<i>Camponotus</i> sp. 3	A	1	0	0	0
<i>Camponotus (Tanaemyrmex)</i> sp. 4	A	5	0	0	0
<i>Camponotus (Tanaemyrmex)</i> sp. 5	A	17(5)	0	0	0
<i>Echinopla</i> sp. 1	A	3(8)	0	0	0
<i>Euprenolepis</i> sp. 1		0	0	5	0
<i>Myrmoteras diastematum</i> Moffett, 1985	G	0	0	3	0
<i>Paratrechina</i> sp. 1		2	0	0	0
<i>Paratrechina</i> sp. 2		0	0	1	0
<i>Paratrechina</i> sp. 3	G	11(4)	0	0	0
<i>Paratrechina</i> sp. 4	G	0	0	7	0
<i>Paratrechina</i> sp. 5	G	0	0	6	0
<i>Paratrechina longicornis</i> (Latreille, 1802)	G	0	0	0	20(10)
<i>Paratrechina</i> sp. 6	A	35	15	0	0
<i>Polyrhachis nigropilosa</i> Mayer, 1872	G	34(20)	0	0	0
<i>Polyrhachis (Myrmhopla)</i> sp. 1	A	12(1)	0	0	0
<i>Polyrhachis rixosus</i> Smith, 1858	A	8(4)	0	0	0
<i>Prenolepis jerdoni</i> Emery, 1893	A	0	0	6	0
Myrmicinae					
<i>Aphaenogaster</i> sp. 1	G	0	0	1	0
<i>Crematogaster (Orthocrema)</i> sp. 1	G	6(35)	0	0	0
<i>Crematogaster coriaria</i> Mayr, 1872	A	7(44)	0	0	0
<i>Crematogaster (Paracrema)</i> sp. 2		1(55)	0	0	0
<i>Crematogaster</i> sp. 3		1	0	0	0
<i>Lophomyrmex longicornis</i> Rigato, 1994	G	3	0	0	0
<i>Monomorium</i> sp. 1		0	0	0	19(5)
<i>Monomorium</i> sp. 2		0	0	0	1(8)
<i>Pheidole (Pheidolacanthinus)</i> sp. 1	G	0	0	5(3)	0
<i>Pheidole (Pheidolacanthinus)</i> sp. 2	G	0	0	2(3)	0
<i>Pheidole plagiaria</i> Smith, 1860	G	0	0	293(204)	0
<i>Pheidole</i> sp. 3	G	2	0	0	0
<i>Pheidole</i> sp. 4	G	0	0	8(5)	0

<i>Pheidole</i> sp. 5	G	4(26)	0	1	0
Dolichoderinae					
<i>Dolichoderus cuspidatus</i> (Smith, 1857)	A	15(5)	0	0	0
<i>Dolichoderus semirugosus</i> (Mayr, 1870)	A	1(64)	0	0	0
<i>Dolichoderus thoracicus</i> group	A	49(8)	0	0	0
<i>Technomyrmex butteli</i> Forel	A	1(5)	0	0	0
<i>Technomyrmex</i> sp. 1	A	0	0	1	0
<i>Technomyrmex</i> sp. 2	A	0	7(8)	0	0
<i>Technomyrmex</i> sp. 3	A	0	23(64)	0	0
<i>Technomyrmex modigliani</i> Emery, 1913	A	0	3(27)	1	0
<i>Technomyrmex</i> sp. 4		0	0	2	0
<i>Technomyrmex</i> sp. 5		0	0	1	0
Ponerinae					
<i>Pachycondyla tridentata</i> Smith, 1858	G	3(14)	0	0	0
Intact adult ants (number of individuals)		224	48	343	40
Parts of adult ants (number of parts)		522	0	0	0
Immature ants		428	147	306	63
Parts of immature ants		58	0	0	0
Other arthropods		28	0	1	0
Total		1,260	195	650	103

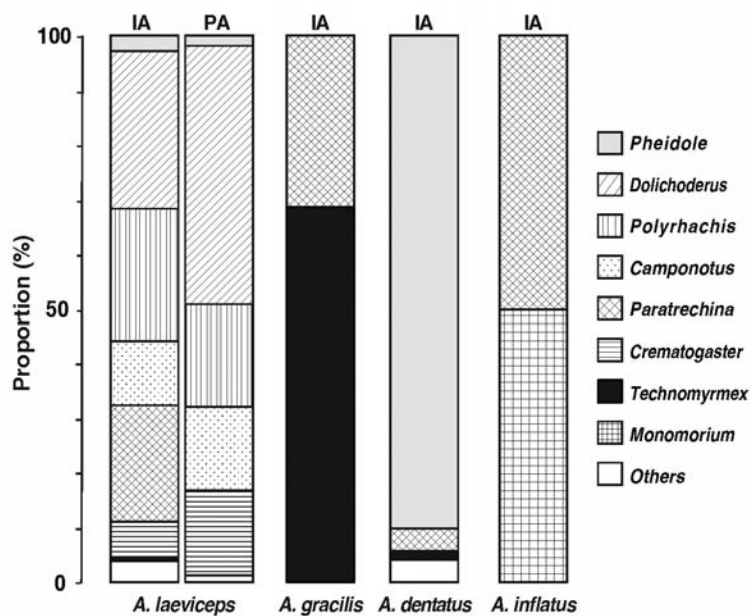


Fig. 2. Proportion of each genus of prey ant adults collected by the four *Aenictus* species in Lambir Hills National Park. IA: Intact ant adults of prey, PA: Parts of ant adults.

Table 2. Food niche overlap (O) expressed as Pianka's index between the four *Aenictus* species in Lambir Hills National Park.

	O
<i>A. dentatus</i> vs. <i>A. gracilis</i>	0.019
<i>A. dentatus</i> vs. <i>A. inflatus</i>	0.032
<i>A. dentatus</i> vs. <i>A. laeviceps</i>	0.080
<i>A. gracilis</i> vs. <i>A. inflatus</i>	0.293
<i>A. gracilis</i> vs. <i>A. laeviceps</i>	0.195
<i>A. inflatus</i> vs. <i>A. laeviceps</i>	0.333

Forty-four species of 15 ant genera were identified among the intact prey items of the four *Aenictus* species, and 17 ant genera were recognized when including non-intact material (Table 1). Taxonomic composition of the prey ants was clearly different between the four *Aenictus* species (Fig. 2). In *A. dentatus*, the most frequently hunted genus was *Pheidole*, which made up 90% of the adult prey. In *A. gracilis*, the dominant genus was *Technomyrmex*, constituting 69% of the adult prey. In *A. inflatus*,

although the estimation was based on only a few observations, *Paratrechina* (sensu lat.) (50%) and *Monomorium* (50%) seemed to be particularly preferred as prey. In *A. laeviceps*, despite a wider prey range at genus level than the other three species, the dominant genus in the adult prey was *Dolichoderus* (29% of whole intact and 47% of dismembered items), followed by *Polyrhachis* (24% and 18% respectively). The Pianka pairwise comparisons indicated a low degree of dietary overlap between the four *Aenictus* species based on measures of relative abundance of each genus of prey ants (Table 2). Null model analysis demonstrated that the observed mean of dietary overlap for all *Aenictus* species combined (0.158) was significantly less than expected by chance, after 5000 randomizations (simulated mean = 0.341, $p = 0.043$).

In addition to the preferences for certain prey taxa in each species, the proportions of immatures and adults in the prey items were different among the four species (Chi-square test, $\chi^2 = 11.34$, $df = 3$, $p < 0.001$) (Fig. 3). Pairwise comparisons after Bonferroni correction showed a significantly high proportion of adult ants in *A. dentatus* (53%), compared with the other three species ($p < 0.001$ after Bonferroni correction). Another difference found in prey composition was in the proportion of arboreal and ground nesting ants (Chi-square test, $\chi^2 = 17.93$, $df = 3$, $p < 0.001$)

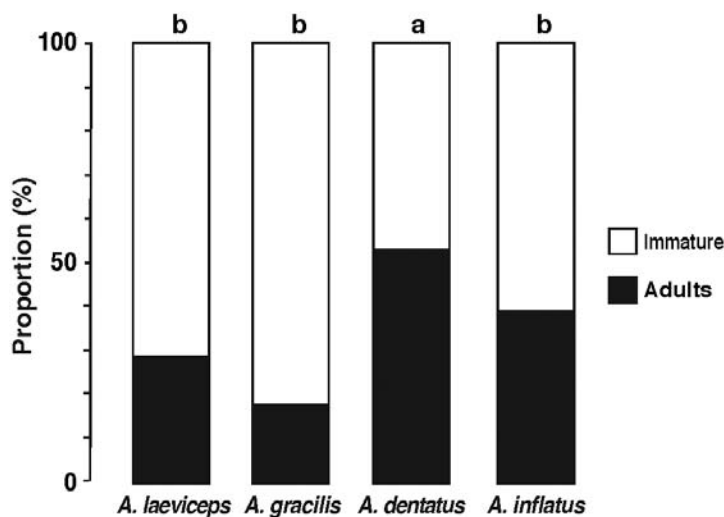


Fig. 3. Proportion of immatures and adults in intact prey items collected by the four *Aenictus* species in Lambir Hills National Park. Different alphabet letters are used to indicate that the data compared are statistically significant ($p < 0.001$) after Bonferroni correction.

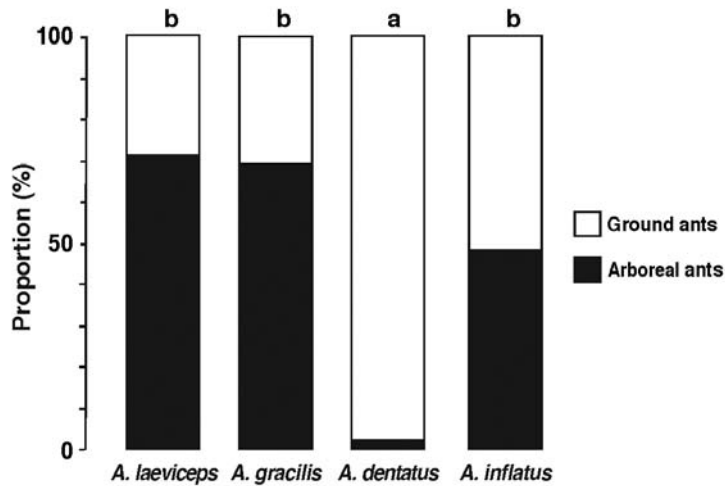


Fig. 4. Proportion of arboreal and ground nesting ants in intact prey items collected by the four *Aenictus* species in Lambir Hills National Park. Different alphabet letters are used to indicate that the data compared are statistically significant ($p < 0.001$) after Bonferroni correction.

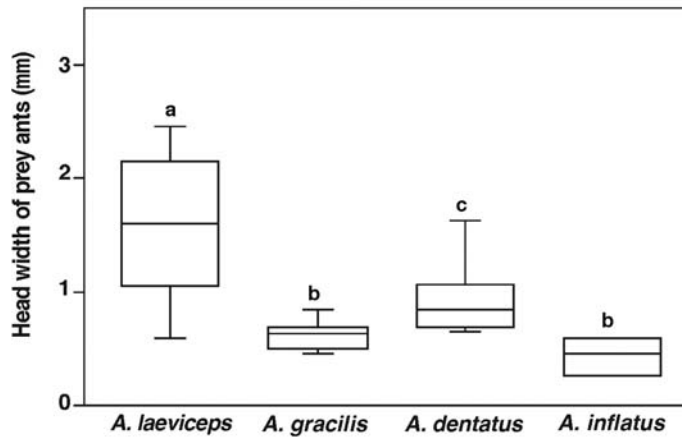


Fig. 5. Head size of intact adult workers for prey ants collected by the four *Aenictus* species in Lambir Hills National Park. Different alphabetic letters are used to indicate that the data compared are statistically significant ($p < 0.001$) using Steel-Dwass tests.

(Fig. 4). For intact adult prey, the proportion of arboreal ants was only 2% in *A. dentatus* and 48% in *A. inflatus*. In contrast, arboreal ant prey accounted for 70% of the prey in *A. laeviceps* and in *A. gracilis*. Pairwise comparisons conducted by the Bonferroni correction test showed a significant smaller proportion of arboreal ant prey in *A. dentatus*, compared with the other three species ($p < 0.001$ after Bonferroni correction). Furthermore, prey size preference was found to vary significantly among the four *Aenictus*

species (1.59 ± 0.69 mm in *A. laeviceps* prey, 0.98 ± 0.36 mm in *A. dentatus* prey, 0.62 ± 0.17 mm in *A. gracilis* prey, 0.44 ± 0.20 mm in *A. inflatus* prey; ANOVA $F_{3,33} = 16.08$, $p < 0.001$) (Fig. 5). Pairwise comparisons conducted using Steel-Dwass tests showed a significant preference for larger prey in *A. laeviceps*, compared with the other three species (Steel-Dwass test $p < 0.001$), and the test also showed significantly larger size of the *A. dentatus* prey than those of the remainder (Steel-Dwass test $p < 0.001$).

DISCUSSION

All of the four sympatric army ant species of *Aenictus* in the investigated area were demonstrated to be specialized on the other ants as food resource. However, notable differences in the composition of prey ants were observed between the species, with very little overlap at genus level. The different patterns of prey composition seem to be explained by the differentiation of foraging mode among the four species. We observed that *A. laeviceps* and *A. gracilis* forage frequently arboreally, while *A. dentatus* and *A. inflatus* forage primarily on the ground. It is known that there is a remarkable taxonomic bias between arboreal and ground ant communities in Bornean tropical forests: there are many arboreal species mainly of the genera *Camponotus*, *Polyrhachis*, *Dolichoderus* and *Technomyrmex*, and many ground ant species of the genera *Pheidole* and *Paratrechina* (Yamane *et al.* 1996, Brühl *et al.* 1998, Eguchi 2001, Widodo *et al.* 2001, Hashimoto *et al.* 2010, Tanaka *et al.* 2010). Consequently, the stratification of foraging sites is expected to yield different patterns of prey composition in the army ant assemblage.

In the present study, we also found that the four species of *Aenictus* army ants preyed on different ants according to their size. *A. laeviceps* apparently preferred larger ants than the other three species, and *A. dentatus* selected larger prey than the remainder. Differentiation of foraging stratum and prey size between sympatric *Aenictus* species was also observed in other areas of Southeast Asia (Rosczewski & Maschwitz 1994 in Pasoh, Peninsular Malaysia; Hirosawa *et al.* 2000 in Poring, Borneo). The similar observations across the different localities seem to support the idea that differences in foraging mode are major mechanisms to facilitate prey partitioning among *Aenictus* army ants.

In addition to the differences in foraging mode, this study showed that prey transportation behaviour differed between *A. laeviceps* and other species. We observed a large number of dismembered ant victims among the prey items carried by *A. laeviceps*. Because *A. laeviceps* apparently prefers a larger prey size than the other *Aenictus* species, the dismembering of prey into small items may be an adaptation to

carry large ants effectively. In the present study, we also found that *A. dentatus* also exhibited a preference for large prey. However, *A. dentatus* usually transports prey in the leaf litter, whereas *A. laeviceps* transports prey primarily above ground. Above-ground activity may expose the prey to scavengers, and army ant columns to predators during prey-transport, e.g., *Oecophylla smaragdina* is known as a predator of surface raiding *Aenictus* species (Gotwald 1995). Assuming that the vulnerability puts a premium on completing transport tasks quickly, it seems reasonable that *A. laeviceps* dismembers prey ants and retrieves the fragments in order to carry large prey at high speeds. This prey dismemberment may also offer *A. laeviceps* advantages in carry large prey items along vertical surfaces, and thus the behaviour seems to aid in its predation on arboreal ants.

Furthermore, we observed that the proportion of immature ants was low in the prey items of *A. dentatus*, but high in those of the other three species. Because *A. dentatus* preyed heavily upon species of *Pheidole* and the other *Aenictus* species ignored or preyed much less frequently on this genus, the observed difference might be due to antipredator behaviour of the prey ants. When the nest of *Pheidole dentata* Mayer, 1886 is heavily invaded by *Solenopsis geminata* (Fabricius, 1804), *Pheidole* ants employ absconding (mass flight) as a predation avoidance behaviour, in which workers holding brood scatter outward in all directions (Wilson 1976). Consequently, some workers of *Pheidole* are easily captured without resistance, but many brood escape predation. The conspicuously low proportion of immatures in the *A. dentatus* prey may indicate the effectiveness of this predation avoidance behaviour against *Aenictus* raids, suggesting that factors such as prey reaction should also affect the pattern found in prey use by *Aenictus* species.

This study presents prey records for *A. inflatus* for the first time, which included both immatures and adults of *Paratrechina longicornis* (Latreille, 1802) and *Monomorium* spp.. *A. inflatus* is exceptional within this genus in having a polymorphic worker caste with the major workers having an inflated propodeum filled with a red liquid (Yamane & Hashimoto 1999). Presently, we have no information about

the function of the red liquid. However, as we did not observe the ants using this liquid during their marching, it is possible that they use it to calm prey ants while raiding. This view seems to be supported by their predation on *Paratrechina longicornis*. This species is known as the “crazy ant” because of its extremely rapid movement, and also has powerful alarm-defense secretions (Witte *et al.* 2007). Capturing *P. longicornis* without chemical means may be very difficult. This is because *Aenictus* species are among the smallest of the true army ants both in body and colony size (Schneirla 1971), and because other ants are potentially dangerous prey. If this assumption is true, such specific predatory behaviours may have caused different prey utilization patterns in most *Aenictus* species.

In conclusion, the present results clearly show that the four sympatric *Aenictus* species prey on different groups/species of prey ants and indicate that this differentiation allows them to co-exist. We consider that interspecific differences in foraging mode, such as foraging stratum and prey size selection, are major factors in facilitating prey partitioning. In addition, our observations suggest that other factors related to difficulties in treating dangerous prey (subduing, handling and capturing) may also have affected the prey menu of each species. Further field surveys on foraging habits in more *Aenictus* species together with studies of their prey ant biology will clarify the behavioural and ecological determinants of prey use pattern and coexistence in these ant-eaters.

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