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Prey specialization of army ants of the genus *Aenictus* in Malaysia

Abstract

Army ants of the genus *Aenictus* in the investigation area Pasoh Forest Reserve (Malaysia, Negeri Sembilan) are specialized on other ants as food source. This is also true for *A. gracilis* EMERY and *A. laeviceps* (F. SMITH), for which a much wider food spectrum is known from the Philippines. Prey could be taken off in 9 of 11 species (4 of them hitherto undescribed) found in the area. The different prey spectrum of each *Aenictus* species indicates resource partitioning, which is shown in preference of particular taxa, strata and prey size. These factors are described and discussed. A list of the prey species is included. An attack of *Aenictus dentatus* FOREL on a *Pheidole* species is described in detail.

Kurzfassung

Beutespezialisierung der Treiberameisen der Gattung *Aenictus* in Malaysia

Im Untersuchungsgebiet Pasoh Forest Reserve (Malaysi Negeri Sembilan) lebende Treiberameisen der Gattung *Aenictus* sind auf andere Ameisen als Nahrungsquelle spezialisiert. Dies gilt auch für *A. gracilis* EMERY und *A. laeviceps* (F. SMITH), für die von den Philippinen ein viel breiteres Nahrungsspektrum bekannt ist. Bei 9 von insgesamt 11 gefundenen Arten – von denen 4 bislang unbeschrieben sind – konnte Beute entnommen und identifiziert werden. Das für jede *Aenictus*-Art unterschiedliche Artenspektrum von Beuteobjekten deutet auf eine Ressourcen-Teilung hin. Sie äußert sich in Bevorzugung bestimmter Taxa, Strata und Beutegröße. Dieses wird beschrieben und diskutiert. Eine Liste der Beutearten ist aufgeführt. Ein Überfall von *Aenictus dentatus* FOREL auf eine *Pheidole*-Art wird detailliert beschrieben.

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1. Introduction

The genus *Aenictus* occurs both in the Indo-Australian region and in tropical Africa, with its centre of distribution in South-East Asia. WILSON (1964) in his revision listed 34 species for the Indo-Australian region. In the last years three new species from Sumatra were described (TERAYAMA & YAMANE 1989), and additional three from Thailand and Vietnam (TERAYAMA & KUBOTA 1993). It is supposed, that all members of this genus are predominantly or exclusively specialized on other ants as prey (CHAPMAN 1964, GOTWALD 1976,

1978, 1982, SCHNEIRLA & REYES 1966, WILSON 1964). However, the extent of the specialization on particular ant species is not known. Solely for *A. gracilis* and *A. laeviceps* some data exist. Both species were investigated by CHAPMAN (1964) and SCHNEIRLA & REYES (1966) in the Philippines. According to these authors, both species have very wide prey spectra, including many arthropodes (spiders, wasps), as well as other invertebrates (earthworms), with other ants being the most common prey. Both species hunt similar prey, that of *A. gracilis* being in general smaller than that of *A. laeviceps*, but with a wide degree of overlapping (SCHNEIRLA & REYES 1966). CHAPMAN (1964) gives a list of ant species taken as prey by both *Aenictus* species in the Philippines (tab. 1), without differentiating between *A. gracilis* and *A. laeviceps*.

Eleven species of *Aenictus* were found in the investigated area in Pasoh Forest Reserve. We presumed resource partitioning as one way to maintain sympatric occurrence of them. We investigated therefore more closely the prey spectra of the *Aenictus* species recorded in this area.

2. Study sites and methods

Most of the observations were made in Pasoh Forest Reserve, a primary lowland rain forest in the state Negeri Sembilan, managed by the Forest Research Institute of Malaysia (FRIM). In the results are also included data gained in the environs of Ulu Gombak and (in one case of *A. camposi*) of Sekinchan, both in the state Selangor.

Pasoh Forest Reserve is one of the few remaining fragments of the primary lowland rain forest in Peninsular Malaysia. It lies about 140 km south-east of Kuala Lumpur (2°59' N, 102°19' E) and consists of a core area of 650 ha of a primary lowland mixed dipterocarp forest surrounded by another 650 ha of buffer zone of partly regenerated and partly virgin forest. A further about 1000 ha of primary hill dipterocarp forest rises to about 600 m a.s.l. to the east. Except for this slope, the terrain is relatively flat with an altitude of 90 m (MANOKARAN & KOCHUMEN 1990, MANOKARAN et al. 1990). The soils are mainly loamy or sandy clay, the pH is 4.3-4.8 (ALLBROOK 1973). Climate data were recorded between 1970 and 1974 (SOEPADMO 1978, AOKI et al., 1978). The annual rainfall varied between 1728 mm and 3112 mm with a mean value of 2054 mm. The months April-May and November-December were relatively wet (250-300 mm rainfall), February-March and July-August relatively dry (30-100 mm rainfall). Somewhat different are data from the nearest meteorological station at Kuala Pilah (about 25 km distance). A mean annual rainfall of 1850 mm is recorded with rain fairly evenly distributed throughout the year,

Table 1. Ant species taken as prey by *Aenictus gracilis* and *A. laeviceps* in the Philippines (CHAPMAN 1964).

Ponerinae
<i>Ponera</i> sp.
Myrmicinae
<i>Crematogaster</i> sp.
<i>Ischnomyrmex longipes</i> EMERY
<i>Myrmicaria brunnea</i>
subsp. <i>subcarinata</i> EMERY
<i>Pheidole</i> sp.
<i>Pheidologeton diversus</i> JERDON
<i>Pristomyrmex</i> sp.
<i>Tetramorium</i> sp.
Dolichoderinae
<i>Dolichoderus bituberculatus</i> MAYR
Formicinae
<i>Acropyga molucca</i> MAYR
<i>Acantholepis chapmani</i> WHEELER
<i>Anopolepis longipes</i> JERDON
<i>Camponotus carin</i> EMERY
<i>Camponotus leonardi</i> EMERY
<i>Camponotus</i> sp.
<i>Echinopla</i> sp.
<i>Paratrechina longicornis</i> LATR.
<i>Polyrhachis armata</i> LEGUILLOU
<i>Polyrhachis bihamata</i> DRURY
<i>Polyrhachis (Myrma)</i> sp.
<i>Polyrhachis</i> sp.

except that monthly rainfall is less than 100 mm in June (MANOKARAN & KOCHUMMEN 1990). Monthly mean temperature in Pasoh 3 m above the ground was 23,0 °C (range 17,5-29,7 °C) in the forest and 24,8 °C (range 19,6-35,9 °C) at the base camp (SOEPADMO 1978, AOKI et al. 1978).

The second locality, Ulu Gombak Field Studies Centre, is a research station of the University of Malaya near Kuala Lumpur (3°19' N, 101°45' E) at an altitude of 220 m. The area is covered with secondary lowland dipterocarp forest. At various locations bamboos were dominant as a result of previous logging (MASCHWITZ et al. 1989).

The third locality (one observation only) is a peat swamp forest near Sekinchan, Selangor, at the west coast of the peninsula (about 3°30' N, 101° E).

To investigate the prey spectra of the army ants their raids were observed whenever encountered, and the visible booty items were picked out. To lesser extent this was done also during emigrations, as probably all encountered *Aenictus* colonies were in the migratory phase and transported the food to new bivouac sites. Almost all of the booty items were taken off from the columns of *Aenictus*. Especially attention was paid to the imagines of prey species. Some were collected directly from attacked colonies, when it was clear, that imagines of these colonies were taken as prey by the army ants (i.e. they were killed and transported away).

The field work was done by K. R. Specimens are deposited in Staatliches Museum für Naturkunde Karlsruhe, Germany, and in the entomological collection of the Forest Research Institute of Malaysia (FRIM), Kepong, Kuala Lumpur. The new species of *Aenictus* will be described elsewhere.

3. Results

In the investigated area (about 25 ha) in Pasoh Forest Reserve a total of 11 species of *Aenictus* was found, four of them undescribed (TERAYAMA, personal com.). They are: *A. aratus* FOREL, *A. camposi* WHEELER & CHAPMAN, *A. cornutus* FOREL, *A. dentatus* FOREL, *A. gracilis* EMERY, *A. hottai* TERAYAMA & YAMANE, *A. laeviceps* (F. SMITH), *Aenictus* sp. n. [near *laeviceps*], *Aenictus* sp. n. 2, *Aenictus* sp. n. 3, *Aenictus* sp. n. 5. This is somewhat less than 30% of the known species number of this genus, and quite a high number of army ants for the small area, though the nomadic habit and comparatively long collecting period (6,5 months) must be considered.

Booty of 9 species of *Aenictus* could be collected. They all seem to be specialized on other ants as food. From 1062 prey items taken off only 4 were no ants. (1 small spider in *A. laeviceps*, 1 leaf hopper in *Aenictus* sp. n. [near *laeviceps*], and 2 unidentified larvae in *Aenictus* sp. 2). However, it was observed, that during an attack of *Aenictus* sp. n. 3 on a nest of *Acropyga acutiventris* and *A. gracilis* on *Acropyga* sp. 3, trophobiontic Homoptera which have been within the prey species' nest, were taken, too.

53 ant species were found as prey of *Aenictus* spp. According to our observations both brood and imagines are taken as prey. All prey species listed in table 2 were determined by the imagines, solely *Odontomachus* sp. was recognized by the heads of the pupae.

The prey spectrum of each *Aenictus* species is clearly different. This is also true for the three epigeically foraging species *A. gracilis*, *A. laeviceps* and *Aenictus* sp. n. [near *laeviceps*] – species from which the highest numbers of food items were taken off.

Some specialization of the *Aenictus* species can be noticed. Particularly, species of the four most epigeic species *cornutus*, *gracilis*, *laeviceps* and sp. n. [near *laeviceps*] possess, despite of quite a wide prey spectrum, at most one prey species in common. Noticeable is also the difference between *A. laeviceps* and *Aenictus* sp. n. [near *laeviceps*], especially the „predilection“ of the last for *Pseudolasius*. In 10 of 13 raids *Pseudolasius* was stated as prey, in seven raids *Pseudolasius* sp. 5. On the contrary, none of the *Pheidole* species was stated, although they occurred with great constancy as prey of *A. laeviceps* (in 5 of 8 raids). Whether *A. aratus* may be specialized on *Pheidole* spp. as prey, as suggested by the few data, must be proofed by more observations. Taxonomic preferences at the subfamily level are recognizable in *A. camposi* (small Formicinae) and *A. gracilis* (Formicinae and Dolichoderinae).

Looking closely to the prey species it seems, that some of them are especially suitable as prey. For example *Technomyrmex* sp. 8 and *Camponotus* sp. 4 were taken by three *Aenictus* species.

prey speci	<i>Aenictus</i> -species								
	1 (3)	2 (6)	3 (2)	4 (7)	5 (12)	6 (1)	7 (8)	8 (13)	9 (1)
<i>Camponotus</i> sp.25							+(1)		
<i>Camponotus</i> sp.29								+(1)	
<i>Camponotus</i> sp.30							+(1)		
<i>Polyrhachis bicolor</i>							+(2)		
<i>Polyrhachis rufipes</i>							+(1)		
<i>Polyrhachis schang</i>							+(1)		
<i>Polyrhachis striata</i>								+(1)	
<i>Polyrhachis</i> sp.13							+(1)		
<i>Polyrhachis carbonaria</i>							+(1)		
<i>Polyrhachis</i> sp.27							+(1)		
<i>Polyrhachis</i> sp.29				+(1)					
<i>Polyrhachis</i> sp.31							+(1)		

Table 3. Nest sites of prey species in Pasoh: A: ground stratum (soil, litter and dead wood on the ground), B: low arboreal stratum (hanging dead wood, tree trunks, silk- and carton nests etc. up to approx. 3 m height), C: high arboreal stratum (from approx. 3 m height up to the top of the canopies).

prey species	stratum	nest site (n)	prey species	stratum	nest site (n)
Ponerinae			<i>Euprenolepis procera</i>	A	dead wood, leaf litter (7)
<i>Hypoponera</i> sp.3	A ²		<i>Euprenolepis</i> sp.2	A	soil (1)
<i>Odontomachus</i> sp.	A ²		<i>Paratrechina</i> sp.1	A	dead wood, litter (9)
Myrmicinae			<i>Paratrechina</i> sp.2	?	
<i>Crematogaster</i> sp.5	B	under bark (1)	<i>Paratrechina</i> sp.4		
<i>Crematogaster</i> sp.8	?		<i>Paratrechina</i> sp.7	A	dead wood (1)
<i>Crematogaster</i> sp.19			<i>Paratrechina</i> sp.8	B	epiphyte (1)
<i>Pheidole longipes</i>	A	dead wood (3)	<i>Paratrechina</i> sp.G-2	?	
<i>Pheidole comata</i>	A	soil (2)	<i>Prenolepis naoroji</i>		
<i>Pheidole</i> sp.3	A	dead wood (4)	<i>Prenolepis</i> sp.2		
<i>Pheidole</i> sp.4	?		<i>Pseudolasius</i> sp.4	A ²	
<i>Pheidole</i> sp.6	A	soil (2)	<i>Pseudolasius</i> sp.5	A ²	
<i>Pheidole</i> sp.8	A	dead wood, litter (9)	<i>Pseudolasius</i> sp.6	A ²	
<i>Pheidole</i> sp.17	?		<i>Camponotus</i> sp.4	A	litter (1)
<i>Pheidole</i> sp.18			<i>Camponotus</i> sp.19	C	foliage (silk nest) (3)
<i>Pheidole</i> sp.19			<i>Camponotus</i> sp.25	?	
<i>Pheidole</i> sp.G-1			<i>Camponotus</i> sp.29		
Dolichoderinae			<i>Camponotus</i> sp.30	C	dead wood
<i>Technomyrmex</i> sp.1	A	dead wood, litter (3)	<i>Polyrhachis bicolor</i>	BC	foliage (silk nest) (2)
<i>Technomyrmex</i> sp.4	B	dead wood, under bark (3)	<i>Polyrhachis rufipes</i>	B	dead wood (2)
<i>Technomyrmex</i> sp.7	B ¹	foliage (1)	<i>Polyrhachis schang</i>	BC	foliage (silk nest) (2)
<i>Technomyrmex</i> sp.8	?		<i>Polyrhachis striata</i>	A	dead wood, litter, soil (4)
<i>Technomyrmex</i> sp.9			<i>Polyrhachis</i> sp.13	?	
<i>Technomyrmex</i> sp.G-1			<i>Polyrhachis carbonaria</i>	AB	dead wood, soil (2)
<i>Technomyrmex</i> sp.G-2			<i>Polyrhachis</i> sp.27	?	
<i>Technomyrmex</i> sp.G-3			<i>Polyrhachis</i> sp.29		
Formicinae			<i>Polyrhachis</i> sp.31	B	foliage (silk nest) (5)
<i>Acropyga acutiventris</i>	A	dead wood (3)			
<i>Acropyga</i> sp.3	A	soil (1)			

¹ One colony was found in approx. 3 m height between leaves.

² No nests of these species were found, but all representatives of these genera were found in Pasoh in the ground stratum.

Table 4. Body size of *Aenictus* spp. and their prey species (total lengths). Data behind the diagonal stroke refer to soldiers. A horizontal stroke marks polymorphic species without a differentiate soldier caste.

<i>Aenictus</i> sp. (length [mm])	prey sp.	length [mm]	<i>Aenictus</i> sp. (length [mm])	prey sp.	length [mm]
<i>aratus</i> (3.8)	<i>Pheidole</i> sp.4	3.0/5.0		<i>Polyrhachis</i> sp.20	6.5
	<i>Pheidole</i> sp.8	1.9/3.0		<i>Polyrhachis</i> sp.27	6.0
<i>camposi</i> (2.5)	<i>Paratrechina</i> sp.1	2.2	sp. n. [near <i>laeviceps</i>] (4.2)	<i>Polyrhachis</i> sp.31	4.3
	<i>Paratrechina</i> sp.2	1.4		<i>Hypoponera</i> sp.3	2.6
	<i>Paratrechina</i> sp.4	1.3		<i>Creumatogaster</i> sp.19	1.7
	<i>Paratrechina</i> sp.7	1.6		<i>Technomyrmex</i> sp.1	3.0
	<i>Paratrechina</i> sp.8	2.0		<i>Euprenolepis procera</i>	4.5-6.0
	<i>Prenolepis naoroji</i>	2.9		<i>Prenolepis naoroji</i>	2.9
<i>cornutus</i> (4.3)	<i>Creumatogaster</i> sp.8	3.0	sp. n.3 (2.9)	<i>Pseudolasius</i> sp.4	3.3/5.1
	<i>Pheidole</i> sp.19	/3.4		<i>Pseudolasius</i> sp.5	3.5/4.9
	<i>Technomyrmex</i> sp.8	3.1		<i>Pseudolasius</i> sp.6	/4.4
	<i>Technomyrmex</i> sp.9	4.4		<i>Camponotus</i> sp.4	9.5/12.8
	<i>Polyrhachis</i> sp.29	5.8		<i>Camponotus</i> sp.29	8.5/11.5
	<i>Pheidole longipes</i>	5.5/7.5		<i>Polyrhachis striata</i>	10.8
<i>dentatus</i> (4.7)	<i>Pheidole comata</i>	5.0/7.5	<i>Acropyga acutiventris</i>	3.8	
	<i>Pheidole</i> sp.3	3.0/5.0			
	<i>Pheidole</i> sp.4	3.0/5.0			
	<i>Pheidole</i> sp.6	3.0/6.2			
	<i>Pheidole</i> sp.17	/3.2			
	<i>Technomyrmex</i> sp.1	3.0			
	<i>Technomyrmex</i> sp.8	3.1			
	<i>Euprenolepis procera</i>	4.5-6.0			
	<i>Euprenolepis</i> sp.2	4.2-5.8			
	<i>Camponotus</i> sp.4	9.5/12.8			
<i>gracilis</i> (4.0)	<i>Technomyrmex</i> sp.4	2.4			
	<i>Technomyrmex</i> sp.7	4.1			
	<i>Technomyrmex</i> sp.8	3.1			
	<i>Technomyrmex</i> sp.G-1	2.5			
	<i>Technomyrmex</i> sp.G-2	2.6			
	<i>Technomyrmex</i> sp.G-3	2.6			
	<i>Acropyga</i> sp.3	2.0			
	<i>Paratrechina</i> sp.1	2.2			
	<i>Paratrechina</i> sp.G-1	3.2			
	<i>Paratrechina</i> sp.G-2	1.9			
<i>hottai</i> (5.2)	<i>Prenolepis</i> sp.2	3.9			
	<i>Odontomachus</i> sp.	10.0 ¹			
<i>laeviceps</i> (4.1)	<i>Creumatogaster</i> sp.5	2.3-4.9			
	<i>Pheidole longipes</i>	5.5/7.5			
	<i>Pheidole</i> sp.18	/3.2			
	<i>Pheidole</i> sp.19	/3.4			
	<i>Pheidole</i> sp.G-1	2.3			
	<i>Prenolepis</i> sp.2	3.9			
	<i>Camponotus</i> sp.4	9.5/12.8			
	<i>Camponotus</i> sp.19	5.2			
	<i>Camponotus</i> sp.25	4.8			
	<i>Camponotus</i> sp.30	7.4/9.0			
	<i>Polyrhachis bicolor</i>	6.2			
	<i>Polyrhachis rufipes</i>	6.4			
	<i>Polyrhachis schang</i>	6.2			
	<i>Polyrhachis</i> sp.13	6.8			

Both species of *Odontomachus* found in Pasoh Forest Reserve (*O. rixosus* F. SMITH and *O. similimus* F. SMITH) have a total length of about 10 mm.

Beside of preferences for certain taxa as prey, spatial distribution of the army ants and their prey species may also have an influence of the prey spectrum of *Aenictus*. With regard to their extranidal activities the observed species of *Aenictus* can be divided in two groups. The first group are epigeic active species, to which belong *A. cornutus*, *gracilis*, *laeviceps* and sp. n. [near *laeviceps*]. The raids and emigrations are proceeded by them on the soil, litter, and wood. To the second group – hypogeic active species – belong all other representatives of this genus. They perform raids and emigrations below roots, in subterranean cavities, and under the litter and usually appear on the surface for short distances, only. This separation does not hold comparing foraging behavior, at the front of the raids. The epigeic species are active then also under the litter, searching for prey, and at least some hypogeic *Aenictus* pursue their prey also quite high on tree trunks. Thus, for example, *A. hottai* was seen at a height of about 3 m on a tree stem, apparently foraging, whereas *A. dentatus* likewise pursued fleeing *Pheidole* several meters high on a tree trunk. In this context the nesting sites of the prey ants are interesting. They are shown in table 3.

As expected all registered prey ants of the hypogeic group of *Aenictus* nest in the ground stratum. In contrast the epigeic active *Aenictus* species seem to prefer distinct strata to forage. It seems to be least pronounced in *A. gracilis*. Successful foraging of this spe-

Table 5. Body size of *Aenictus* spp. and their prey species: total lengths of *Aenictus* spp., arithmetic means of the total lengths of prey species (\pm standard deviation [SD], soldiers omitted, species without differentiated soldiers averaged), and ratio between the two quantities. Data ordered after increasing size of the *Aenictus* spp.

<i>Aenictus</i> sp.	<i>Aenictus</i> length [mm]	prey length ($\bar{x} \pm$ SD [mm])	ratio prey length/ <i>Aenictus</i> length
<i>camposi</i>	2.5	1.9 \pm 0.6	0.76
sp. n.3	2.9	3.8	1.31
<i>aratus</i>	3.8	2.5 \pm 0.8	0.66
<i>gracilis</i>	4.0	2.8 \pm 0.7	0.70
<i>laeviceps</i>	4.1	5.6 \pm 1.7	1.37
sp. n. [near <i>laeviceps</i>]	4.2	5.1 \pm 3.3	1.21
<i>cornutus</i>	4.3	4.1 \pm 1.3	0.95
<i>dentatus</i>	4.7	4.5 \pm 2.1	0.96
<i>hottai</i>	5.2	10.0	1.92

cies was observed as well in the litter as on tree trunks and lianas in the B-stratum. *A. laeviceps* showed a distinct preference of the arboreal strata, whereas *Aenictus* sp. n. [near *laeviceps*] was obviously restricted to the ground stratum while foraging. Data relating to foraging behavior are unfortunately lacking for *A. cornutus*. The foraging activity is apparently not restricted to particular nest sites of the prey species, but rather to a particular stratum as whole.

Another factor which may influence the prey selection of *Aenictus* is the body size. According to SCHNEIRLA & REYES (1966) the prey of (somewhat smaller) *A. gracilis* is in general smaller than that of *A. laeviceps*. Prey ants of the neotropical Ecitoninae range up to 1.5 times the length of the largest army ant workers (RETTENMEYER et al. 1983). Table 4 gives a survey about the total lengths of *Aenictus* and their prey species. The length was measured on single, apparently average specimens in dorsal view from the tip of the mandibles to the end of the gaster. If the specimens were not outstretched, measurements were made in two or three planes and the results were summed.

Arithmetic means of the body size of the prey species and their ratio to the body size of *Aenictus* spp. are shown in table 5.

It seems, that generally the larger species of *Aenictus* take indeed bigger prey on average than smaller ones. However, the correlation is rather poor. The correlation coefficient is significant if all *Aenictus* species are taken into account ($r = 0.735$, $P < 0.05$), but not significant if both species with single observations (*Aenictus* sp. n. 3 and *A. hottai*) are omitted ($r = 0.705$, n.s.). Noticeable is the difference between *A. gracilis* and *A. laeviceps*, the average prey size of the latter being two times bigger than of the former species. Compared with its own length *A. gracilis*, beside of *A. aratus* and

A. camposi, take the smallest prey species. Generally the prey species are smaller or only slightly longer than their predators (see tab. 4 and 5). However, in some cases the prey's length is more than two times the length of the *Aenictus*: *Polyrhachis striata* and *Camponotus* sp. 4 in *Aenictus* sp. n. [near *laeviceps*], and *Camponotus* sp. 4 in *A. laeviceps*.

Though specialized on ants, *Aenictus* species did not take all ant species as prey. They ignored many species, showed avoidance behavior, particularly against other army ants, and sometimes became prey themselves, as show the following observations:

1. Ignoring of other ants during a raid or emigration:

- *Dolichoderus* sp. 1, *Crematogaster* sp. 3, and *Meranoplus* sp. were completely ignored by *A. gracilis* during a raid, although their trails intersected with the trails of the other ant species.
- Individuals of *Polyrhachis* sp. and *Diacamma* sp. went repeatedly on the same branches as *A. gracilis*, without provoking any attack.
- The same observation was also made for *Polyrhachis* sp. 16 and *A. laeviceps*.
- An unidentified ant male fell in a column of *A. gracilis*, but could withdraw without difficulties.
- A single worker of *Odontomachus rixosus*, which was tentatively placed into a raid of *A. hottai*, was not attacked and could retire without difficulties. (In one case brood of *Odontomachus* was found to be booty of *A. hottai*. Possibly the imagines of this species are not regarded as prey, at least outside of the nest area. This is also known from other investigated species of *Aenictus* in Afrika; GOTWALD 1976, 1982).
- An emigration column of *A. cornutus* ran partly on the same route as a trail of *Cataulacus insularis*. No aggression was observed, although single *Cataulacus* went into the *Aenictus* column.

Plate 1. a) Encounter of two army ant raids: *Aenictus camposi* (yellow) and *Aenictus* sp. n. [near *laeviceps*] (black). The raids have been temporarily interrupted but no hostilities occurred. Eventually both species changed the routes and continued their raids; Photograph: ROŚCISZEWSKI.



Plate 1. b) *Aenictus* sp. n. [near *laeviceps*] killing during a raid a worker of *Polyrhachis striata*, one of the prey species; Photograph: ROŚCISZEWSKI.

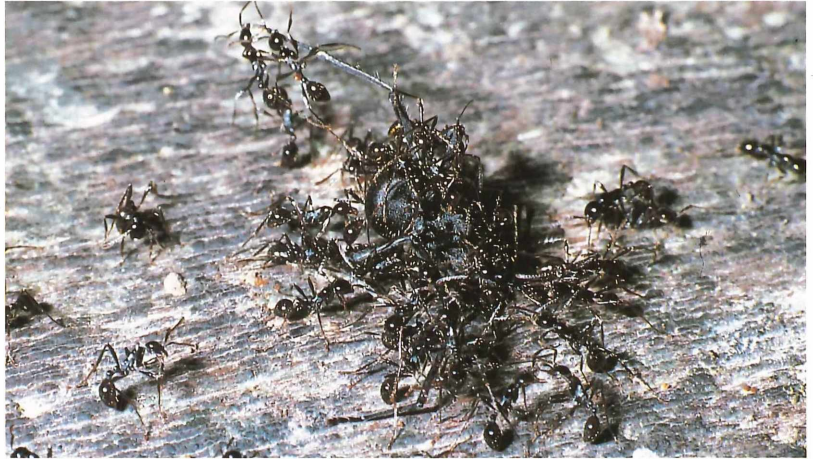


Plate 1. c) Nest evacuation of a prey species (apparently belonging to the tribe Prenolepidini: *Paratrechina* sp., *Prenolepis* sp. or *Euprenolepis* sp.) after detection of their nest by *Aenictus*; Photograph: MASCHWITZ.



2. Ignoring of other ants despite of disturbances caused by them:

- A raid of *A. gracilis*, as well as one of *Aenictus* sp. n. [near *laeviceps*] was disturbed by *Lophomyrmex bedoti*, which stood on both sides of the *Aenictus* trail. Occasionally short fights with the *Aenictus* „guards“ setting against them occurred, but generally the army ants behaved very passive.
- In similar way a raid of *A. gracilis* was disturbed by *Gnamptogenys* sp.

3. Avoidance behavior:

- A raid of *Aenictus* sp. n. [near *laeviceps*] was forced by *Paratrechina* sp. 8 to change its route by gathering and blocking the stretch. The same species of *Paratrechina* was found to be the prey of *A. camposi*.
- During a contact of a raid of *A. hottai* with an emigration column of *Leptogenys* cf. *borneensis* there were no hostilities: The ants of both colonies got out of the way after short hesitation.
- During an encounter between raid columns of *A. camposi* and *Aenictus* sp. n. [near *laeviceps*] no aggressions were observed. Both species changed their trails in such a way, that these did not intersect (*Aenictus* sp. n. [near *laeviceps*] used a „bridge“ of litter, whereas *A. camposi* continued on the soil: plate 1a).

4. *Aenictus* as prey of other ants:

- Workers of *Oecophylla smaragdina* (mostly several individuals) were repeatedly observed picking out single workers of *A. gracilis* from the trail, killing, and carrying them to the nest.
- *Odontoponera transversa* picked up single individuals from the trails of *A. hottai* and *A. cornutus*.

CRAWLEY (1924, cited after CHAPMAN 1964) describes an attack of *A. aitkeni* var. *dentata* FOREL (= *dentatus* FOREL: WILSON 1964) on a colony of *Pheidole plageria* F. SMITH nesting in the roof of a house. According to him only brood was taken as prey, but no imagines. This does not at all agree with our observations. We therefore describe here an attack of *A. dentatus* on two nests of *Pheidole comata* F. SMITH, which took place on February 13, 1990 from 11 until 13 o'clock:

The *Aenictus* ran preferably below, but sometimes also on the litter – searching for the prey in the litter. Under the roots of a young tree they discovered a nest of *Pheidole*, which fled with their brood upwards. The *Aenictus* pursued them approx. 2 m high. On this occasion several *Pheidole* were killed. The gaster of the soldiers were cut off and taken as booty, otherwise also whole imagines, but mainly brood. Several metres apart of the tree the *Aenictus* discovered in the litter some individuals of the prey species and killed them, too. At the time, some *Pheidole* ants from another nest, which was also located under tree roots 1-2 m apart, ran out with their brood. They also fled on the tree trunk upwards, parts of the brood were robbed

by *Bengalia* flies. (*Bengalia* flies, family Calliphoridae, are known to rob prey and brood from different ant species; MASCHWITZ & SCHÖNEGGE 1980. In Pasoh they could be regularly observed robbing prey from columns of epigeic active *Aenictus* species during the day.) The *Aenictus*, however, did not become aware of the *Pheidole* and passed the tree. The *Pheidole* returned slowly into their nest. We guided now the *Aenictus* raid to the *Pheidole* nest by offering them some prey ants on suitable places. The army ants soon discovered the nest of the prey and came on, whereas the *Pheidole* fled again with their brood on the trunk upwards. They were pursued by *Aenictus* workers several metres high and offered no resistance, many dropped on the ground and were killed there. After approx. 15 minutes the *Aenictus* slowly descended the trunk, followed hesitatingly by the *Pheidole*, mainly soldiers. They snapped occasionally at the *Aenictus* and sometimes short fights happened, but the opponents separated always from each other after a short time. During the next 15 minutes the *Aenictus* entirely drew back from the tree and remained only at the robbed nest. Occasionally individual *Pheidole* soldiers which ventured to approach too close, were still seized and killed. A lot of booty was carried off: whole brood, parts of brood, whole imagines of the minor workers, and gaster of the soldiers; seldom other parts of the soldiers. About 1 hour after the beginning of the attack, the army ants abandoned definitely the robbed nest, and the *Pheidole* returned slowly. However, the raid of *Aenictus* continued, branched out, and a part of the troop came back from the other side of the trunk. The *Pheidole* fled again upwards – several were seized and killed. But this time the *Aenictus* pursued them only approx. 1 m high on the trunk and did not enter the robbed nest once more. Finally, after about 1.5 hour the *Pheidole* moved back to their nest with the rescued brood. The queen was not seen.

In a similar pattern *A. dentatus* proceeded an attack on a colony of *Pheidole longipes* (F. SMITH). Also in that case the prey left their nest in time, and would probably have remained undiscovered by the *Aenictus* without the intervention of the observer. In the case of the subterranean *Acropyga acutiventris* ROGER many imagines fled with brood being attacked by *Aenictus* sp. 3. Though the nest got robbed, the colony survived, as the *Aenictus* did not pursue them on the ground surface.

4. Discussion

Our observations allow the following conclusions:

1. All species of *Aenictus* in the investigated area take ants as prey and at least some are apparently fully specialized on other ants as food resource. This is also true for *A. gracilis* and *A. laeviceps* – species

which tend to be food generalists in the Philippines (CHAPMAN 1964, SCHNEIRLA & REYES 1966).

2. The different prey spectrum indicates resource partitioning. The observed factors are:
 - Preference of particular taxa (*A. camposi*: Formicinae, mainly *Paratrechina* spp.; *A. aratus* and partly *A. dentatus*: *Pheidole* spp.).
 - Foraging in different strata (e.g. *A. laeviceps* and *Aenictus* sp. n. [near *laeviceps*]).
 - Preference of particular prey size (*A. gracilis* and *A. camposi*: small prey; *A. laeviceps* and *Aenictus* sp. n. [near *laeviceps*]: also bigger prey – see plate 1b and tab. 4 and 5).
3. Both brood and imagines are taken as prey. This was observed in 8 of 9 species. No imagines as prey were noticed in the only occasion in which *A. hottai* could be observed. Thus, for this species a definitive statement is not possible. The preponderance of the juvenile stages in other investigations (CHAPMAN 1964, MIRENDA et al. 1980) could be a result of the higher mobility of the imagines (flight). It is more likely, however, that the immobile, nutrient-rich brood is preferred, but not exclusively taken.
4. The flight reaction of some prey species (*Pheidole longipes*, *Pheidole comata*) can be interpreted as a specific behavior pattern.
5. Ant species which do not belong to the prey spectrum of particular *Aenictus* species are ignored or avoided.
6. *Aenictus* species seem not to take congeners, and probably also no other ants with army ant habits (e.g. *Leptogenys*) as prey. To our knowledge fights between *Aenictus* colonies have never been observed. CHAPMAN (1964) succeeded even in mixing of workers of two different species. The phenomenon of avoiding conflicts between army ant colonies is also known from the neotropis. No one species of Ecitoninae has been seen to injure or capture other ants of the subfamily (RETTEMEYER et al. 1983).

According to RETTEMEYER et al. (1983) about 20 sympatric species of army ants can be expected in a lowland moist tropical forest in the neotropis. This number could be true for the Pasoh Forest Reserve, too. Beside of the 11 *Aenictus* species (almost certainly some representatives of this genus remained undiscovered) several more species of ants with army ant life habits have been found in this locality: *Dorylus laevigatus* F. SMITH, *Leptogenys crassicornis* EMERY, *L. distinguenda* (EMERY), *L. mutabilis* (F. SMITH), and *Pheidologeton silenus* (F. SMITH). However, all of them can be regarded as generalists (MASCHWITZ et al. 1989, MASCHWITZ & STEGHAUS-KOVAC 1991, MOFFETT 1988, WEIßFLOG & MASCHWITZ unpublished data). Ant adults are reported to be prey of *Pheidologeton silenus*, but only as a minor diet component (MOFFETT 1988). Thus *Aenictus* species seem to be the only army ants of this region specialized in ants as prey.

Ants of the genus *Cerapachys*, of which 13 species were found in Pasoh Forest Reserve, are also, as far as it is known, specialized ant predators. However, because of their solitary scouting and group recruitment to the discovered prey nests, they are not regarded as army ants (HÖLLDOBLER 1982, HÖLLDOBLER & WILSON 1990).

Leaving the nest in time or an immediate flight in the case of detection of the nest by *Aenictus* seems to be a quite successful strategy for a prey species to avoid the total extinction of the colony (plate 1c). At least a part of the brood and the imagines keep alive and occupy their nest again. A repeated attack on the nest robbed just short time ago seems unlikely, as the *Aenictus* went on after the raid. One can suppose, that for the army ants it is more efficient to search for other prey nests which offer concentrated food supply in form of motionless brood, as to catch the dispersed fleeing ants. Such flight reaction was described also for two species of relatively large *Pheidole*, prey of *Neivamyrmex nigrescens* (MIRENDA et al. 1980). This American army ant is like the *Aenictus* species a column raider, has a comparable colony size (up to approx. 100000 individuals), and is specialized on other ants (and some species of termites) as prey. A very strong reaction shows *Camponotus festinatus*, one of the prey species of *N. nigrescens*. Already one single worker, which takes notice of the army ants, can cause the flight of the whole colony, including the queen. The ants stay for several hours in the vegetation outside of the nest. This reaction is of the all-or-none type, and can not be caused by mechanical disturbances or blowing into the nest. Hence, it is possibly a specific reaction against the threat by the army ants (LAMON & TOPOFF 1981). Mass evacuation as a reaction on the odour of single crushed worker of *Eciton hamatum* shows also *Dolichoderus rugosus* (RETTEMEYER et al. 1983). Nest defence as an alternative reaction on the presence of *N. nigrescens* occurs in smaller species of *Pheidole* (MIRENDA et al. 1980) and some *Camponotus* species (LAMON & TOPOFF 1981).

The prey spectrum of army ants depends probably on the composition and availability of the ant fauna (or of the potential prey generally) in space and time. This suggests the results of the investigations of MIRENDA et al. (1980) for *Neivamyrmex nigrescens*. Also the different prey spectrum of *A. gracilis* and *A. laeviceps* on the Philippines and in Pasoh Forest Reserve, is an indication of this assumption. According to CHAPMAN (1964), and SCHNEIRLA & REYES (1966) neither prey specialization nor resource partitioning between the two species is existing (except that prey of *A. gracilis* is in general smaller than prey of *A. laeviceps*). Both species take almost any invertebrate that they can find and overcome, and their prey lists overlap widely (SCHNEIRLA & REYES 1966). As ant prey the authors mention representatives of the genera *Polyrhachis*,

Camponotus, *Formica*, *Crematogaster* and *Pheidole*, without citing a detailed list of species. On contrary, our data show clear differences in prey spectra of the two species and specialization on other ants as prey. Looking on our results for these two species two factors must be taken into consideration:

- The still relative small number of prey registered (53 raids in all).
- Different sampling localities – Gombak for *A. gracilis*, mainly Pasoh for *A. laeviceps*.

We expect little differences in the ant fauna composition between both localities because of their relative similarity (about 150 km distance, about 130 m altitude difference, mostly similar vegetation structure). However, such differences cannot be fully ruled out and it is still possible, that the prey spectrum of *A. gracilis* in Pasoh differs in some way from that in Gombak.

Also other unknown factors may play a role in prey selection of army ants. *Eciton hamatum* is a neotropical army ant which feeds largely on ant brood. RETTENMEYER et al. (1983) reported differences in prey spectrum of *E. hamatum* in two localities, though the composition of ant faunas was at least partly similar in both areas. Attine ants are common in Panama, as well as in Ecuador, but are commonly raided by the army ant in the first, and rarely in the second locality. It is likely, however, that both ant faunas differ in their species composition and relative abundance of species. Thus, their similarity may be in fact superficially. Considering the poor data material to our opinion nothing can be stated about a prey specialization of *A. hottai* and *Aenictus* sp. 3. The presumption expressed by GOTWALD (1978, 1982), that the hypogeic foragers are usually trophic specialists, whereas the epigeic foragers become general predators, is not supported by our data. It may be simply a result of greater difficulties in observing of the former.

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