PATTERNS OF ABUNDANCE OF FOUR SPECIES OF WANDERING SPIDERS (CTENIDAE, *CTENUS*) IN A FOREST IN CENTRAL AMAZONIA

Thierry R. Gasnier: Depto. de Biologia/ICB, Fundação Universidade do Amazonas, Av. Gal. R.O. J. Ramos 3000, CEP 69067-000, Manaus, AM, Brazil

Hubert Höfer: Staatliches Museum für Naturkunde Karlsruhe, Postfach 6209, D-76042 Karlsruhe, Germany

ABSTRACT.   We studied spatial and temporal patterns of abundance of *Ctenus amphora*, *C. crulsi*, *C. manauara* and *C. villasboasi*, four syntopic species of medium-to-large sized wandering spiders that forage on the ground in a neotropical rainforest. We found temporal variation, apparently seasonal, in abundance for two of the four species. The four species are sympatric in the study area, but with very distinct spatial patterns of abundance. *Ctenus amphora* was more abundant in areas with sandy soil but are also common on clay soils, *C. manauara* and *C. crulsi* are the dominant species in areas with clay soil and are infrequent in sandy soils, and *C. villasboasi* had a more homogenous abundance in the study area. Previous studies suggested that a predator, army ants, could have an important impact on the abundance of these spiders. We estimated the frequency of attacks by army ants using pitfall traps in sandy and clay soil areas. The estimated probability of attack by army ants was higher in areas with clay soil (92% per 3 months), where all species are frequently found, than in sandy soil areas (21%), where *C. crulsi* and *C. manauara* were almost absent. However, it is still not clear if predation by army ants is a key factor that facilitates coexistence in clay soils, and this factor can not explain the difference on the dominant species between areas with different soil types. We also discuss the description of spatial patterns of abundance as a simple, but powerful, tool seldom used for preliminary studies on the coexistence of spiders.

RESUMO.   Nós estudamos padrões espaciais e temporais de abundância de *Ctenus amphora*, *C. crulsi*, *C. manauara* e *C. villasboasi*, quatro espécies sintópicas de aranhas errantes que forrageiam no chão em uma floresta neotropical úmida. Nós encontramos uma variação temporal, aparentemente sazonal, na abundafancia de duas das quatro espécies. As quatro espécies são simpátricas na área de estudo, mas com padrões espaciais de abundância muito distintos. *Ctenus amphora* foi mais abundante em áreas de solos arenosos, mas também foi comum em solos argilosos *C. manauara* e *C. crulsi* foram as espécies dominantes em solos argilosos, e foram infreqüentes em solos arenosos, e *C. villasboasi* teve uma abundância mais homogênea na área de estudo. Estudos anteriores sugeriram que um predador, formigas de correição, poderia ter um forte impacto sobre a abundância destas aranhas. Nós estimamos a freqüência de ataques por formigas de correição usando armadilhas de fosso (pitfall traps) em áreas de solo arenoso e argiloso. A probabilidade estimada de ataques por formigas de correição foi maior em áreas de solo argiloso (92% em 3 meses), onde todas as espécies são freqüentemente encontradas, que em solo arenoso (21%), onde *C. crulsi* e *C. manauara* foram raras. Entretanto, ainda não está claro se a predação é um fator chave para facilitar a coexistência em solos argilosos, e este fator não pode explicar a diferença de espécies dominantes entre as áreas com tipos de solo diferentes. Nós também discutimos a descrição de padrões espaciais de abundância como um ferramenta simples, mas poderosa e pouco usada para o estudo da coexistência de aranhas.

Studies on the ecology of wandering spiders have been performed mainly in temperate regions and mostly with spiders of the family Lycosidae (e.g., Edgar 1971a, b; Ford 1977, 1978; Greenstone 1978, 1979, 1980; Hallander 1970 a, b; Suwa 1986; Van Dyke & Lowrie 1975; Wise 1993). Although the family Ctenidae is rich in species and abundant in the tropics, there are few studies on their ecology. One exception is the genus *Cupiennius*, which

was intensively studied by Barth and collaborators (e.g., Schuster et al. 1994 and citations in it); however, in this genus only the males are considered wandering spiders (Schmitt et al. 1990).

Höfer, Brescovit & Gasnier (1994) studied the wandering spiders of the genus *Ctenus* (Walckenaer 1805) in ''Reserva Florestal Adolfo Ducke'' (RFAD) in central Amazonia. They found seven species, four of which (*Ctenus amphora* Mello-Leitão 1930; *C. crulsi* Mello-Leitão 1930; *C. manauara* Höfer, Brescovit & Gasnier 1994; and *C. villasboasi* Mello-Leitão 1949) are very similar in behavior and use of microhabitat. They forage in and on the leaf litter and are the dominant medium-to-large sized wandering spiders on the ground in most parts of this forest.

Vieira & Höfer (1994, 1998) studied swarm-raiding army ants (*Eciton burchelli* and *Labidus praedator*) in central Amazonia (100 km north of RFAD) and concluded that the spiders of the genus *Ctenus* are among the major prey items of these ants. The effect of army ants on ground-living spiders, including *Ctenus*, was also discussed by Gasnier, Höfer & Brescovit (1995). These ants forage in massive groups of many thousands of individuals, and these authors suggest that they probably have a strong impact on the abundance and on the structure of this guild of wandering spiders. However, although *Ctenus* is an important prey for army ants, the impact of the ants on the spiders is unknown because there is no estimation of how frequently they pass by a given area. The objective of this study was to describe spatial and temporal patterns of abundance of these four *Ctenus* species and to evaluate how army ants influence them.

METHODS

Study area.—The study was conducted in ''Reserva Florestal Adolfo Ducke'' (RFAD), 25 km North of Manaus, Amazon, Brazil. The reserve has 10,000 ha of ''terra-firme'' primary forest, over poor soils of tertiary origin (Chauvel, Lucas & Boulet 1987). Collections were made in an area of 2×5 km (Fig. 1). The northern half of this area is formed by plateaus, slopes and flat valley bottom of the stream ''Barro Branco.'' In this area clay soils (''latossolo amarelo álico'' or ''aplic acrorthox'') predominate, mainly in the plateaus and slopes, but there are sandy soils (''podzol
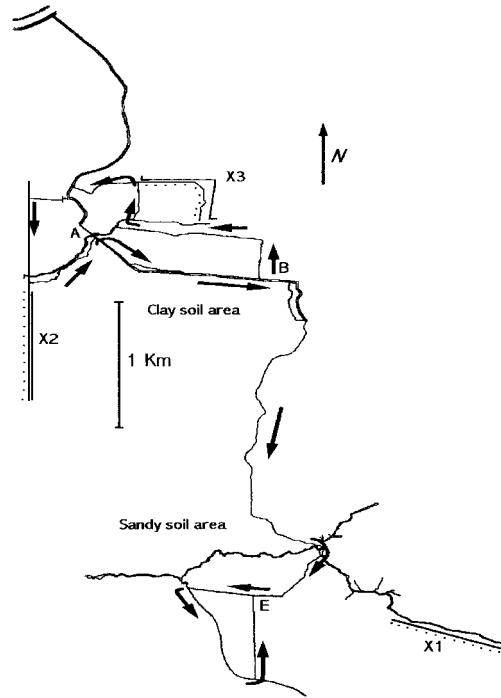

Figure 1.—Study area and the trails used in the extensive censuses. B = start and E = end of the main 12 km trail; arrows indicate the direction followed in this trail. ''X1,'' ''X2'' and ''X3'' are additional trails. A = administration of the reserve.

álico'' or ''arenic tropaquod'') in some of the lower parts of the slopes and in the valley bottom. Close to the streams the hydromorphic soils (''podzólicos vermelho-amarelo latossólicos'' or ''epiaquic paleudults'') dominate. This area is covered by a dense forest called ''Floresta de Terra-Firme'' (in the restricted sense), except for the valley bottom, where the forest is dense, but lower, more humid and with more palms, a vegetation called ''Floresta de Baixio'' (descriptions in Guillaumet 1987). The southern half is the drainage basin of the stream ''Acará.'' Clay soils are present on the more elevated areas next to the plateaus, but most of the work in the ''Acará'' valley was on sandy areas. The vegetation in this area is lower than the ''terra-firme'' forest on clay soils, and is generically called ''Campinarana'' (Guillaumet 1987). Next to the streams in the southern half there is also a predominance of hydromorphic soils. The temperature in the region of Manaus varies little annually, with a mean temperature of

25.8 °C in February and 27.9 °C in September (Salati et al. 1991). Mean annual rainfall in RFAD is 2480 mm, with a dry season from July–November (Marques-Filho et al. 1981). Data presented here were collected from November 1995 to March 1997.

Identification of spiders.—The size (measured as prosoma length) of adults varies among species: *C. manauara* (4–6 mm); *C. crulsi* (5.5–10.5 mm); *C. amphora* (5.5–11 mm); *C. villasboasi* (10–12.5 mm). Identification of spiders at species level is based mainly on reproductive structures (palp in male and epigynum in females), but inside RFAD all species of *Ctenus* are known, and the adults and larger juveniles can be identified based on color and design patterns on their body (descriptions and photographs in Höfer, Brescovit & Gasnier 1994). However, in the smaller juveniles the patterns of color and designs may be confused. During a preliminary phase of this study, we compared color and design patterns in juveniles of different sizes of the four species to provide criteria to distinguish the juveniles of each species in our study area. This was important because it allowed us to get much more data for the evaluation of abundance patterns. We present these criteria below. Vouchers were deposited in the aracnological collection of the Instituto Nacional de Pesquisas da Amazônia under the numbers INPA-001 to INPA-023.

On the back side of the opisthosoma of these *Ctenus* there is a white design similar to an amphora (Greek jar), generally followed by a series of triangles (a very similar pattern is also found in sympatric *Centroctenus*, which made us believe that this is a primitive characteristic for this and related genera). In the adults of *C. villasboasi* this design almost always disappears completely, but it is still visible in the smaller juveniles. *Ctenus villasboasi* can be identified after they reach 2–3 mm because the anterior part of the design is brighter and has the shape of the letter ''U.'' Besides that, individuals larger than 5 mm have a distinct longitudinal white line on the ventral surface of the prosoma, unique in *C. villasboasi*. In *C. amphora* the triangles of the design almost always have disappeared completely in juveniles of size 3–4 mm, resulting in the typical amphora-shaped marking. Besides that, the pattern of coloration of the

body, especially the ventral surface of the opisthosoma, is generally very dark.

Ctenus crulsi and *C. manauara* have the complete pattern of the design (amphora and triangles) from eclosion from the egg sac through the adult phase. Adults and subadults can be distinguished since adults of *C. manauara* are smaller than adults of *C. crulsi*, and the presence of the external copulatory organ (developed in adults or underdeveloped in subadults) is visible to the naked eye. Furthermore, they have some coloration differences, especially on the venter. Adults of *C. manauara* generally are brighter brown on the ventral surface, sometimes pink like the smaller juveniles of all species, and generally with a black spot near the spinnerets. The other species, including *C. crulsi*, have a large triangular design covering most of the ventral surface after they reach 3–4 mm. However, throughout the study, we found this pattern with ventral triangles on the opisthosoma also in adults of *C. manauara*, and possibly the ventral triangle may be delayed in appearing in the juveniles of *C. crulsi*. This means that we could have misidentified some juveniles of *C. manauara* as *C. crulsi* and *vice versa*. Therefore, we counted as identified only spiders larger than 4 mm, which was probably sufficient in avoiding misidentifications.

Censuses.—We captured spiders at night only, using rechargeable battery head lamps (Koehler Electric Cap Lamp). With these lamps the reflection of the light by the eyes of the spiders is visible up to 25 m, even for small individuals, but this depends on the position of the spider, the amount of litter and the density of the lower vegetation. Even when the position does not favor the reflection of the light, spiders may be localized by recognizing the spider's body or part of it.

In the censuses, the spiders were captured, identified, and immediately released at their capture site to minimize disturbance of the population. We employed two types of censuses: intensive censuses, for evaluation of temporal variation of the abundance of spiders, and extensive censuses, for evaluation of spatial patterns of abundance. In the intensive censuses we counted, at intervals of about two months, spiders in 10 small transects (each one of 60 × 1.5 m) per collection for a total of seven collections. The search was intensive, and we tried to capture all visible spiders

with prosoma length larger than 4 mm, which required 20 minutes to one hour per transect. Except for the first collection trip, the transects were in the same 10 defined areas, but in different positions inside the areas at each trip. With this procedure, we tried to include the variability inherent in the system and to obtain similar samples throughout the year, although not at exactly the same points. After the first sampling we realized that *C. crulsi* and *C. manauara* were nearly absent from all 9 selected areas, so we added an area, where individuals of these species were known to be abundant. An index to standardize the effort was applied to the abundance data for the first trip (abundance per species $\times$ 1.11), which compensates for one less transect, but this does not avoid an underestimation for the latter two species because this corrected mean still lacks the area where they are more abundant.

We identified and recorded the position of spiders on 15 km of trails in the extensive censuses, in June and October of 1995 and in February of 1996. Most of the trails constituted an almost continuous line of 12.5 km (Fig. 1), with small interruptions to avoid disturbed areas. The other three trails of about 1 km were outside this continuous line, but were included because they were the spatial extremes of the study area. These three trails are the last three segments in the graphical presentation of the abundance of spiders along the trails. The search for spiders was less intensive than in the previous census; and, depending on their abundance, we spent 30 minutes to two hours counting spiders in 1 km. The number of spiders found by this method was low per meter of transect, especially for small spiders, like juveniles and *C. manauara* (the smallest species), but the total number of spiders, even of *C. manauara*, was high.

The extensive censuses were used to show graphically how the abundance changed along these long transects and to calculate covariation indices among species. The trails were divided into segments of 100 m, which were our sample units. Data used to describe abundance graphically were the number of individuals of each species in each excursion per sample unit. We excluded from the covariation analyses sample units close to disturbed areas, and half of the sample units, avoiding contiguous segments of 100 m, to minimize

the dependency of the data. Data used for the evaluation of covariation were the sum of spiders in each sample unit in the three excursions. Based on the recapture rate of 100 marked adult spiders, we concluded that the sum of spiders per sample unit in three excursions was not biased by the fact that spiders could be counted more than once, because only 1% of the marked animals were found in one transect after one month. Soils type definition in the sample units consisted on a division first in hydromorphic and non-hydromorphic soils, and a division of the non-hydromorphic in clay and sandy soils. This categorization was rough, but sufficient for the analyses, as most places were inside one of the extremes of soil types. We used Pearson's index (Ludwig & Reynolds 1988) for the description of the interspecific covariation by pairs of species, excluding sample units where both elements of the pair were absent.

Estimating the frequency of raid occurrence of army ants.—We installed 40 pitfall traps, with a minimum distance between each of them of 200 m. Each trap consisted of a plastic container (diameter of opening 8 cm, 20 cm deep) buried flush with the surface, and an aluminum cover 10 cm above the trap for protection against rain, not obstructing the entrance of invertebrates. We used picric acid inside the trap as a preservative liquid. Two samples were made for periods of 90 days, from March–June 1995, and from October–February 1996. The samples were preserved in 70% alcohol. We counted the number of army ants of the species *Eciton burchelli* and *Labidus predator*, which are the swarm-raiding species that attack *Ctenus*. Considering that a spider could be where a trap was, we used the proportion of traps with more than 10 army ants of the same species (a probable raid), as an index of frequency of risky encounters for *Ctenus*.

RESULTS

We recorded 494 individuals of *Ctenus* during seven excursions with intensive censuses and 1304 individuals during three extensive censuses. The abundance of *Ctenus amphora* and *C. villasboasi* was high in December 1994, gradually decreased until July, and increased again after August (Fig. 2), suggesting seasonal variation. The abundance of *Ctenus manauara* was also low during the dry season.
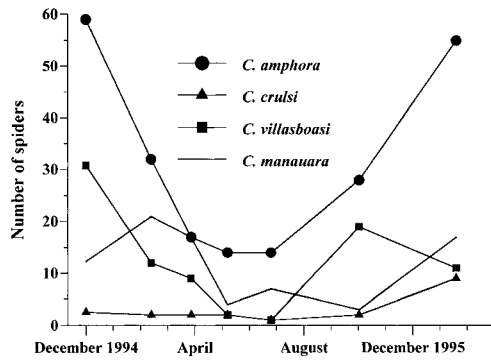
Figure 2.—Number of individuals per species collected in the intensive censuses throughout one year.

Because the census value for December 1994 was probably underestimated (see methods), it is reasonable to assume that it followed the same pattern of the above species. Data from intensive censuses, which was used to describe the patterns above, were not enough to evaluate temporal variation for *C. crulsi*. However, the totals of *C. crulsi* counted in the three extensive censuses in July, October and February 1995 were respectively 63, 129 and 191, a similar temporal variation compared to *C. amphora*, 77, 171 and 235, which means that all species have similar temporal patterns of abundance—or at least that they do not differ strongly.

Comparing the abundance between pairs of species per sample unit, we found significant negative covariation only in the pairs *C. amphora* × *C. crulsi* and *C. amphora* × *C. manauara* (Table 1). The comparison of spatial patterns of abundance (Fig. 3) facilitated the interpretation of these negative correlations. There were large areas with dominance of *C. amphora* where *C. crulsi* and *C. manauara* had low abundance, and *vice versa*. Although the abundances of *C. crulsi* and *C. manauara* were not positively correlated, the comparisons revealed very similar spatial patterns of abundance. Apparently, covariance analysis was not appropriate to evaluate patterns of abundance in this case because the number of individuals per sampling unit was low and because there were many points where both species of the pair were absent. There were three consistent large scale spatial patterns of abundance: *C. amphora* had the highest densities between positions 80 and 150; *C. crulsi* and *C. manauara* had the highest densities between 1–80 and between 150–180; and *C. villasboasi* had a relatively homogeneous distribution.

The total abundance varied through time, but the spatial patterns of abundance within each species were very similar in the three censuses. The positions 80–150, where *C. amphora* was more abundant, were mostly on sandy (55%) or hydromorphic (38%) soils, while the positions 1–80 and 150–180, where *C. crulsi* and *C. manauara* were more abundant, were mostly on clay (64%) or hydromorphic (27%) soils. There are two pieces of evidence suggesting that soils could, directly or indirectly, determinate which species dominates an area: a) the change in dominance from *C. crulsi* and *C. manauara* to *C. amphora* between positions 70 and 90 was coincident with a change in predominant soil from clay to sandy; b) *C. crulsi* and *C. manauara* were almost absent in a large area of white sandy soils, but both appeared in two censuses inside this area, in the only place with a small segment of about 500 m of intermediate sandy-clay soil in the trail.

Table 1.—Interspecific covariation between pairs of *Ctenus* species. Pearson = Pearson's correlation coefficient after excluding sample units where both species in the pair were absent; P = probability associated to the correlation; n = sample size; Sign = significance calculated considering 6 tests: * = significant, ns = non significant.

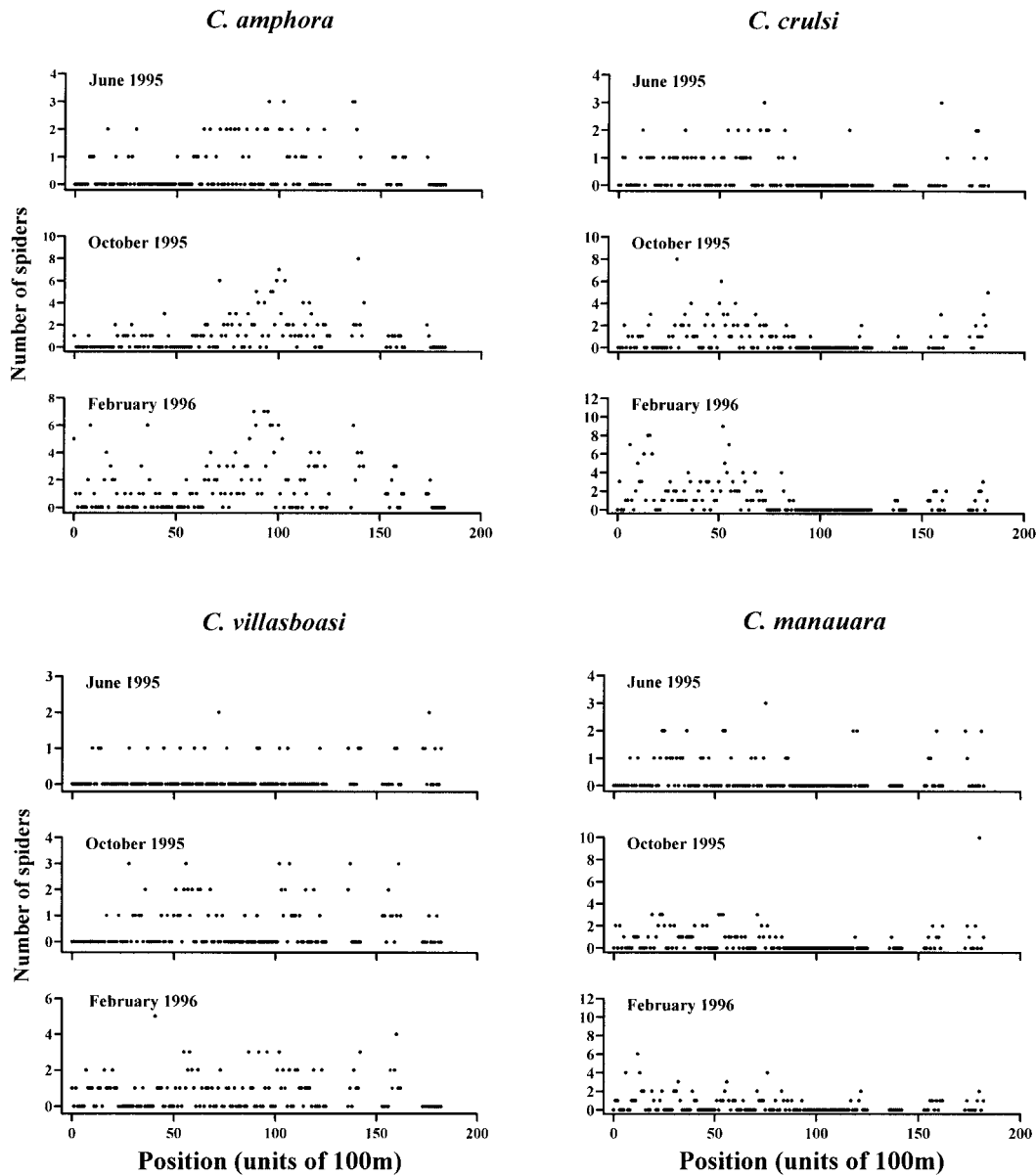| Pairs of species	Pearson	P	n	Sign
C. amphora × *C. crulsi*	−0.48	<0.001	67	*
C. amphora × *C. manauara*	−0.34	0.006	64	*
C. amphora × *C. villasboasi*	0.00	0.99	62	ns
C. crulsi × *C. manauara*	0.02	0.91	49	ns
C. crulsi × *C. villasboasi*	−0.23	0.07	61	ns
C. manauara × *C. villasboasi*	−0.26	0.05	57	ns

Figure 3.—Number of individuals collected along the extensive censuses trails for each species in three periods. Three patterns of abundance were detected: one for *Ctenus amphora*, one for *Ctenus crulsi* and *Ctenus manauara*, and one for *Ctenus villasboasi*.

Considering these differences in relation to soils, we calculated two indices of frequency of risky encounters with army ants, one for clay soil areas and another for sandy soil areas. The traps in hydromorphic soils areas were in insufficient number to be included in the analysis. The proportion of traps with army ants and the amount of army ants were higher in the clay soil areas (Table 2). Clay soil areas had a much higher index of risk of encounters with army ants (0.92) than sandy soil areas (0.21). We suppose that life span for *Ctenus* is between 6–12 months; therefore, it is highly probable that every *Ctenus* individual encounters army ants at least once during its life in clay soils, while many *Ctenus* will

Table 2.—Number of pitfall traps with different amounts of army ants in sandy and clay soils in two periods of the year.

Soil	Absence of ants	1–10 ants	10–100 ants	>100 ants
April–June 1995				
Clay	1	1	2	7
Sandy	1	2	1	1
December 1995–February 1996				
Clay	0	0	8	7
Sandy	3	5	1	0

probably never encounter army ants on sandy soils.

DISCUSSION

The four *Ctenus* species are sympatric throughout the study area. However, there were strong differences in the spatial patterns of abundance of the species, which were stable during the study. Although the amount of spiders changed throughout the year, the general pattern of locational dominance remained. The predominant species in a given place is probably determined by local characteristics of the environment, which favor one species more than the other. However, it is not clear what these environmental characteristics are, and why the favored species in a given place do not exclude the others.

Based on our data, we can conclude that army ants are important predators of *Ctenus*, but a more detailed study would be necessary to determinate if they are a key factor that facilitates coexistence in this system. One evidence that the ants may be important for coexistence is that on clay soils, where army ants are more abundant, the four species are relatively common. However, predation alone would not explain why the dominant species is not the same all over the area.

The temporal variation in the abundance of spiders probably reflected seasonal variation of the environment. Evidence of seasonal variation in the abundance of ctenid-pisaurid spiders was not detected by Gasnier et al. (1995) in this forest; however, this was observed in a year with less pronounced seasons. The cause of variation in the present study is not clear, there are many possible reasons, e.g., a seasonal variation of the amount of leaf litter could restrict the amount of refuges or prey

available, or the absence or excess of rain could cause a seasonal variation in mortality. Whatever the cause, seasonality may facilitate the coexistence of species either by maintaining the species under a level in which their interactions would influence coexistence or by differentiation in seasonal peaks of activity or abundance. Sympatric species of forest-floor spiders may differ by seasonal peaks of abundance (Niemelä et al. 1994), but we did not find this difference among the *Ctenus* species. For a further discussion on how seasonality could affect coexistence in this system it will be necessary to evaluate the mechanism by which environmental seasonality affects the abundance of these spiders.

Evaluations of spatial patterns of abundance or distribution (e.g., Cutler & Jennings 1992; Fernandez-Montraveta, Lahoz-Beltra & Ortega 1991; Greenstone 1979, 1980) are not frequent in the spider literature. Authors defending the use of an experimental approach as the safer mode to evaluate coexistence of species recognize the importance of basic knowledge (e.g., spatial patterns of abundance) to plan and interpret the experiments (e.g., Hairston 1989; Wise 1993). However, there is little discussion on the procedures of how to build this knowledge. The use of interspecific covariation is one of the standard forms to detect patterns of coexistence (Ludwig & Reynolds 1988). However, in our study, the evaluation by interspecific covariation did not show any evidence for the similar patterns of abundance of *C. crulsi* and *C. manauara*. We recommend the interpretation of the indices of covariation in conjunction with an evaluation of spatial patterns of abundance. Evaluations based on graphics of abundance along transects (or on bidimensional maps of abundance) may help to detect important factors that affect a species, especially if the repetition of the censuses indicates that the pattern is stable in time, which probably reflects a local factor. After the pattern is established, and considering the dimension of the areas of higher abundance, the researcher may go back to the field and consider potential factors affecting the abundance. During the comparison of spatial patterns of abundance among species by superposition of graphs unexpected differences may arise, which makes this a powerful tool in the development of hypothesis for the abundance and coexistence of species.

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