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FACTORS AFFECTING THE "ACTIVITY DENSITY" OF SPIDERS ON TREE TRUNKS IN AN AMAZONIAN RAINFOREST

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Abstract. We studied the influence of rainfall, availability of prey and hunting by army ants on "activity density" (captures dependent on activity and abundance) of spiders on tree trunks, using three arboreal funnel traps. Spiders were sorted into 16 groups, based on taxonomic affinities, to investigate whether these factors act on spiders in general or only on some groups. Hunting swarms of two species of army ants near the traps led to an increase in the total number of spiders captured of up to 3.5 times, and these ants occurred in 16 out of 74 weeks. These increases in capture rates were observed mainly on medium to large ground-living spiders. Weekly rainfall and food availability (weight of arthropods in traps) were not significantly correlated with the number of individuals of the studied groups of spiders. Capture rates throughout the year are described by a graphical smoothing technique, and those of the most abundant groups compared. In general, seasonality of "activity density" of spiders on tree trunks was absent or much weaker than in other studies of spiders in tropical areas.
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Key words: Brazil, Amazon rainforest, spiders, Araneae, seasonality, tree trunks.

INTRODUCTION

The trunk and canopy of trees are known to be suitable habitats for spiders. Whereas the canopy regions, especially of tropical forests, have received much attention during the last years because of the high species richness expected, few studies have addressed rhe spider fauna of tree trunks (Manhart 1994, Vincent & Frankie 1985, Wunderlich 1982). We studied the trunk fauna in a tropical rain forest reserve in central Amazonia within the framework of an ecological project dealing with mechanisms maintaining high diversity in the tropics. The project is based on an intensive sampling of spiders in all strata (Höfer *et al.* 1994a,b) and continuously functioning arboreal funnel traps were used to collect spiders on tree trunks during 17 months. Here we present a pattern analysis of these samples, based on correlations and regressions of spider capture rates with rainfall, prey availability and presence of army ants. Such analysis represents a necessary step to propounding realistic hypotheses about ecological processes linked with species richness of tropical communities, which subsequently can be tested in experimental work.

Capture rates in pitfall traps, arboreal funnel traps and other similar traps are denominated "activity density" (Funke 1971, Schaefer & Tischler 1992) because they simultaneously depend on abundance and activity of the trapped animals (Curtis 1980, Höfer 1990, Uetz & Unzicker 1975). Although those traps do not measure pure abundance, they have been used in studies of temporal and spatial variation in abundance of spiders (Bultman 1992; Nentwig 1982, 1989; Uetz 1975, 1976; Young & Lockley 1994).

In temperate and subtropical ecosystems, seasonality in activity and density of arthropods (including spiders) has been primarily associated with temperature (Basset 1991, Campos & Peraza 1986, Dondale & Binns 1977, Russell-Smith 1981, Schaefer 1987). The relative importance of rainfall was generally low or undetected in these ecosystems, but higher densities of spiders were observed during the rainy season in a tropical savanna in Ivory Coast (Blandin 1971), in low vegetation on a tropical oceanic island (Tanaka & Tanaka 1982) and in deciduous tropical rainforests (Nentwig 1985, 1993), all sites where annual variation in temperature is low. Activity density of spiders in two tropical floodplain rainforests ("Igapó" and "Várzea" forests) was strongly determined by the annual cycle of inundation (Adis 1981; Höfer 1990, Höfer, *in press*). The degree of seasonality of spiders might be stronger in open areas than in woodland, at least when comparing closely situated sites (Russell-Smith 1981).

Prey availability is a potential cause of variation in activity density of spiders, resulting either in numerical or functional responses (foraging mode, activity) to prey densities (overview *in* Riechert & Harp 1986). Other sit-and-wait predators frequently change activity as a function of food supply (e.g., Huey & Pianka 1981, Dunham 1983).

A third factor influencing spider activity density is predation. Swarm-raiding army ants are known to forage in large numbers on the ground in many tropical forests, leading to sudden local increases in arthropod activity as they escape from the swarm fronts (Hölldobler & Wilson 1990). Swarms of two species, *Eciton burchelli* and *Labidus praedator*, appeared repeatedly in our study area, and both have been shown to be important predators of spiders in central Amazonia (Vieira & Höfer 1994).

METHODS

The study was conducted in the "Reserva Florestal Adolfo Ducke", 26 km northeast of Manaus, Brazil, between September 1991 and February 1993. Spiders were collected on a plateau area in "terra firme forest" (*sensu* Guillaumer 1987), with three funnel traps (arboreal photo-eclectors, described in Adis 1981, 1988), mounted at a height of 1.5 m on three trees of different species about 50-70 m distant from each other. Picric acid was used as a preservative in the sample containers. All arthropods were removed from traps at weekly intervals and preserved in 70 % ethanol. Adult spiders were identified as morphospecies, and juveniles in most cases were sorted to family, genus, and if possible allotted to morphospecies. Details of the composition of the spider community will be described elsewhere (Höfer *et al., in prep.*). The rest of the arthropods were divided into three size-classes. Size 1 included those that passed through a sieve of 4 mm mesh width (rinsed with water at low pressure) and held in another sieve of 0.063 mm mesh width. From the arthropods retained on the sieve of 4 mm mesh, size 2 included all individuals of less than 1 g, and size 3 those of more than 1 g. The total weight of each size-class was measured. The presence of the swarm-raiding army ants *Eciton burchelli* and *Labidus praedator* was registered.

Rainfall and temperature data during the study period were furnished by the "Coordenadoria de Pesquisas em Hidrometeorologia" of the "Instituto Nacional de Pesquisas da Amazônia", from a meteorological station 2 km distant from the study site. Data from previous years are from Marques-Filho *et al.* (1981) from the same station.

We did not test the effect of temperature on weekly activity density, because the temperature was almost constant throughout the year. The weekly mean of daily minimum temperatures was previously chosen for analysis because it represents the temperature at night, when most spiders are active. It varied only between 21.0° C and 23.4° C during the study period, and we considered this a range too narrow to have any significant effect on spider activity. So we restricted the weather analysis to rainfall. Rainfall analysis included: 1) regressions between weekly rainfall and the number of spiders captured, and 2) a graphical comparison of the variation in rainfall and the variation in the number of spiders during the study. Considering the high variation of rainfall from one week to another, even within the same season, these approaches reveal different phenomena. The first approach mainly detects the effect of rainfall on the weekly activity, and the second allows a comparison of seasonality curves and detection of trends (e.g., time lags or cumulative effects of rainfall) in activity density of spiders and other arthropods. The graphical comparison was performed by "Robust Locally Weighted Regression" (Cleveland 1979), using the LOWESS smoothing function from the statistical package SYSTAT (Wilkinson 1990). The LOWESS function is an algorithm to analyze a time series without prejudging its shape or monotonicity. The only parameter to be adjusted is "tension", from 0 (local detail) to 1 (global smoothing). We compared different tensions, and chose the one closest to a seasonal pattern, with one positive and one negative peak per year. We considered that tension 0.3 was reasonable for most observed patterns, and tension 0.2 for small mygalomorph spiders because they had a strong seasonal pattern restricted in duration.

The significance level for tests was = 0.05, the probabilities were recalculated for multiple tests in each column of our table following Rice (1989). The significance of regressions was tested with ANOVA, and the calculated values of "F" are presented in a table. The significance of correlation between two arthropod size classes was calculated with Student's T-test (Zar 1974).

In a few cases spiderlings from recent clutches, with up to 160 individuals (*Idiops* sp., Idiopidae) in one week, appeared in the traps, and we considered it inappropriate to count each one as an independent captured individual. Thus, when more than five spiderlings of the same species and nymphal stage appeared in one trap, they were counted as one capture. Pholcid spiders were excluded from analysis, because they could build webs within or on the traps, and although these webs were regularly removed, the capture of these spiders was considered to be strongly biased.

RESULTS

A total of 3872 individuals belonging to 32 families and approx. 150 morphospecies were collected. Salticidae were the dominant family (15-20 %) in all three traps, followed by Corinnidae (9-13 %) and Ctenidae (9-11 %). Pisauridae made up 3-5 %, but 20 % in one single trap, and Oonopidae made up between 4 and 9 % of all individuals.

The number of individuals per species was too low for evaluations at this level, so we made 16 groups based on taxonomic affinities, which made it also possible to include juveniles in the analysis. We grouped spiders generally by family, except for Mygalomorphae (Dipluridae, Idiopidae, Theraphosidae) and Orbiculariae (*sensu* Coddington & Levi 1991). In samples of pitfall traps and ground photo-eclectors in central Amazonia we recognize a guild of leaf litter-inhabiting tiny web spiders (Höfer, *in press*), consisting of Anapidae, Araneidae, Linyphiidae, Mysmenidae, Symphytognathidae, Theridiidae and Theridiosomatidae (all Orbiculariae) and Ochyroceratidae. The latter family, also not belonging to the same taxonomic clade, was counted with the Orbiculariae in our analyses, because we expect ecological similarities. Families with a mean capture rate of < 0.1 individuals per week were excluded from analysis. The total of individuals considered for analysis was 2640. Families with higher capture rates were further divided into adults and juveniles. Ctenidae (e.g., *Ctenus*) and Pisauridae (e. g., *Ancylometes*) were grouped together in some analyses, because immature individuals cannot be separated and they are presumed to have very similar life history strategies (Höfer *et al.* 1994a). We separated *Gephyroctenus* from other Ctenidae, because spiders of this genus have a different morphology (flattened and cryptic) and ecology (trunk-dwelling).

Hunting swarms of the swarm-raiding army ants *Eciton burchelli* (EB) and *Labidus praedator* (LP), passing on the ground below the traps, were usually detected by their occurrence in the traps in 16 of the 74 weeks. They were found in 11 capture weeks in only one trap, 3 capture weeks in two traps and 2 capture weeks in all traps. They were once present in 9 consecutive capture weeks (between 13 July and 21 September 1992, mainly *L. praedator*). They were also present in February (EB), March (EB+LP), April (LP), June (EB), July (LP) and November (LP) 1992. Army ants were only assumed to be present around the traps in one week in 1991 (7-14 October), when the number of spiders in traps suddenly increased from 40-60 to 170, decreasing to 40-60 in the following weeks. This week was classified as "week with army ants" in the analysis shown here, because it was the major change in activity of spiders observed, and evidence of army ants was strong: unusually high numbers of other arthropods, especially ground-dwellers, similar changes in family composition of spiders compared to other weeks with army ants and absence of any major change in weather. However, the trend and statistical signif-icance of tests did not change when this week was excluded from analyses.

Based on a ratio of 23% of weeks with army ants hunting near the trunks with traps, we tested if the total of spiders per group captured when these ants were hunting was proportionally higher (>23%) than the total captures per group when there was no evidence of their presence, using the Chi^2-test (Table 1). A statistically significant and strong increase was observed for Mygalomorphae and juveniles of Ctenidae plus Pisauridae. Capture rates of adult Ctenidae doubled but the increase was not significant. A significant decrease was observed for Oonopidae. For the other groups, variations in capture rates were small and not statistically significant, but may still show a tendency. Most taxa showing a positive increase represent ground-dwelling, agile wandering spiders, (Corinnidae, Ctenidae, Pisauridae, Salticidae) or flattened mimetic spiders (*Gephyroctenus*, Heteropodidae) that live on trunks, all medium- to large-sized (5 - 15 mm body length). Spider groups showing no increase in capture rates during weeks with army ants, included generally small-sized spiders (< 5 mm) with a more stationary life style (Caponiidae, Oonopidae, Orbiculariae, Palpimanidae, Scytodidae, Segestriidae).

TABLE 1. Statistical significance of tests of relationships between activity density of spiders and presence of army ants, weekly rainfall and biomass of arthropods in the traps. Spider groups: if not otherwise stated juveniles (juv.) and adults were included; "no army ants" = weekly mean number of spiders captured in the absence of army ants (n = 57); "army ants" = mean in the presence of army ants (n = 17); % = increase between the two means in percent of the first mean; Chi² = Chi square value for null hypothesis that captures were not affected by army ants. The values of "F" for regressions with rainfall and arthropods are presented in the columns "rain (F)" and "arthrop. (F)" (n = 57). "stat.sign."= statistical significance of the tests of the previous column, adjusted by column following Rice (1989)". * = $P < 0.05$.

spider group	no army ants	army ants	∆%	Chi²	stat.sign. ants	rain (F)	stat.sign. rain	arthrop. (F)	stat.sign. arthrop.
Mygalomorphae	0.32	3.12	887	106	*	0.99	—	0.42	—
Ctenidae/ Pisauridae - juv.	3.47	19.5	462	470	*	1.21	—	0.41	—
Ctenidae - adult	0.26	0.53	101	2.85	—	0.31	—	1.00	—
Corinnidae - adult	2.37	3.47	47	6.01	—	0.10	—	3.45	—
Gephyroctenus	1.26	1.65	42	2.45	—	> 0.1	—	4.12	—
Heteropodidae	0.63	0.82	30	0.71	—	> 0.1	—	1.02	—
Pisauridae - adult	0.70	0.88	25	0.57	—	1.21	—	1.37	—
Salticidae - juvenile	4.97	6.06	22	2.96	—	0.10	—	0.60	—
Gnaphosidae	1.19	1.53	13	0.27	—	> 0.1	—	0.18	—
Salticidae -adult	5.4	5.82	10	0.41	—	> 0.1	—	2.44	—
Corinnidae - juvenile	3.84	4.12	7	0.24	—	1.42	—	0.70	—
Caponiidae	0.29	0.30	1	< 0.1	—	0.73	—	0.27	—
Orbiculariae	0.47	0.47	0	< 0.1	—	0.43	—	0.41	—
Hersiliidae	0.12	0.12	-4	< 0.1	—	> 0.1	—	0.95	—
Scytodidae	0.70	0.47	-33	1.09	—	4.48	—	< 0.1	—
Oonopidae	3.72	2.12	-43	10.1	*	1.61	—	1.50	—
Segestriidae	0.63	0.30	-53	2.70	—	0.26	—	0.44	—
Mimetidae	0.39	0.18	-54	1.72	—	1.06	—	< 0.1	—
Palpimanidae	0.21	0.00	-100	3.58	—	2.48	—	< 0.1	—

The weeks with army ants were excluded from the subsequent analysis.

During our study period the monthly rainfall values differed moderately from the long term mean (Fig. 1). During the dry season, 1991 and 1992 (May-October), most monthly rainfall values were higher than the mean of 11 years and during the rainy season (November 1991 - April 1992) all values except one were considerably lower than the mean. The highest daily rainfall value was in March 1992 (120 mm). On the whole, the rainy season of 1992 might be considered relatively weak. The deviations from the long term mean were probably caused by the El Niño-Southern Oscillation 1991-92 (Adis, *pers. comm.;* see Marengo & Hastenrath 1993).

The regression analyses showed no significant relationship between weekly rainfall and activity density of any of the spider groups (Table 1).

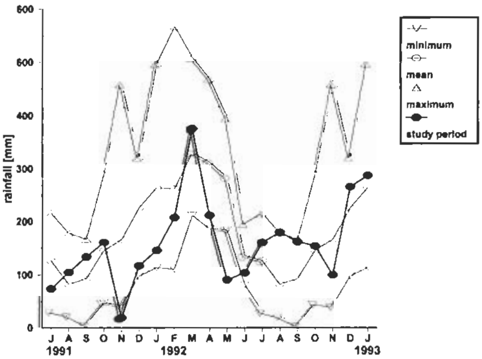
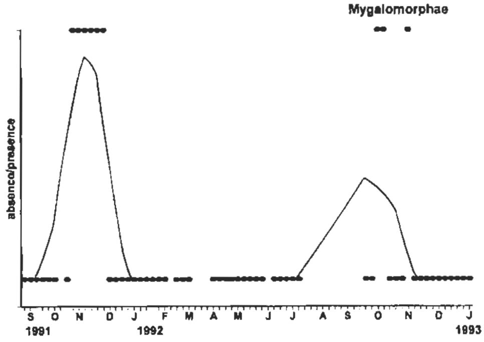
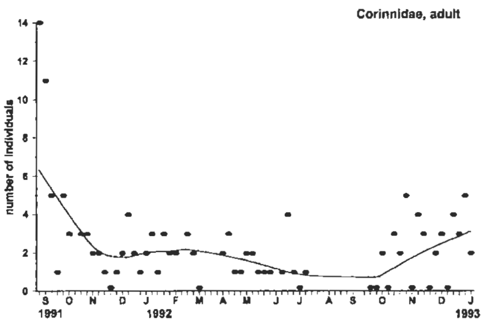


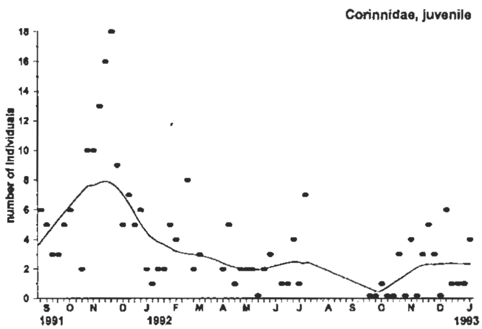
FIG. 1. Monthly minimum, mean and maximum rainfall during 11 years (fine lines, data modified from Marques-Filho *et al.* 1981) and monthly rainfall during the study period September 1991 - January 1993 (bold line, data from CPHM-INPA), all measured in Reserva Ducke.

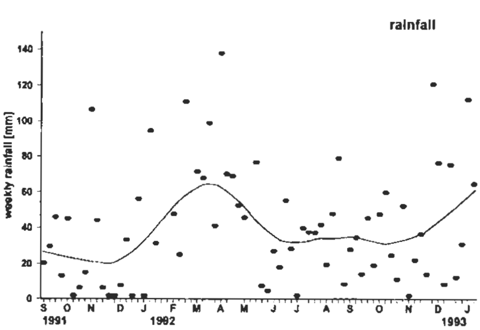
Five families were captured in sufficient numbers to allow a consistent analysis of variation in activity density throughout the year (Fig. 2). Annual fluctuations in activity densities seem generally weak; however, some temporal variation was observed. Juveniles and adults of Salticidae decreased in numbers during the second half of the rainy season, but recovered their mean numbers by the middle of the next dry season. Higher numbers of Oonopidae and juveniles of Corinnidae were collected at the end of the dry season in 1991, but not in the same period in 1992. Captures of Ctenidae and Gnaphosidae were almost constant throughout the year. Clear evidence of a seasonal pattern was observed only for small juveniles of one mygalomorph species (*Idiops* sp., Idiopidae). These spiders appeared between 21 October and 2 December 1991 in all three traps, and between 2 and 19 October 1992 in two traps, in most cases in very high numbers (up to 160 individuals per trap and week) - and in the absence of army ants. These captures represent clutches or part of clutches of recently hatched spiderlings, and thus only presence-absence data were used in the graphical evaluation (Fig. 2) and the regression analyses (see above). The captures clearly indicate a restricted reproduction period of this species at the beginning of the rainy season, but no significant correlation with weekly rainfall.

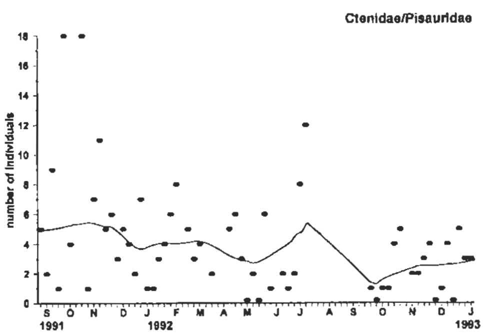
The arthropods of size-class 3 (individual mass > 1g) were excluded from analysis of prey availability because they are too large to be considered prey for most spiders and were collected only in small numbers, showing high variability among samples. Variation in activity density throughout the year between arthropods of size-classes 1 and 2 covaried significantly (r^2= 0.31, T= 4.92, P<0.001, Fig. 2) so they were summed to a single index of prey availability. However no significant relationship between weekly capture of spiders and this index of prey availability could be detected (Table 1).

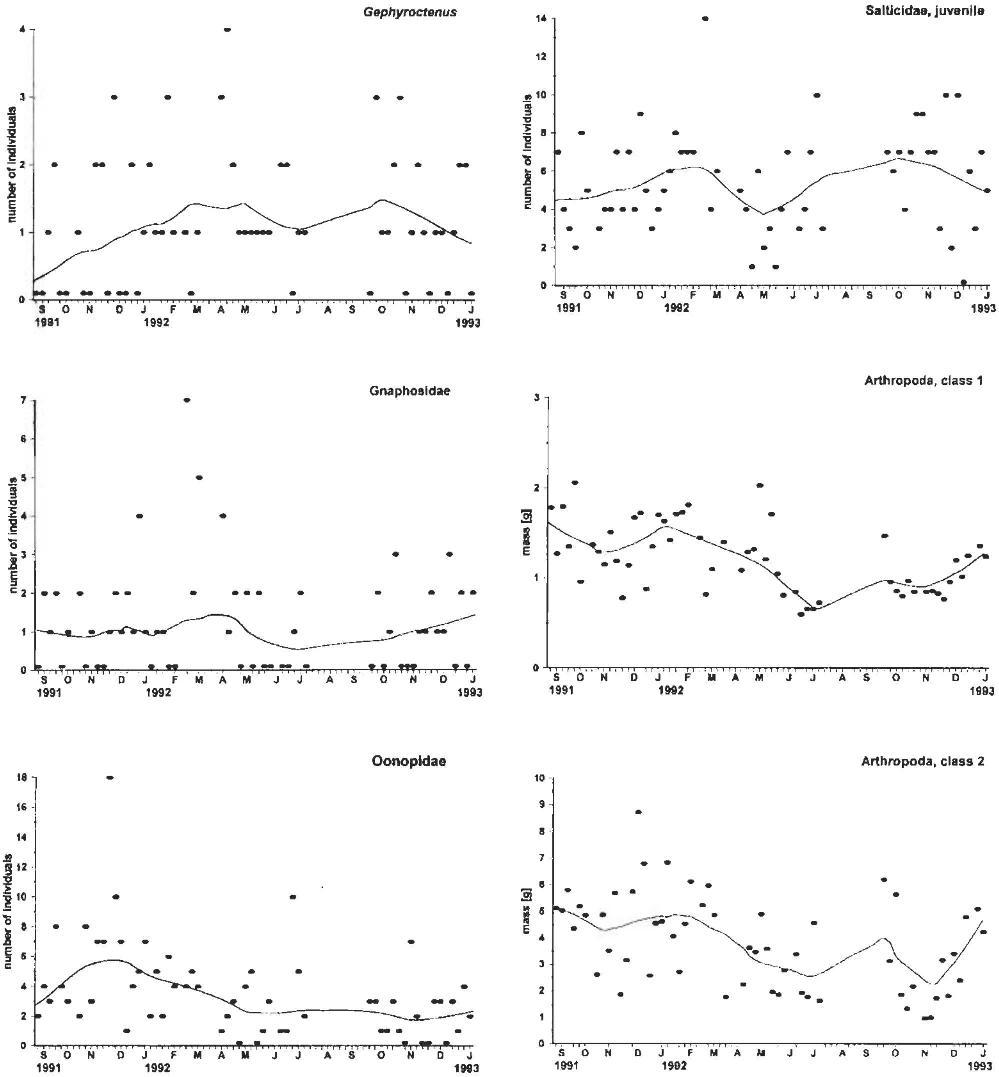












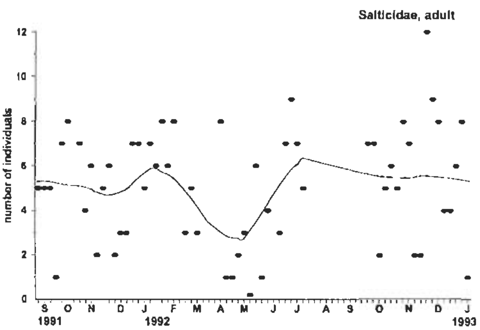


FIG. 2. Phenology of - a. rainfall (weekly precipitation in mm), b. absence/presence of recent clutches of juvenile mygalomorph spiders (*Idiops* sp.), c - j. capture rates of araneomorph spiders, k - l. biomass of arthropods in the traps - during the study period September 1991 - January 1993.

DISCUSSION

More than 3800 spiders were collected during a period of 17 months on three tree trunks. Roughly 30 % (150 species) of the total number of spider species collected in this tropical forest site (450 morphospecies) appeared on these tree trunks, showing the importance of the trunk region as microhabitat, refuge area and pathway to the canopy. This also shows the efficiency of arboreal funnel traps for species inventories.

Although activity density is a mixed index of abundance and activity, it may, given certain assumptions, allow a reasonable understanding of both activity and abundance. When it is reasonable to assume that one has remained constant or has varied in a predictable way, it is possible to estimate the other. For spiders, sudden increases or decreases in captures are generally more likely to reflect changes in activity than in abundance. Furthermore, a constant activity density of spiders as a group throughout the year probably reflects a constancy in both activity and abundance; it is unlikely that one decreases, and the other increases at the same rate and at the same time. However, single species may certainly show seasonal variations in abundance and activity which do not covary, and only a better knowledge of the life cycles and behaviour of tropical spiders will prevent erroneous conclusions.

Hunting by swarm-raiding army ants led to an increase in weekly capture of spiders on tree trunks. When these ants hunted, many more ground-living, large and agile spiders were caught. Medium-sized Ctenidae and Mygalomorphae are the most important spider prey of those army ants (Vieira & Höfer 1994) and climbing trees is probably the most effective way for them to escape. During our nocturnal observations of *Labidus praedator* foraging, those medium-sized spiders, and large adults of *Ctenus*, were the most obvious group of spiders escaping from ants. We could not evaluate the exact intensity of predation, but we were surprised by the high frequency of hunting events. Army ants appeared in almost one quarter of all study weeks, with at least 16 distinct foraging events, and during 9 consecutive weeks. The three traps were too close to consider them as true replicates and to evaluate if such a hunting frequency is common. However, the presence of army ants is an important factor to be considered in sampling programs with traps that measure activity density of arthropods in tropical forests.

The only clear evidence of a seasonal pattern was shown by one species of mygalomorph spiders (*Idiops* sp.). The ecology of mygalomorph spiders in the tropics is poorly known. Many of the large species live in burrows in the ground, but especially the smaller species are difficult to observe. There is evidence that many species spend part of their life on trunks or in the canopy. Some species may disperse aerially from the trees by ballooning, thus increasing their vagility (Coyle 1983, Coyle *et al.* 1985).

On a weekly scale, rainfall apparently did not much affect the activity of spiders on the lower part of tree trunks. However, regression analysis would not detect if one single intensive rain affected spiders in some weeks. This may have happened to Salticidae, where a reduction in activity density following the most intensive rain was observed. However, further observations, with more specific methods, will be necessary to test the effect of strong rains on spiders. In general, rainfall and activity of spiders had no tendency to covary in our study, in contrast to another rainforest in Panama (Nentwig 1993), with more distinct dry and wet seasons.

We believe that the weight of arthropods in the traps was a good measure of the general availability of food for spiders that live on trunks, because a) most arthropods captured climbed the trunks, so they are potential prey to be captured by spiders on trunks, b) most spiders are generalist opportunistic predators, and c) activity density (more than abundance alone) reflects the frequency with which spiders encounter their prey. However we found no evidence that activity density of spiders was affected by the variation of arthropod abundance during the year.

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