Prey spectrum of two army ant species on Central Amazonia, with special attention on the effect on spider populations

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Abstract

During six months of field work in a terra firme rainforest near Manaus in the central Amazon we collected prey fragments from 28 colonies of the large swarm-raiding army ant species *Eciton burchelli* and from 9 colonies of the smaller swarm-raiding ant *Labidus praedator*. Regarding the presence of prey fragments from 20 arthropod orders in samples of both army ant species, these might be considered generalist predators. But relative abundances of the prey fragments showed that only four arthropod orders made up 89 % of the prey of *Eciton burchelli* and nine arthropod orders 95 % of the prey of *Labidus praedator*. Spiders made up 13 % respectively 17 % of the prey. Identification of the spider fragments on the morphospecies level showed that *Eciton burchelli* hunted principally on spiders of one genus (*Ctenus*), which is represented by seven species in the study area. Comparison of preliminary density data for these spiders from the same site with the extrapolated number of spiders, caught during one day by a colony of *Eciton burchelli*, points out that the army ants have a high effect on *Ctenus* populations. *Labidus praedator* hunted on a wider variety of spiders, but *Ctenus* fragments were also found. We conclude, that repeated hunting of the two army ant species in the same area, which was observed in another site near Manaus, can have a very high impact on ground living spider assemblages.

Kurzfassung

Das Beutespektrum zweier Treiberameisen-Arten in Zentralamazonien, unter besonderer Berücksichtigung ihres Einflußes auf Spinnenpopulationen

Während sechsmonatiger Feldarbeiten in einem nicht-überschwemmten Regenwald bei Manaus in Zentralamazonien wurden Beutefragmente von 28 Kolonien der schwarmjagenden Treiberameisenart *Eciton burchelli* und von 9 Kolonien der ebenfalls schwarmjagenden Art *Labidus praedator* gesammelt. In den Aufsammlungen beider Arten waren Beutefragmente aus 20 Arthropodenordnungen zu finden, so daß diese Treiberameisen als Generalisten zu bezeichnen wären. Allerdings zeigen die relativen Abundanzen ein differenzierteres Bild. Nur vier Arthropodenordnungen stellten im Mittel 89 % der Beute von *Eciton burchelli* und neun Arthropodenordnungen im Mittel 95 % der Beute von *Labidus praedator*. Spinnen stellten mit 13 % bzw. 17 % für beide Ameisenarten eine wichtige Beutegruppe dar. Identifizierung der Spinnenfragmente bis auf Morphospezies-Ebene zeigte, daß *Eciton burchelli* hauptsächlich Spinnen der Gattung *Ctenus* jagte, einer Gattung, die im Untersuchungsgebiet mit 7 Arten vertreten ist. Ein Vergleich vorläufiger Daten zur Dichte dieser Spinnen im selben Gebiet mit der extrapolierten Zahl der Spinnen, die pro Tag von den Treiberameisen erbeutet wurden, weist auf einen hohen Effekt der Ameisen auf die Spinnenpopulation hin. *Labidus praedator* erbeutet eine größere Varietät von Spinnen, darunter auch *Ctenus*. Aufgrund von Beobachtun-

gen in einem zweiten Waldgebiet bei Manaus, die zeigen, daß *Eciton burchelli* und *Labidus praedator* innerhalb eines Jahres wiederholt in den gleichen Flächen jagen, schließen wir auf einen beträchtlichen Einfluß der Treiberameisen auf die Struktur von Spinnenpopulationen und -assoziationen des Waldbodens.

Resumo

Espectro de presas de duas espécies de formigas de correição na Amazônia central, com ênfase no efeito das formigas sobre as populações de aranhas

Durante seis meses de trabalho de campo numa floresta de terra firme na Amazônia central perto de Manaus coletamos fragmentos de presas de 28 colónias de *Eciton burchelli* e de 9 colónias de *Labidus praedator*, ambas espécies de formigas de correição predando em forma de enxame. Através da presência de 20 ordens de artrópodos nas coletas de presa das duas espécies de formigas, estas poderiam ser consideradas predadores generalistas. Porém as abundâncias relativas dos fragmentos de presa mostraram que somente quatro ordens de artrópodos forneceram 89 % da presa de *Eciton burchelli* e nove ordens 95 % da presa de *Labidus praedator*. Aranhas representaram 13 % e 17 % da presa, respectivamente. A identificação dos fragmentos de aranhas até o nível de espécie mostrou que *Eciton burchelli* caçou principalmente aranhas de um só gênero (*Ctenus*), o qual está representado por sete espécies na área estudada. A comparação de dados préliminares sobre a densidade destas aranhas da mesma área com o número de aranhas capturado por *Eciton burchelli* - extrapolado para um dia inteiro de caça, indica que as formigas de correição prejudicam fortemente as populações de *Ctenus*. *Labidus praedator* caçou uma variedade mais ampla de aranhas, incluindo *Ctenus*. Nos concluímos que caçadas repetidas das duas espécies de formigas de correição na mesma área, o que foi observado numa outra reserva perto de Manaus, podem afetar fortemente populações e associações de aranhas errantes do chão.

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1. Introduction

Much of the recent discussion in community ecology has focused on the importance of predation versus competition in structuring communities (CONNELL 1983, SCHOENER 1983, SIH et al. 1985). For tropical areas a greater predatory pressure than in temperate areas has been hypothesized as a mechanism of maintaining high species diversity (CONNELL 1975, 1978; PAINE 1966). Intense predation in the tropics has been shown mostly in marine environments and by herbivores on trees (CONNELL 1971, 1975; JANZEN 1970), but seldom in terrestrial invertebrate communities.

Ants are among the most abundant and species rich invertebrate predators in the tropics, and it has been shown that the rate of predation by ants on wasps increases towards the tropics (JEANNE 1979). Especially army ants could be expected to have a substantial impact on the ground fauna because they are not only carnivorous predators, but, due to their nomadic lifestyle, they forage over a vast area during their activity cycle (SCHNEIRLA 1971). Unlike most of the other neotropical army ants of the tribe Ecitonini, *Eciton burchelli* and *Labidus praedator* are swarm-raiding ants and prey on a wide variety of arthropods (HÖLLDOBLER & WILSON 1990, RETTENMEYER et al. 1983, SCHNEIRLA 1971).

During studies on spider communities in central Amazon rain forests, repeated movements of *E. burchelli* and *L. coecus* were observed within a 400 m² experimental plot (GASNIER & HÖFER, unpublished data). An apparently low density of spiders and a decline of spider abundance during one year within the experimental area led to the hypothesis that predation by army ants could affect spider populations and influence the structure of spider assemblages in leaf litter. To evaluate such effects, we initiated a field study on the ecology of two army ant species, with special emphasis on the prey spectrum of these ants. In this paper, we present a preliminary analysis of the prey item data of two species of army ants and estimate the effect of army ants on spider populations.

2. Study area and Methods

The study was conducted between June and November 1993 in a terra firme rainforest (reserve 1501) of the „Biological Dynamics of Forest Fragments Project" (BDFFP, INPA/Smithsonian Institution), approximately 80 km north of Manaus, in central Amazonia (2° 25' S, 59° 48' W). The reserve, which has been described in detail by LOVEJOY (1980) and LOVEJOY et al. (1983), has a grid of trails with interdistances of 100 meters. *Eciton burchelli* colonies were located by walking the trails during the morning (7:00 - 14:00) until ants were detected visually or audibly (by listening for the typical noises of antbirds, RETTENMEYER 1963, WILLIS 1967). When the raid column was found, it was followed in the opposite direction in order to locate the bivouac. The sampling of prey items was done from a point (usually regular surfaces such as tree trunks or open soil), where the collector had a sufficient view on the main column of ants returning to the nest. Depending on the position of the bivouac, the sampling point was at different distances from the nest.

Labidus praedator colonies were not easily found in the forest due to the smaller size of the ants and their more hypogeic lifestyle. Consequently we searched along a dirt road and prey items were collected from the columns crossing the road.

Army ants carry prey under their body and secure them firmly even when disturbed. We collected prey items by using tweezers to pick up the ants which carried prey and putting them into 80 % alcohol for preservation. This was done during periods of two hours. Unfortunately the ants run so fast, that is was not possible to collect every ant passing with prey. We checked the efficiency of our samples by counting *Eciton* ants passing with prey during 40 periods of 10 seconds each and compared the resulting median number of prey items for two hours with the median number of prey items we were able to collect during our samples. The number of ants carrying food in the 10 second samples was similar to that given in the literature (see below). Thus we calculated an efficiency of 4.4 % for our samples of *Eciton* prey. No measurement of the efficiency was taken for samples of *Labidus* prey.

In the laboratory, all prey fragments were separated from ants and sorted to taxonomic orders. So far only spiders were sorted to morphospecies. Due to our experience in identifying Amazon spiders, we were often able to identify a genus or species even with incomplete (prosomas) and juvenile material (e.g. *Ctenus*). Each prosoma in the sample was counted as one individual spider. The number of individual spiders of the genus *Ctenus* in our samples was used to estimate the number of *Ctenus* spiders caught by the ant colony during a whole day (Iday, tab. 3). This was done by the following formula: Iday = Is · ef · tf, where Is is the number of individual *Ctenus* spiders in our samples, ef the factor adjusting to an efficiency of 100 % (= 100/4.4) and tf the time factor, adjusting the number of individual spiders in two hour samples to a daily eight hour period (= 4).

The effect of ants preying on *Ctenus* spiders was expressed as the proportion of the *Ctenus* population which would have been caught by the ants during one day by using Iday and data for the density of *Ctenus* in 40 areas of 160 m² in the same reserve (median 15 *Ctenus*/160 m², GASNIER unpubl.), extrapolated to a hunting area of 1000 m². *Ctenus* densities were studied by searching spiders at night with the aid of headlamps. Only spiders with a body size (length of prosoma and abdomen) of about 1 cm or more were considered. We made no attempt to measure the hunting area of *Eciton burchelli*, but instead used a mean of 1000 m², which seems to us as a realistic mean of the many values for width and length of the daily hunting area, given in literature (see appendix).

As most of the data are not expected to be normally distributed we calculated the median instead of the mean, and present the lower and upper quartile (lQ, uQ) together with the interquartile range/2 in percent of the median (IQ %) to give an idea of the relative variability (LAMPRECHT 1992).

3. Results and Discussion

3.1 *Eciton burchelli*
3.1.1 Prey spectrum of *Eciton burchelli*
Twenty-eight colonies of *Eciton burchelli* were found and thirty-one prey item samples (2 hours each) were

Table 1. Prey spectrum of *Eciton burchelli*: absolute numbers of prey fragments in two hour-samples (Ara-Araneae, Sco-Scorpionida, Opi-Opilionida, Amb-Amblypygi, Uro-Uropygi, Schiz-Schizomida, Aca-Acari, Chilo-Chilopoda, Isopo-Isopoda, Thys-Thysanura, Derm-Dermaptera, Blatt-Blattodea, Isopt-Isoptera, Ortho-Orthoptera, Het-Heteroptera, Dipt-Diptera, Col-Coleoptera, Hym-Hymenoptera, Form-Formicidae, Lep-Lepidoptera, Rept-Reptilia, n. i.-not identified; IQ-lower quartile, uQ-upper quartile, IQ%-half of interquartile in % of median; sample no. 30 was a 4-hour sample and thus divided).

| sample | | Systematic category | | | | | | | | | | | | | | | | | | | | | | |
no.	date	Ara	Sco	Opi	Amb	Uro	Schiz	Aca	Chilo	Isopo	Thys	Derm	Blatt	Isopt	Ortho	Het	Dipt	Col	Hym	Form	Lep	Rept	n.i.	sum
1	07-Jul	46	4	0	3	18	0	0	1	0	1	1	56	0	1	0	0	0	0	49	0	1	2	183
2	20-Jul	43	1	0	1	0	0	2	4	0	0	0	67	0	12	0	0	0	0	43	0	0	6	179
3	21-Jul	44	3	0	0	0	0	0	16	0	2	0	115	0	12	1	0	1	0	41	4	1	3	243
4	22-Jul	60	5	0	4	0	0	0	14	0	1	0	85	0	22	1	0	2	0	21	0	0	3	218
5	13-Aug	26	4	0	4	0	0	0	0	0	3	0	57	0	16	0	0	3	2	65	1	0	15	196
6	14-Aug	24	1	0	3	0	0	0	3	0	0	0	71	0	25	1	0	4	3	107	1	0	7	250
7	15-Aug	89	11	0	0	2	0	1	9	0	0	0	70	0	41	0	0	3	2	129	1	0	13	371
8	17-Aug	99	6	0	1	0	0	0	4	0	2	0	144	0	35	0	1	1	6	37	1	1	1	339
9	17-Aug	21	1	0	0	2	0	0	6	0	0	0	27	0	2	0	0	1	7	16	0	0	3	86
10	18-Aug	74	13	0	2	22	0	0	3	1	0	2	111	0	17	0	0	1	5	102	2	1	10	366
11	18-Aug	23	5	0	1	1	0	0	2	0	0	0	80	0	22	2	0	3	2	21	2	2	6	172
12	26-Aug	68	9	0	0	2	0	0	7	0	3	0	60	0	7	0	0	0	8	105	0	0	9	278
13	27-Aug	47	9	0	6	9	0	0	0	0	0	0	91	0	29	0	0	0	0	27	0	0	7	225
15	15-Sep	33	13	0	6	1	0	0	14	0	2	1	76	0	44	10	1	3	0	240	0	3	4	453
17I	16-Sep	96	13	0	9	3	0	0	5	0	2	0	84	0	73	7	0	2	2	118	1	0	9	424
17III	16-Sep	51	14	0	9	0	0	0	6	0	0	0	51	6	52	6	0	2	0	140	1	2	9	349
17V	16-Sep	18	25	0	12	0	0	0	14	0	3	0	37	5	23	4	0	1	9	305	1	2	3	462
18	21-Sep	61	12	0	0	21	2	0	24	0	0	6	144	5	58	6	2	0	3	174	0	1	18	537
19	06-Okt	111	46	0	0	6	0	0	0	0	10	2	163	1	72	5	0	20	3	283	0	0	53	775
20	21-Okt	72	5	0	1	2	0	0	0	1	6	0	82	0	50	2	1	2	1	219	1	1	7	453
22	05-Nov	35	10	0	0	3	0	0	8	0	8	0	77	0	51	3	0	1	5	35	0	2	10	248
23	07-Nov	26	24	0	3	8	0	0	7	0	0	0	117	0	56	1	0	1	2	47	0	2	10	304
24	09-Nov	40	8	0	0	11	0	0	7	0	8	0	81	0	56	0	1	1	0	72	1	0	26	312
25	17-Nov	13	2	1	1	0	0	0	2	0	0	0	58	1	45	3	1	1	0	52	0	3	3	186
26	20-Nov	28	5	0	1	1	0	0	0	0	0	0	127	0	62	3	2	0	0	107	5	0	26	367
27	21-Nov	26	0	0	1	2	0	0	3	0	15	0	73	0	56	0	0	1	0	50	0	4	4	235
28	22-Nov	11	2	0	0	0	0	0	1	0	1	2	22	0	11	0	0	0	0	350	0	0	4	404
29	23-Nov	29	26	0	0	0	0	0	13	0	0	2	120	0	114	0	0	1	0	209	3	0	10	527
30	24-Nov	29.5	1.5	0.5	0	0	0	0	0	0	17	0	82.5	1	56	1	1	1	0.5	64	0.5	5	10.5	271.5
30	24-Nov	29.5	1.5	0.5	0	0	0	0	0	0	17	0	82.5	1	56	1	1	1	0.5	64	0.5	5	10.5	271.5
31	25-Nov	35	12	0	3	0	0	3	1	0	0	0	51	0	58	4	2	3	1	113	1	2	16	305
sum		1408	292	2	86	120	2	3	174	2	110	16	2562	15	1234	60	10	63	62	3405	26	30	308	9990
median		35	6	0	1	1			4	0	2	0	80	0	44	1	0	1	1	72	0.5	0.0	7.0	304.0
lQ		9	4	0	1	1			3	0	2	0	22	0	27	1	0	0	1	29	0.5	0.0	4.0	79.0
uQ		26	7	0	3	2			4	0	3	0	31	0	12	2	1	2	2	68	0.5	1.0	3.5	100.0
lQ%		50	91.7	150	200	150			87.5	125			33.1		44.3	150		100	150	67.4	100.0		53.6	29.4

Table 2. Prey spectrum of *Eciton burchelli*: relative numbers of fragments in two hour-samples.

sample no.	date	Araneae	Blattodea	Orthoptera	Formicidae	not id.	sum	others
				Systematic category				
1	07-Jul	25.14	30.60	0.55	26.78	1.09	84.2	15.8
2	20-Jul	24.02	37.43	6.70	24.02	3.35	95.5	4.5
3	21-Jul	18.11	47.33	4.94	16.87	1.23	88.5	11.5
4	22-Jul	27.52	38.99	10.09	9.63	1.38	87.6	12.4
5	13-Aug	13.27	29.08	8.16	33.16	7.65	91.3	8.7
6	14-Aug	9.60	28.40	10.00	42.80	2.80	93.6	6.4
7	15-Aug	23.99	18.87	11.05	34.77	3.50	92.2	7.8
8	17-Aug	29.20	42.48	10.32	10.91	0.29	93.2	6.8
9	17-Aug	24.42	31.40	2.33	18.60	3.49	80.2	19.8
10	18-Aug	20.22	30.33	4.64	27.87	2.73	85.8	14.2
11	18-Aug	13.37	46.51	12.79	12.21	3.49	88.4	11.6
12	26-Aug	24.46	21.58	2.52	37.77	3.24	89.6	10.4
13	27-Aug	20.89	40.44	12.89	12.00	3.11	89.3	10.7
15	15-Sep	7.28	16.78	9.71	52.98	0.88	87.6	12.4
17I	16-Sep	22.64	19.81	17.22	27.83	2.12	89.6	10.4
17III	16-Sep	14.61	14.61	14.90	40.11	2.58	86.8	13.2
17V	16-Sep	3.90	8.01	4.98	66.02	0.65	83.5	16.5
18	21-Sep	11.36	26.82	10.80	32.40	3.35	84.7	15.3
19	06-Okt	14.32	21.03	9.29	36.52	6.84	88.0	12.0
20	21-Okt	15.89	18.10	11.04	48.34	1.55	94.9	5.1
22	05-Nov	14.11	31.05	20.56	14.11	4.03	83.9	16.1
23	07-Nov	8.55	38.49	18.42	15.46	3.29	84.2	15.8
24	09-Nov	12.82	25.96	17.95	23.08	8.33	88.1	11.9
25	17-Nov	6.99	31.18	24.19	27.96	1.61	91.9	8.1
26	20-Nov	7.63	34.60	16.89	29.16	7.08	95.4	4.6
27	21-Nov	11.06	31.06	23.83	21.28	1.70	88.9	11.1
28	22-Nov	2.72	5.45	2.72	86.63	0.00	97.5	2.5
29	23-Nov	5.50	22.77	21.63	39.66	0.76	90.3	9.7
30	24-Nov	10.87	30.39	20.63	23.57	3.87	89.3	10.7
30	24-Nov	10.87	30.39	20.63	23.57	3.87	89.3	10.7
31	25-Nov	11.48	16.72	19.02	37.05	5.25	89.5	10.5
median		12.8	26.5	12.9	23.7	2.6	89.3	10.7
lQ		1.2	2.0	5.3	4.6	1.0	2.5	2.6
uQ		2.3	1.0	1.9	11.1	0.4	2.6	2.5
IQ%		13.9	5.6	27.9	33.1	25.9	2.9	23.8

taken. *Eciton burchelli* ants immobilize their prey and depending on prey size, carry it whole or cut into pieces (GOTWALD 1982, DA SILVA 1972). For large prey (generally >1cm length) legs, wings, and antennas are cut off at the insertion point or at articulations, and heads or prosomas are separated from abdomens. Most items were large, the samples, therefore, consist of few complete individuals and a large number of fragments of arthropods. The number of prey fragments collected during the two hour-sampling periods varied from 86 to 775, with a median of 304 and an IQ of 29.4 % (tab. 1). To check the efficiency of our own samples, we counted the number of ants passing by with prey during periods of 10 seconds. The median

number was 9.5 ants in 10 seconds (n = 40, IQ = 24.5 %), which is similar to other reported values (FRANKS 1990). Thus a total of 27360 prey fragments would have been collected during 8 hours of foraging. FRANKS (1990) calculated 29000 prey fragments/ colony/day from studies in Panama.

Altogether the 31 samples contained 9990 fragments, which were sorted into Reptilia and 20 arthropod orders belonging to Arachnida, Crustacea, Myriapoda and Insecta (tab. 1). We were unable to identify 308 fragments. Cockroaches (Blattodea) were the most abundant group with a median of 26.5 %, followed by ants (Formicidae) with 23.7 % (including adults, eggs, larvae and pupae), grasshoppers (Orthoptera) with

12.9 % (including a few mantids) and spiders (Araneae) with 12.8 %. All remaining groups made up 10.7 %, and no individual group more than 2 % of the median (tab. 2). None of these remaining groups made up more than 8 % of any single sample. Maximum values for the relative portion of the four major prey groups for single samples were 29 % for spiders, 47 % for cockroaches, 24 % for grasshoppers and 87 % for ants (tab. 2).

Published data on prey spectrum of *Eciton burchelli* (RETTENMEYER 1963, SCHNEIRLA 1971, DA SILVA 1972, WILLIS 1967) show Formicidae, Blattodea, Orthoptera and Araneae as the most important groups, but no study reports absolute or relative numbers. One exception is FRANKS (1990), who showed that social Hymenoptera (adults and larvae) represent 55 % of the dry weight of all prey, whereas crickets and cockroaches make up 34 % in the rainy season and 30 % in the dry season, other arthropods constituting the remaining 12 and 15 % of the prey.

In this study, the four most abundant prey groups (Blattodea, Formicidae, Orthoptera, Araneae) also showed the lowest IQ % values, indicating that they were also the most regularly sampled prey. This is especially true for these four groups as a whole, which had a minimum of 80 % of every sample (median 89.3) and show very low variation (IQ 2.9 %) compared with the single groups (tab. 2). However, variation of both absolute and relative number of prey fragments was higher for ants than for cockroaches and spiders (tab. 1, 2), reflecting the more uneven distribution of ants as social insects (nests with many individuals), compared with the individually living arthropods.

In studies of ground living arthropods in the Manaus area, Formicidae, Orthoptera, Blattodea and Arachnida are among the dominant groups, their relative abundances changing only slightly, depending on the sampling method (pitfall traps or quadrat sampling, ADIS & SCHUBART 1984, MALCOLM 1991, MORAIS 1985). Arthropod orders which were not represented in the prey spectrum of *Eciton burchelli* in proportion to their availability in the leaf litter are termites (Isoptera), and insects and arachnids of very small size, such as Diplura, Symphyla, Pauropoda, Protura and Pseudoscorpiones.

3.1.2 Spiders as prey of *Eciton burchelli*

A median of 35 spider fragments was collected from *Eciton* ants during the two-hour samples (minimum 11, maximum 111, IQ = 50 %, table 3). Spiders were most often cut in ten fragments (prosoma, abdomen, eight legs), only a few small spiders appeared intact in the samples. Consequently, the ratio between fragments and individuals should be close to 10. When using prosomas as indicative of individual spiders in our samples this ratio is clearly below 10 (median 4.9; IQ 33 %, table 3), which means that legs and abdomens

are underrepresented. Because legs carried by ants are even more visible for the collector than prosomas we suppose that principally legs and sometimes abdomens get lost on the way to the bivouac. Thus prosomas represent the best basis to calculate the total number of spider individuals caught during one day. The median number of individual spiders, based on the number of prosomas in the two hour-samples, was 9 (minimum 2, maximum 24, IQ = 50 %, table 3).

Most of the 312 individual spiders could be identified to family and some to genera and species. Species iden-

Table 3. Spiders as prey of *Eciton burchelli* in two hour-samples (frag-spider fragments, ind-number of fragments representing individual spiders, Is-number of *Ctenus* individuals in two hour-samples, Iday-extrapolated number of *Ctenus* caught by the ants per day).

sample	date	frag	ind	frag/ind	Is	Iday
1	07-Jul	46	5	9.2	3	272.7
2	20-Jul	43	5	8.6	5	454.5
3	21-Jul	44	6	7.3	6	545.5
4	22-Jul	60	11	5.5	10	909.1
5	13-Aug	26	5	5.2	4	363.6
6	14-Aug	24	3	8.0	1	90.9
7	15-Aug	89	9	9.9	9	818.2
8	17-Aug	99	24	4.1	21	1909.1
9	17-Aug	21	3	7.0	2	181.8
10	18-Aug	74	21	3.5	19	1727.3
11	18-Aug	23	7	3.3	6	545.5
12	26-Aug	68	14	4.9	14	1272.7
13	27-Aug	47	21	2.2	21	1909.1
15	15-Sep	33	4	8.3	4	363.6
17I	16-Sep	96	18	5.3	16	1454.5
17III	16-Sep	51	10	5.1	8	727.3
17V	16-Sep	18	6	3.0	4	363.6
18	21-Sep	61	14	4.4	12	1090.9
19	06-Okt	111	21	5.3	20	1818.2
20	21-Okt	72	18	4.0	16	1454.5
22	05-Nov	35	13	2.7	10	909.1
23	07-Nov	26	14	1.9	12	1090.9
24	09-Nov	40	7	5.7	4	363.6
25	17-Nov	13	2	6.5	2	181.8
26	20-Nov	28	9	3.1	8	727.3
27	21-Nov	26	9	2.9	5	454.5
28	22-Nov	11	3	3.7	1	90.9
29	23-Nov	29	9	3.2	8	727.3
30	24-Nov	29.5	7	4.2	6	545.5
30	24-Nov	29.5	7	4.2	6	545.5
31	25-Nov	35	7	5.0	5	454.5
median		35.0	9.0	4.9	6.0	545.5
IQ		9.0	4.0	1.6	2.0	181.8
uQ		26.0	5.0	1.6	6.0	545.5
IQ%		50.0	50.0	33.1	66.7	66.7

Table 4. Species list of spiders, preyed by *Eciton burchelli*.

family	morphospecies	sum	%
Clubionidae	*Elaver* sp.	1	0.3
Clubionidae ?	sp.	1	0.3
Corinnidae	*Corinna* sp.	10	3.2
Ctenidae	*Ctenus manauara*	5	1.6
Ctenidae	„*Ctenus*" cf. *auberti*	27	8.7
Ctenidae	*Ctenus amphora*	8	2.6
Ctenidae	*Ctenus crulsi*	2	0.6
Ctenidae	*Ctenus* spp.	221	70.8
Ctenidae	*Enoploctenus* sp.	1	0.3
Ctenidae	gen.? sp.	3	1.0
Deinopidae	*Deinopis* sp.	1	0.3
Heteropodidae	Sparianthinae sp.	7	2.2
Mygalomorphae	spp.	18	5.8
Pholcidae	sp.	2	0.6
Salticidae	pluridentatae sp.	2	0.6
Theraphosidae	sp.	2	0.6
Zodariidae	sp.	1	0.3
sum		312	100

tification was possible only in the case of adult male and female fragments of spiders of the genus *Ctenus* and some juveniles with the typical abdominal design (e.g. „*Ctenus*" cf. *auberti*). The genus *Ctenus* represented 84 % of all spiders in the samples, and 4 species of *Ctenus* were identified. Most mygalomorphs could not be identified to family, but most probably belong to Dipluridae or Theraphosidae. In total, 18 morphospecies are represented in the samples (tab. 4).

The spider prey spectrum represented only a fraction of the total spider availability in the area (HÖFER, BRESCOVIT, GASNIER unpubl.; VIEIRA unpubl. data). *Eciton burchelli* almost never preyed upon web-building spiders (Araneidae, Pholcidae, Pisauridae, Theridiidae) and very small spiders (Anapidae, Ochyroceratidae, Oonopidae), and never caught the abundant but cryptic and motionless remaining spiders of the genus *Paratropis* (Paratropididae). The fact that some abundant wandering spiders which are slightly smaller than *Ctenus* spiders are not or underrepresented in the prey samples (e.g. Caponiidae, Heteropodidae, Pisauridae, Salticidae, Zodariidae) suggests that *Eciton burchelli* prefers medium sized spiders of 1-2 cm body length. In reserve 1501, this size class is represented mainly by adults of two smaller species of *Ctenus* (*C. manauara*, *C.* n.sp.) and juveniles of *Ctenus amphora*, *Ctenus crulsi*, „*Ctenus*" cf. *auberti* and *C. tapereba* (see HÖFER et al. 1994, this volume). The ants seem not to be able to prey on larger ctenid and pisaurid spiders (*Ctenus villasboasi*, *Phoneutria* spp., *Ancylometes* spp.), nor to catch the burrowing mygalomorphs (Actinopodidae, Nemesiidae, Theraphosidae).

The number of *Ctenus* prosomas in the two hour-samples (minimum 1, maximum 21, median 6, IQ = 66.7, table 3) was extrapolated by the formula above to a number of *Ctenus* individuals theoretically caught by the ants during eight hours. Thus, a median of 545 *Ctenus* individuals would have been caught by a colony during one day (Iday in table 3: minimum 91, maximum 1909, IQ = 66.7 %).

3.2 *Labidus praedator*
3.2.1 Prey spectrum of *Labidus praedator*

Nine colonies of *Labidus praedator* were found and one sample of two hours was taken from each. *Labidus praedator* preys in the same manner as *Eciton burchelli*, but individual prey usually is smaller or is cut into smaller pieces (SCHNEIRLA 1949, cited in RETTENMEYER 1963). This makes identification of fragments more difficult, resulting in a higher portion of unidentified fragments (229 fragments = 5.2 %, table 5, 6). The number of prey fragments collected during two hours varied from 73 to 339, with a median of 177 and an IQ of 75 % (tab. 5). A total of 1911 fragments was collected from the ants, including fragments of 20 arthropod orders and of reptiles (tab. 5). Cockroaches (Blattodea) were the most abundant prey with a median of 31.6 %, followed by spiders (Araneae, 17 %), centipedes (Chilopoda, 5.5 %), larvae of Lepidoptera (4.3 %), and whip scorpions (Holopeltidia, 3.5 %). Ants (Formicidae) had low representation with a median of 3 %, as well as grasshoppers (Orthoptera) and scorpions (Scorpionida) with 2.7 % (tab. 5). Together with earwigs (Dermaptera, 2.3 %) and the unidentified fragments, these 9 arthropod groups represented 94.5 % (median), the remaining 11 groups accounting for only 5.5 % (median, table 6). Maximum values for relative abundance of the major prey groups in a single sample were 24.7 % for spiders, 19.7 % for whip scorpions, 16.7 % for earwigs, 39.2 % for cockroaches. Only cockroaches and spiders showed IQ values below 50 % (20,8 and 42.2 respectively) and thus were the most regularly sampled prey (tab. 6).

Labidus praedator is also considered to be a generalist arthropod predator (RETTENMEYER 1963, DA SILVA 1972). In our prey samples of *Labidus* the same number of arthropod orders is present as in samples of *Eciton*. Differences in the representation of prey groups include the absence of Amblypygi and Hymenoptera (excl. ants) and the presence of Protura and Neuroptera in the prey samples of *Labidus*. Regarding the relative abundance of arthropod groups in the prey samples *Labidus* seems to make use of a wider spectrum than *Eciton burchelli* (tab. 2 vs. 6). Hunting in the same habitats and strata and consequently having the same prey spectrum available, *Labidus* caught relatively more Arachnids (spiders, scorpions and whipscorpions), centipedes and larvae of Lepidoptera. Ants were less important.

Table 5. Prey spectrum of *Labidus praedator*: absolute numbers of fragments in two hour-samples (for abbreviations see table 1; Prot-Protura, Neuro-Neuroptera).

sample		Systematic category																						
no.	date	Ara	Sco	Opi	Uro	Schiz	Aca	Chilo	Isopo	Prot	Neuro	Thys	Ortho	Het	Dipt	Isopt	Blatt	Derm	Col	Form	Lep	Rept	n.i.	sum
1	24-Jun	63	1	6	7	2	1	11	0	1	0	3	2	9	0	0	65	12	6	4	29	0	62	284
2	24-Jun	18	0	0	1	0	0	3	0	0	0	0	9	1	0	0	27	4	1	1	6	0	2	73
3	03-Aug	13	4	0	10	0	0	28	0	0	0	1	3	2	2	1	68	1	3	6	2	0	56	200
5	16-Aug	63	9	5	12	2	5	18	10	0	0	4	27	21	1	2	107	16	5	15	11	0	6	339
6	26-Aug	32	12	0	37	0	0	5	0	0	1	0	0	0	0	0	16	0	6	12	2	1	64	188
7	14-Sep	10	5	1	3	0	0	15	0	0	0	0	2	2	0	0	39	1	1	8	10	0	10	107
8	15-Sep	19	0	0	20	0	0	21	9	0	0	4	9	2	0	0	85	5	4	12	22	0	5	217
9	22-Nov	37	7	0	5	0	2	24	0	0	0	14	14	3	0	0	47	2	3	3	4	2	7	174
10	25-Nov	40	24	4	30	0	1	18	0	0	0	2	9	1	0	0	99	55	9	5	14	1	17	329
sum		295	62	16	125	4	9	143	19	1	1	28	75	41	3	3	553	96	38	66	100	4	229	1911
median		32	5	0	10	0	0	18	0	0	0	2	9	2	0	0	65	4	4	6	10	0	10	177
lQ		16.5	4.5	0				10				2	7	2			32	3	2	2.5	7	0	4.5	98
uQ		19.5	5.5	4.5	15	1	1.5	24	4.5			2	9	4	0.5	0.5		10	1.5	6	8	1	49	168
lQ%		56.3	100		105			40.3	4.5			100	52.8	125			45.4	162.5	43.8	70.8	75		267.5	75.1

3.2.2 Spiders as prey of *Labidus praedator*

A median of 32 fragments of spiders was collected with *Labidus* ants during two hours (minimum 10, maximum 63, IQ = 56 %, table 7). Most of the larger spiders (Ctenidae, Heteropodidae, Mygalomorphae) were in smaller pieces than in the samples from *Eciton* (e.g. parts of the prosoma), but many smaller spiders were found intact or only with a few legs cut off. This resulted in a very low ratio between fragments and individuals (median 1.7; IQ 13 %, table 7). As in the *Eciton* samples prosomas were counted as individual spiders and a median of 16 spiders was present in the two hour samples (minimum 6, maximum 39, IQ = 72 %, table 7). Because of the rapid movement of the small *Labidus* ants no efficiency test was executed and thus, no extrapolation of the data to the amount of prey taken during one day could be made.

From a total of 173 individual spiders collected, 28 morphospecies could be identified (tab. 8). Fragments of Ctenidae were most abundant with 27 %, followed by Salticidae (19.1 %) and Dipluridae (12.7 %).

The sampled *Labidus* colonies preyed upon a wider variety of spiders than *Eciton*, including web spiders (Araneidae, Deinopidae, Mysmenidae, Pholcidae, Uloboridae), a large number of the small wandering spider mentioned above and the medium sized *Ctenus* spiders (tab. 8).

4. Conclusion

Both *Eciton burchelli* and *Labidus praedator* have been considered polyphagous predators (generalists), in comparison to other army ant species of the tribe Ecitonini (GOTWALD 1982, RETTENMEYER et al. 1983). However, our data show that four arthropod groups dominate the prey spectrum of *Eciton burchelli*. Arthropod representation in the prey samples seems to be dependent partly on the availability (relative abundance and frequence) of these arthropods in the habitat. However, some small-sized arthropods and termites, very abundant in the leaf litter, were rare in the prey samples of *Eciton burchelli*. The ants might prefer some prey (e.g. larvae) or avoid others (aggressive, distasteful, smooth and armoured) and fail to detect cryptic motionless animals, but this will only be visible below the level of orders. Among spiders *Eciton burchelli* shows preference for wandering spiders of the genus *Ctenus*, which in fact might be a preference for a certain size class.

Labidus praedator showed a higher evenness in the prey spectrum, both on the level of arthropod orders and in spiders. They also seem to make use of some of the smaller arthropod groups. However, overlap with the prey spectrum of *Eciton burchelli* is considerably high.

The extrapolation of our samples resulted in a median number of 545 *Ctenus* spiders, caught by a colony of

Table 6. Prey spectrum of *Labidus praedator*: relative numbers of fragments in two hour-samples (for abbreviations see table 1).

sample	date					Systematic category							
no.		Ara	Sco	Uro	Chilo	Derm	Blatt	Ortho	Form	Lep	n.i.	sum	others
1	24-Jun	22.2	0.4	2.5	3.9	4.2	22.9	0.7	1.4	10.2	21.8	90.1	9.9
2	24-Jun	24.7	0.0	1.4	4.1	5.5	37.0	12.3	1.4	8.2	2.7	97.3	2.7
3	03-Aug	6.5	2.0	5.0	14.0	0.5	34.0	1.5	3.0	1.0	28.0	95.5	4.5
5	16-Aug	18.6	2.7	3.5	5.3	4.7	31.6	8.0	4.4	3.2	1.8	83.8	16.2
6	26-Aug	17.0	6.4	19.7	2.7	0.0	8.5	0.0	6.4	1.1	34.0	95.7	4.3
7	14-Sep	9.3	4.7	2.8	14.0	0.9	36.4	1.9	7.5	9.3	9.3	96.3	3.7
8	15-Sep	8.8	0.0	9.2	9.7	2.3	39.2	4.1	5.5	10.1	2.3	91.2	8.8
9	22-Nov	21.3	4.0	2.9	13.8	1.1	27.0	8.0	1.7	2.3	4.0	86.2	13.8
10	25-Nov	12.2	7.3	9.1	5.5	16.7	30.1	2.7	1.5	4.3	5.2	94.5	5.5
median		17.0	2.7	3.5	5.5	2.3	31.6	2.7	3.0	4.3	5.2	94.5	5.5
IQ		8.0	2.5	0.9	1.5	1.6	6.6	1.6	1.5	2.6	2.6	6.4	1.5
uQ		4.7	2.9	5.6	8.4	2.8	5.2	5.3	3.0	5.5	19.7	1.5	6.4
IQ %		42.2	125	167	91.6	225	20.8	166	91.1	99.8	275	4.2	100.6

Eciton burchelli during one day. Assuming a daily hunting area of 1000 m² and a mean density of 94 *Ctenus* spiders per 1000 m² (GASNIER unpubl.) the ants would have an efficiency of 580 %. Using the maximum density in GASNIER's samples, 175 *Ctenus* spiders per 1000 m², they still would have an efficiency of 311 %. Obviously the ants cannot kill more prey than actually exists and so estimates of >100 % are biased. There is a series of possible sources for such bias. First, daily hunting area and daily hunting time were not measured for every ant colony, but instead were generalized from information in the literature. Next, the hunting efficiency of the army ants fluctuates during the day (SCHNEIRLA 1971) and a linear extrapolation from two hour-samples to eight hours might cause an error. During the morning the ants set up booty caches, where they retain prey fragments and they make a midday break (RETTENMEYER et al. 1983). The activity cycle of the ants consists of a migratory and a statary phase, which influences hunting effort (SCHNEIRLA 1971), and we do not know in which phase our sampled colonies were. We also do not know the size of the colony which was observed hunting. Another possible source of error lies in the assumption that we collected 4,4 % of all actual prey taken by the ants. The probability to loose the smallest prey fragments is certainly higher and thus, the efficiency for the large spider fragments could be higher than the overall efficiency. However, most of the above mentioned sources of error should be partially eliminated by using 30 samples, which were taken from different colonies, at different times of the day.

On the other hand our field experience leads us to the assumption that ants are much better collectors of *Ctenus* than we are, principally because they are searching every centimeter of the forest floor and the lower vegetation, and even enter in burrows and crevices.

They should encounter close to 100 % of the *Ctenus* spiders. *Ctenus* densities attained by visual censusing of large areas (160 m²) by men are certainly underestimates. Spider density also fluctuates considerably with area and army ants are supposed to adjust their foraging behavior to prey densities (CHADAB & RETTENMEYER 1975). Using a probably more realistic density of 1 *Ctenus*/m², the ants would still prey on 54 % of them. This estimation for *Ctenus* spiders is not contradicted by the numerous observations of several workers that many spiders flee from the advancing raid, because these „spiders" were never identified. We assume that mostly larger spiders (see above) are frequently observed escaping at the front of the raids. A more reliable estimate of the effect on prey populati-

Table 7. Spiders as prey of *Labidus praedator* in two hour-samples (frag-spider fragments, ind-number of fragments representing individual spiders).

sample				
no.	date	frag	ind	frag/ind
1	24-Jun	63	39	1.6
2	24-Jun	18	12	1.5
3	03-Aug	13	8	1.6
5	16-Aug	63	31	2.0
6	26-Aug	32	16	2.0
7	14-Sep	10	6	1.7
8	15-Sep	19	7	2.7
9	22-Nov	37	30	1.2
10	25-Nov	40	24	1.7
median		32.0	16.0	1.7
IQ		16.5	8.5	0.15
uQ		19.5	14.5	0.3
IQ %		56.3	71.9	13.2

Table 8. Species list of spiders, preyed by *Labidus praedator*.

family	morphospecies	sum	%
Araneidae	spp.	5	2.9
Araneidae	*Hypognatha* sp.	1	0.6
Caponiidae	*Nops* sp.	2	1.2
Clubionidae	sp.	2	1.2
Corinnidae	spp.	16	9.2
Ctenidae	*Ctenus* spp.	47	27.2
Deinopidae	*Deinopis* sp.	1	0.6
Dipluridae	spp.	22	12.7
Gnaphosidae	gen.? sp.	3	1.7
Heteropodidae	sp.	1	0.6
Heteropodidae	sp.f	3	1.7
Lycosidae	sp.	1	0.6
Mygalomorphae	spp.	8	4.6
Mysmenidae	sp.	2	1.2
Pholcidae	*Blechroscelis* sp.	1	0.6
Pholcidae	gen.? sp.	1	0.6
Pisauridae	cf. *Dossenus* sp.	1	0.6
Pisauridae	sp.	1	0.6
Salticidae	spp.	33	19.1
Scytodidae	*Scytodes* sp.	1	0.6
Uloboridae	*Miagrammopes* sp.	1	0.6
Zodariidae	sp.	5	2.9
Zoridae ?	sp.	8	4.6
indet.		7	4.0
sum		173	100

ons should involve the measurement of spider availability in the same area where army ants forage, before and after the hunt. This was done by OTIS et al. (1986), and they reported that spider populations were not at all affected by *Eciton burchelli* raids, whereas pseudoscorpion density was significantly reduced. In their study, however, they were only able to collect two quadrats of 1 m² in front and behind each raiding swarm, and the non-homogeneous distribution of arthropods on the forest floor resulted in a very high variability. *Ctenus* spiders are not even expected to be captured by this method; for these relatively large spiders reliable density measurements are not rapidly made and because the hunting area of the ants is not predictable, such measurements cannot be made in advance (e.g. before army ants pass), at least not in sufficiently high numbers to allow statistically significant results.

In another rainforest reserve near Manaus (Reserva Ducke) we were able to mark an area of 30 m² during the day, when *Eciton burchelli* hunted, and came back to count spiders in this area at night and we did not count even one spider.

We conclude from our data that *Eciton burchelli* can have a high direct effect (mortality) on *Ctenus* popula-

tions. Also, by prefering certain *Ctenus* species (by prefering a certain size class) over others, they might have a considerable effect on the structure of this guild of wandering spiders. This is strengthened by our observations on foraging frequence within a certain area. In an experimental plot in Reserva Ducke, during each of three sampling periods of four weeks within one year *Eciton burchelli* was caught in pitfall traps, making it highly probable that they hunted there at least three times in one year.

Labidus makes use of a larger portion of the existing spider assemblage and consequently should have a smaller effect on single species populations. On the other hand, observations in Panguana, Peru (VERHAAGH pers. comm.) and our own studies in Reserva Ducke indicate that *Labidus* colonies stay much longer in the same area. Samples of arboreal funnel traps (2 m above ground) have shown that the flushing effect of *Labidus praedator* on large and medium sized spiders is high (GASNIER & HÖFER unpublished). The flushing effect on spiders (and other arthropods) from the litter during foraging, exposes them to other predators like ant following ant-birds and woodcreepers (WILLIS & ONIKI 1978), monkeys (RYLANDS et al. 1989), and parasites like Tachinidae and Conopidae (RETTENMEYER 1961). This indirect impact may be higher than the direct impact by the ants (FRANKS 1982, FRANKS & BOSSERT 1983). Therefore repeated foraging by *Labidus*, in addition to foraging of *Eciton burchelli* in the same area within a short period should lead to a substantial impact on spider assemblages.

5. Literature

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Appendix:

Author   measurements of hunting area of *Eciton burchelli*

	width	distance	area
FRANKS 1982		105 m	
FRANKS 1990			500 m²/day
FRANKS & BOSSERT 1983		116 m (migratory fase)	
		89 m (statary fase)	
FRANKS & FLETCHER 1983		105 m	
FRANKS et al. 1991			1000 m²/day
SCHNEIRLA 1971	> 15 m (max. 25 m)	70-140 m	1050-2100 m²/day
DA SILVA 1972		89 m (migratory fase)	
		76 m (statary fase)	
WILLIS 1967	< 15 m (mean 6 m)		