

ADULT SIZE OF EIGHT HUNTING SPIDER SPECIES IN CENTRAL AMAZONIA: TEMPORAL VARIATIONS AND SEXUAL DIMORPHISMS

Thierry Ray Gasnier: Depto. de Biologia/ ICB, Fundação Universidade do Amazonas, Av. Gal. R.O. J. Ramos 3000, CEP 69067-000, Manaus, AM, Brazil.
E-mail: thierry@internext.com.br

Clarissa Salette de Azevedo and Martha Patricia Torres-Sanchez: Instituto Nacional de Pesquisas da Amazônia Caixa Postal 478, 69011-970, Manaus, AM, Brazil

Hubert Höfer: Staatliches Museum für Naturkunde Karlsruhe, Postfach 111364, D-76063 Karlsruhe, Germany

ABSTRACT. We studied temporal variation in adult size and sexual size dimorphism (SSD) of seven hunting spider species, *Ctenus amphora*, *C. crulsi*, *C. manauara*, *C. villasboasi* (Ctenidae), *Phoneutria fera*, *P. reidy* (Ctenidae), and *Ancylometes rufus* (Pisauridae) in a tropical rainforest, and one species from a relatively open vegetation habitat, *C. minor*, in central Amazonia. Size variation was great within and among field trips. Spiders were generally smaller in October (end of dry season) when compared with other months: adults of *C. amphora*, *C. crulsi* and *C. manauara* were significantly smaller in October 1995 when compared to February 1996; *P. fera* were smaller in October 1998 than in June 1998; and *A. rufus* were smaller in October 1998 than in August 1998. The temporal variation in size is possibly a result of low prey availability during the dry season. Six species had significant differences in prosoma length between males and females: *C. amphora*, *C. crulsi*, *C. manauara* and *C. minor* had larger males (which is considered rare in spiders), and *P. reidy* and *P. fera* had larger females. However, considering an alternative index of size, the “rough area” (an approximate measure of the area of the spider as seen from above), the males were significantly larger for all species (up to 2.8 times in *C. minor*), because they have longer legs relative to their prosoma length. We suggest that selection for high mobility may be the reason for adult males with longer legs, and that the smaller species had higher degrees of sexual dimorphism in leg length because of the relative size of obstacles in the leaf litter.

RESUMO. Estudamos a variação temporal de tamanho de adultos e o dimorfismo sexual de tamanho de sete espécies simpátricas de aranhas errantes, *Ctenus amphora*, *C. crulsi*, *C. manauara*, *C. villasboasi* (Ctenidae), *Phoneutria fera*, *P. reidy* (Ctenidae), e *Ancylometes rufus* (Pisauridae) em uma floresta tropical úmida, e uma espécie em um habitat de vegetação relativamente aberta, *C. minor*, na Amazônia Central. A variação de tamanho foi grande dentro e entre excursões de coleta. As aranhas foram geralmente menores em outubro (final da estação seca) comparado com outros meses: adultos de *C. amphora*, *C. crulsi*, *C. manauara* e *C. minor* foram significativamente menores em outubro de 1995 comparado a fevereiro de 1996; *P. fera* foram menores em outubro de 1998 do que em junho de 1998 e *A. rufus* foram menores em outubro de 1998 do que em agosto de 1998. A variação temporal em tamanhos observada é possivelmente um resultado de baixa disponibilidade de presas durante a estação seca. Seis espécies tiveram diferenças significativas em comprimento do cefalotórax entre machos e fêmeas, *C. amphora*, *C. crulsi*, *C. manauara* e *C. minor* tiveram machos maiores (o que é considerado raro em aranhas), *P. reidy* e *P. fera* tiveram fêmeas maiores. Entretanto, considerando um índice alternativo de tamanho, a “área aproximada” (uma medida da área da aranha em vista superior), os machos foram significativamente maiores em todas as espécies (até 2,8 vezes em *C. minor*), porque eles têm pernas mais longas em relação ao tamanho do cefalotórax. Nós sugerimos que uma seleção para alta mobilidade pode ser a razão para machos com pernas maiores, e que as menores espécies tem maior dimorfismo sexual no comprimento das pernas devido ao tamanho relativo dos obstáculos na serapilheira.

Keywords: *Ancylometes*, *Ctenus*, Ctenidae, *Phoneutria*, Pisauridae, seasonality, sex ratio, sexual-size-dimorphism, wandering spiders

The size of adult spiders may vary considerably in individuals of the same species and sex. Studies on such variation contributed to the evaluation of spatial and temporal variation in spider growth and abundance (e.g. Jocqué 1981a, b; Olive 1981; Vollrath 1988; Vertainen et al. 2000), and to the discussion of food limitation in spiders (Wise 1993). However, there are relatively few studies documenting spatial and temporal size variation in tropical hunting spiders.

Besides the variation in the size of spiders of the same sex, the differences in size between sexes are remarkable in some species, and the reasons for sexual dimorphism in spiders have received much attention (e.g. Petersen 1950; Jocqué 1983; Elgar 1991; Vollrath & Parker 1992; Head 1995; Prenter et al. 1997; Prenter et al. 1999; Coddington et al. 1997; Hormiga et al. 2000; Schneider 1997; Schneider et al. 2000, Vertainen et al. 2000). Prenter et al. (1999) argued that fecundity selection provides the only general explanation for the evolution of sexual dimorphism in spiders. However, most studies focused on the selective pressures for different degrees of dimorphism in which females are larger; less attention has been paid to the phenomenon that males are slightly larger in a few species.

We studied the temporal variation in the size of adults and the degree of sexual size dimorphism of seven ground hunting spider species in a tropical forest: *Ctenus manauara* Höfer, Brescovit & Gasnier 1994 (Ctenidae), *C. amphora* Mello-Leitão 1930, *C. crulsi* Mello-Leitão 1930, *C. villasboasi*, Mello-Leitão 1949, *Phoneutria fera* Perty 1833 (Ctenidae), *P. reidyi* (F. O. P.-Cambridge 1897) and *Ancylometes rufus* (Walckenaer 1837) (Pisauridae). These species are sympatric in our main study area ("Reserva Ducke"); however, they have differences in relative abundance among habitats and microhabitats. The *Ctenus* species forage exclusively ambushing on the ground litter, but *C. manauara* and *C. crulsi* are more abundant in dry clay soils areas, *C. amphora* more abundant in dry sandy soil areas, and *C. villasboasi* has a more homogeneous distribution including dry and wet clay and sandy soils (Gasnier & Höfer 2001). The *Phoneutria* species forage on the vegetation as young juveniles, and on the ground and on the vegetation when late instar juveniles or adults. *Phoneutria reidyi* is almost absent on dry

sandy soils while *P. fera* is well distributed in dry and wet sandy and clay soils (Torres-Sanches 2000). *Ancylometes rufus* forage exclusively on the ground, where they feed mostly on arthropods, close to or far from bodies of water; however, it is much more abundant close to streams and natural pools, where they find extra food (e.g., tadpoles, toads and small fishes) and may dive to escape from predators (Azevedo 2000; Höfer & Brescovit 2000). These species, specially the *Ctenus* in the dry areas and *A. rufus* in the wet areas, are the dominant medium to large sized hunting spiders in "Reserva Ducke." Another species, *Ctenus minor* F. O. P.-Cambridge 1897, was included in the evaluation of size dimorphism. It forages on the ground in places with a relatively open vegetation on dry sandy soils locally called "campina" (Höfer et al. 1994). This species was collected about 100 km from "Reserva Ducke" (see Methods).

METHODS

Most of the study was conducted in "Reserva Florestal Adolpho Ducke" (2°57' S, 59°57'W), a forest reserve in contact with the city of Manaus, Amazonia, Brazil. The reserve has 10,000 ha of "terra-firme" primary forest (description of vegetation in Guillaumet 1987). We collected data in an area inside the reserve of about 2 by 5 km, where three different habitats occur: "Baixio," or forest close to streams in small flat valleys on hydromorphic soils; "Campinarana," or forest on dry sandy soils, and "terra-firme forest" in a strict-sense, on dry clay soils. A more detailed description of the study area is presented in Gasnier & Höfer (2001). The wettest months are November–May, the driest June–October, and the mean annual rainfall is 2480 mm (Marques-Filho et al. 1981). We collected *C. minor* in the "Reserva da Campina" (01°40'S, 60°50'W). This species apparently occurs in "Reserva Ducke," but not in the area where we collected spiders. We included data on *C. villasboasi* collected by L. Mestre in "Reserva Ducke" and in the reserves of the "Projeto de Dinâmica Biológica de Fragmentos Florestais" (02°38'S, 59°93'W).

Data presented here were part of one doctoral and two master dissertations on *Ctenus* (Gasnier 1996), *Phoneutria* (Torres-Sanchez 2000) and *Ancylometes* (Azevedo 2000), which are deposited (with the raw data) in the

library of the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus. Therefore, there are some differences in the methods and time of collection. We searched for spiders with head lamps at night, their active period. Spiders of the genus *Ctenus* were collected by forcing them to enter small glass vials for identification and measurement of the prosoma length. The measurement was made with a ruler in the field, because collection of individuals was avoided during the study. Comparing field and laboratory measures, we considered this to be a sufficiently accurate method even for the smallest species *C. manauara*, since the same person did all measurements. Spiders of the genus *Phoneutria* were collected with a plastic vial large enough for a safe catch, and killed in the place of the capture with 70% alcohol for later identification and measurement of the prosoma length. *Ancylometes rufus* were immobilized by hand and measured in the field with a ruler (always by the same person), because the study of this genus included the marking and recapture of the spiders.

We used prosoma length as our main index of size instead of prosoma width, a more standard measure of spider size (Jocqué 1981b), because the prosomas of these spiders are elongate, and we considered it a more accurate measure when it has to be done in the field with a ruler, as we did for *Ctenus*, and we maintained it for the other spiders. A factor to transform prosoma length into an approximate measure of prosoma width for all these spiders for comparative studies is 0.8. A second index of size was the "rough area" (RA), which was an area of a circle (πr^2) calculated using the mean of the leg lengths (fully spread) as radius (r). This index is a simplified measure of the area of a spider as seen from above; unlike the former index, this measure of size takes into account the lengths of the spiders' legs. We also calculated an index of the length of legs corrected by size, the leg/prosoma ratio (LPR), which was the mean of the leg lengths divided by the prosoma length. We decided to use the latter indices after field work, therefore the evaluations with these indices were restricted to the study of the degree of sexual dimorphism, and the measurements were from the spiders that we deposited in the Arachnological Collection of INPA as vouchers (INPA 001–INPA 063 and "Iote TG01"),

from Reserva Ducke and other from the region close to Manaus. Spiders without at least one leg of each pair intact were not measured. For all these indices, we calculated the degree of sexual size dimorphism (SSD) as the mean of the index of the males divided by the mean of the females. We also calculated the maximum prosoma length differences (MD) as percentages as follows: $MD = 100 * (\text{largest size} - \text{smallest size}) / \text{smallest size}$.

We measured the prosoma length of *Ctenus* found along 12 km of trails inside primary forest that included the three different habitats types of the reserve in October 1995 and in February 1996. We included extra data of *C. villasboasi* (see above) in the analysis of SSD, because sample size of adults of this species was low. *Phoneutria* were collected, along 9 km of trails (mostly the same used in the *Ctenus* study) in June and October of 1998 and April and August of 1999, and in other places of the reserve in the same years. We used all data of this genus for evaluation of SSD, but only the data of the trails in the evaluation of temporal variation of size, to avoid an influence of combining data from different localities in the evaluation. Furthermore, we only used data of field trips in which more than five adults of the considered species were collected. *Ancylometes rufus* were measured along 0.5 km of the stream "Barro Branco," from 1 km above the administration building of the reserve. We made bimonthly field trips from June 1998–August 1999, but we used only data from June–October of 1998 in the analysis of temporal variation of size, because in the other months we could not find more than five adults in a trip.

We used a non-parametric ANOVA (Mann-Whitney U test and Kruskal Wallis KW) to test the differences of sizes between sexes and among field trips, and Mann-Whitney corrected by Bonferroni for multiple pairwise comparisons (Zar 1984), which were made only between one trip and the next to reduce the number of comparisons. The significance level was $\alpha = 0.05$, but we generally presented exact values, and the significance levels were adjusted to 0.025 for two comparisons and to 0.017 for three comparisons. The presented indices of the calculated U and KW are the number of cases in each category in order of time or first males then females. We did not use evolutionary covariance regression (Head

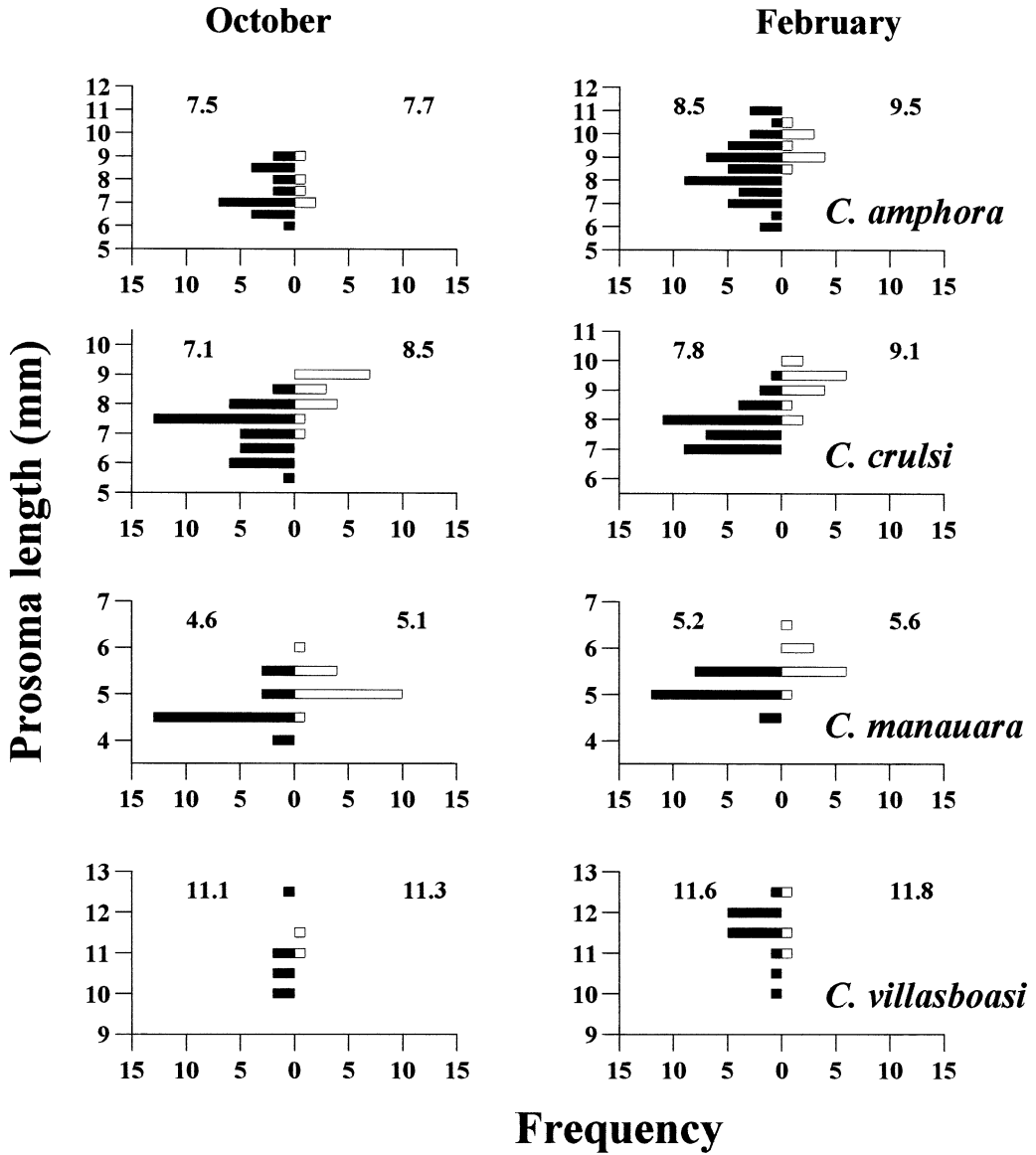


Figure 1.—Frequency distribution of prosoma length classes of four *Ctenus* species in October 1995 and February 1996. Closed bars = females, open bars = males. The numbers are the mean size for each sex in each occasion.

1995), or any other comparative biology method to correct for inflated degrees of freedom, for the relationships between RA and prosoma length, and between LPR and prosoma length, because the phylogenetic relationship among these genera is still controversial (Huber et al. 1993), and among species in *Ctenus* is unknown. All measures of prosoma length are in mm.

RESULTS

We observed significant temporal variation in size for most species. Spiders of three *Ctenus* species were significantly smaller in October 1995 compared to February 1996 (*C. amphora*, $U_{27,55} = 334$, $P < 0.001$; *C. crulsi*, $U_{55,50} = 883$, $P = 0.001$; *C. manauara*, $U_{41,34} = 339$, $P < 0.001$; *C. villasboasi*, $U_{10,14} = 43$, $P = 0.11$; Fig. 1). Size varied for *P. fera*

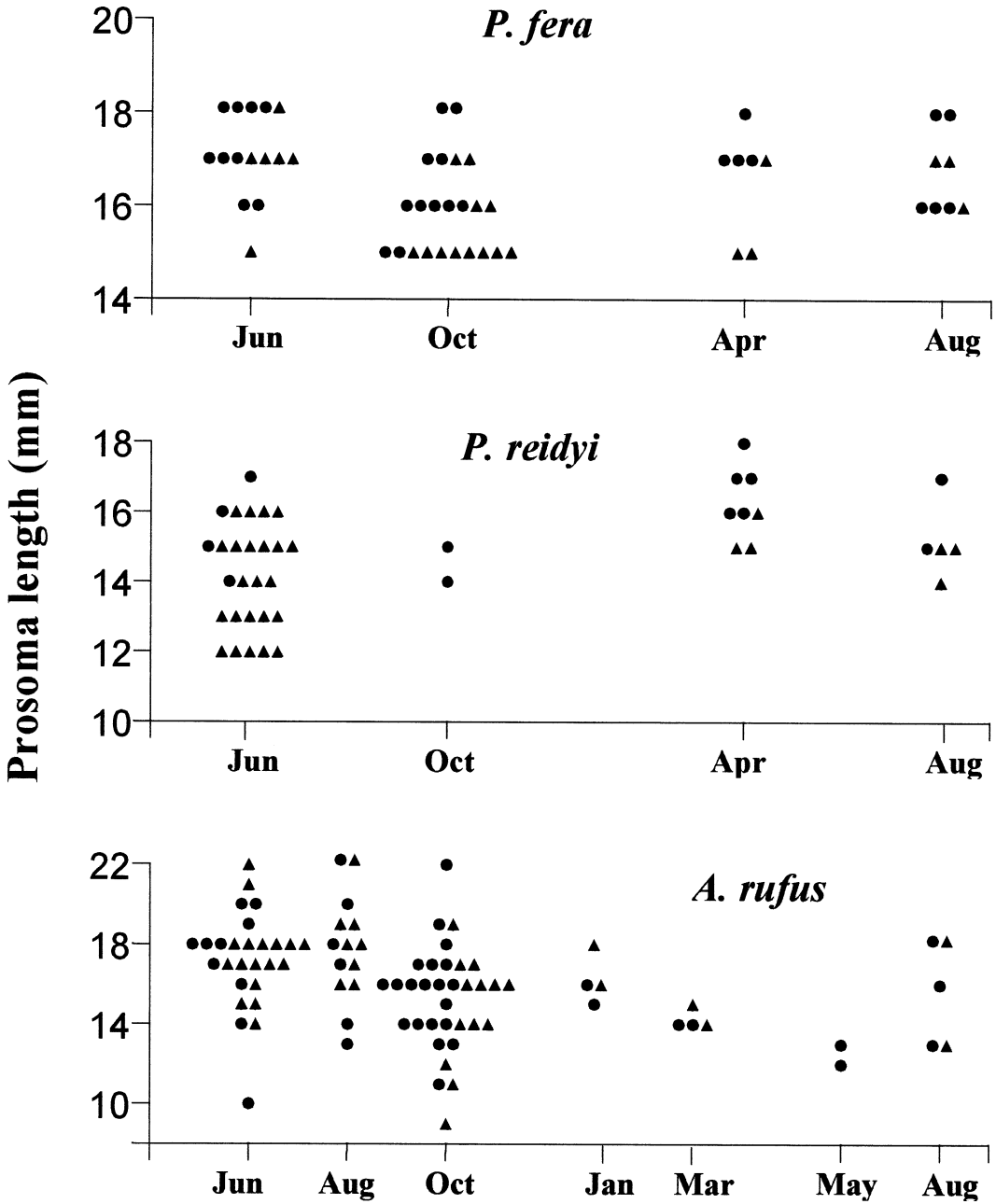


Figure 2.—Prosoma length of females (●) and males (▲) of adults of *Phoneutria fera*, *P. reidyi* and *Ancylometes rufus* on each field trip.

($KW_{15,23,7,8} = 11.6$, $P = 0.009$), with the following differences of means on the pairwise comparisons: June 1998 (17.1) > October 1998 (15.9) = April 1999 (16.6) = August 1999 (16.8) (Fig. 2). Only in June 1998 and April 1999 did we collect enough adults of *P.*

reidyi for evaluation, and we found larger adults in April ($U_{27,8} = 35.5$, $P = 0.002$, respectively 14.2 and 16.3). However, an unusual sex ratio was found on the first field trip (Table 1); 85% of the adults were males, compared to 46% in the other three months, and

Table 1.—Size data of the spiders measured in the field. n_1, n_2, n_3 and n_4 = sample size of females and males respectively in each field trip (see text for field trip dates in each genus); MPLF = mean prosoma length for females; MPLM = mean prosoma length for males; StD = standard deviation; MDF = maximum prosoma length difference for females (percentages); MDM = maximum prosoma length difference for males; SDPL1 = degree of size dimorphism in prosoma length (first sample); Significance levels of SDPL1: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$, ns = non significant.

Species	n_1	n_2	n_3	n_4	MPLF	StD	MPLM	StD	MDF	MDM	SDPL1	Sign
<i>C. manauara</i>	22:19	22:12			4.90	0.46	5.32	0.44	38	44	1.09	***
<i>C. crulsi</i>	38:17	34:16			7.46	0.79	8.76	0.7	73	43	1.17	***
<i>C. amphora</i>	22:5	45:10			8.15	1.25	8.87	1.09	83	50	1.09	*
<i>C. villasboasi</i>	8:2	11:3			11.4	0.93	11.6	0.65	44	25	1.02	ns
<i>P. reidyi</i>	4:23	2:0	5:3	2:3	15.9	1.26	14.2	1.39	36	75	0.89	***
<i>P. fera</i>	9:6	11:12	4:3	5:3	16.8	0.97	16.2	1.28	20	20	0.96	**
<i>A. rufus</i>	10:17	6:8	20:13		16.0	2.71	16.5	2.57	144	133	1.03	ns

this species presented sexual size dimorphism in prosoma length (see below). Therefore, this difference probably does not reflect the variation in the size of the spiders, but rather the change in the sex ratio in our captures. This was not a problem in the analysis of *P. fera*, because sex ratio was approximately constant among trips to the field, and no size dimorphism was detected for *A. rufus* (see below). The size of the adults of *A. rufus* varied from June to October 1998 ($KW_{27,14,33} = 14.6, P < 0.001$), with the following differences in pairwise comparisons: June (17.3) = August (17.8) > October (15.3).

Adult males had a prosoma length significantly larger than females in three species of *Ctenus*: *C. amphora* ($U_{15,67} = 682, P = 0.030$), *C. crulsi* ($U_{33,72} = 2110, P < 0.001$), and *C. manauara* ($U_{31,44} = 986, P < 0.001$) (Table 1). Significant difference in prosoma length between sexes was not found for *C. villas-*

boasi, neither for those collected in October 1995 or February 1996 ($U_{5,19} = 54, P = 0.64$), nor for more than 36 females and 17 males measured on other occasions (see methods; $U_{22,55} = 750, P = 0.09$). Both *Phoneutria* species had females with larger prosoma length: *P. reidyi* ($U_{29,13} = 72, P = 0.001$) and *P. fera* ($U_{24,29} = 200, P = 0.006$). There was no significant difference in prosoma length between males and females of *A. rufus* ($U_{44,45} = 1135, P = 0.23$). The degrees of sexual dimorphism in prosoma length of the spiders measured in the field (SDPL1- Table 1) were similar to those from the Arachnological Collection of INPA (SDPL2- Table 2).

Although some species had females with greater prosoma length, all species had males with larger “rough area” (RA) (Table 2, $P < 0.05$ for *U* test), because they all had legs significantly longer relative to their prosoma lengths ($P < 0.05$). *Ctenus minor* had males

Table 2.—Size data of the spiders measured in the Arachnological Collection of INPA. n = sample size of females and males respectively; MFPL = mean female prosoma length; MMPL = mean male prosoma length; StD = standard deviation; SDPL2 = degree of sexual dimorphism in prosoma length (second sample); SDRA = degree of sexual dimorphism in “rough area” (see text); SDLPR = degree of sexual dimorphism in leg/prosoma ratio.

Species	n	MFPL	StD	MMPL	StD	SDPL2	SDRA	SDLPR
<i>C. minor</i>	15:16	4.33	0.56	4.81	0.60	1.11	2.78	1.53
<i>C. manauara</i>	41:28	4.59	0.45	5.00	0.47	1.09	2.52	1.46
<i>C. crulsi</i>	20:12	7.15	0.61	8.13	0.53	1.14	2.54	1.40
<i>C. amphora</i>	8:10	7.55	0.72	8.63	0.44	1.14	2.45	1.37
<i>C. villasboasi</i>	3:3	11.3	1.15	11.7	0.58	1.02	2.14	1.42
<i>P. reidyi</i>	6:6	16.2	1.72	14.3	1.97	0.95	1.33	1.31
<i>P. fera</i>	6:6	17.7	1.03	16.8	1.47	0.87	1.32	1.21
<i>A. rufus</i>	4:4	17.5	1.73	16.6	1.75	0.95	1.63	1.35

significantly larger in all indices ($P < 0.05$). This dimorphism in RA and LPR is evident even by sight in the field (specially for *Ctenus*), and occurs when the males become adults; we could not distinguish a female from a male of an instar before maturity based on the relative size of the legs. The degree of sexual size dimorphism in RA and LPR decreased significantly with the female prosoma length of the eight species ($r^2 = 0.92$; $P < 0.001$ for RA and $r^2 = 0.68$; $P = 0.007$ for LPR).

DISCUSSION

The size variation of these species within an area of 10 km² was remarkable: the mean difference in prosoma length between the largest and smallest individuals for females was 63%. Based on the relationship between length and size for immature *Phoneutria*, we estimate that this variation in length is equivalent to a difference of almost four times in weight, and that the variation found in *A. rufus* between the largest and the smallest adult females is greater than 10 times in weight. Jocqué (1981) found similar size and weight variations, and our results corroborate his suggestion that large size variations among individuals are a rule rather than an exception in spider populations. Laboratory studies have shown that the size of adults depends on the amount of food during development (e. g. Nakamura 1987; Vertainen et al. 2000), and this probably also explains most of the intraspecific spatial and temporal variation in the size of spiders in nature (Jocqué 1981 a, b; Wise 1993). Therefore, the observed size variation reflects a great phenotypic plasticity which may be important for habitats with unpredictable food supply in space and time.

There is evidence that seasonality in the availability of prey causes variation in size for these spiders. Most species had smaller adult sizes in October, the end of the dry season, when the abundance of the arthropods in the leaf litter in this forest is considered low (Luizão & Luizão 1991). Even the abundance of *Ctenus* and *Phoneutria* is smaller during the dry season (Gasnier & Höfer 2001; Torres-Sanchez 2000). Assuming a significant level of mortality, specially for the smaller species, most of the adults found in this month probably developed mostly during a period with low availability of prey. In the case of *A. ru-*

fus, availability of food is likely to be larger in the wet season for the additional reason that during this time there are pools close to the streams. *Ancylometes rufus* migrate to pools apparently in search of prey as small fishes, tadpoles and toads, and, latter, in the dry season, they return to the stream borders, where it is probably safer than in the dry pools, but more difficult to capture these prey (Azevedo 2000).

Based on body size (body length), Head (1995) stated that males larger than females is a rare phenomenon, and only with a small degree of size dimorphism. Males larger than females is an exception in the records of sexual dimorphism of spiders: from the 1181 species listed by Head (1995) and Prenter et al. (1997), only about 1% consisted of species with larger males. However, sample size to detect a small size dimorphism should be large, because natural size variation in each sex may be large in spiders, specially if body size is the measure used, instead of prosoma length or width, because the first index also varies with the nutritional and reproductive status of the spider. We believe that further studies with species with smaller degree of sexual dimorphism may show that larger males (in prosoma length) are more common than previously stated. In this study, we contribute with the record of four species (but all from a single genus) to the list of males with greater prosoma length.

Prosoma length (or width) is certainly the most important index of size to start the comprehension of sexual size dimorphism in spiders; however, indices related to the leg lengths are also important (Prenter et al. 1995). Based on the "rough area" (RA), we found that a high degree of sexual dimorphism of size in spiders (up to 2.78 in *C. minor*) is not restricted to larger females. Furthermore, we detected negative correlations between the degree of sexual size dimorphism and prosoma length for the RA and LPR indices. There is an unidentified spider species of the family Heteropodidae in our study area that forages in the leaf litter and is a little smaller than *C. manauara* which also has adult males with legs distinctly longer than the juveniles and adult females (unpublished). It is not clear if these correlations would remain after considering the phylogenetic relationships among these species (Ridley 1989). However, in the

absence of these data, the correlations and the recent observations are enough to suggest that this relationship should be investigated.

Sexual dimorphism may be the result of different selective pressures (Hedrick & Temeles 1989). Males may be larger as a result of the competition for access to mates and to mates' choice, or the dimorphism may have evolved from food competition between sexes, or the sexes may have intrinsic differences between the reproductive roles (such as a more active search for mates by males). Legrand & Morse (2000) suggest that males of a species of crab spiders (*Misumena*) probably evolved relatively longer legs because it would be advantageous for locating females under low density, and Kotiaho et al. (1999) found that large males of *Hydrolycosa rubrofasciata* (Lycosidae) have advantages in mate searching. We believe that the same may apply for the species of the present study. Males of *Ctenus* are much more active than females and juveniles (Salvestrini & Gasnier 2001), which seems to be a common pattern for Ctenidae (Schmitt et al. 1990). Although *Ctenus* are relatively abundant, the density of adults is low during most of the year (Gasnier & Höfer 2001), and the density of *Phoneutria* is certainly much lower. Males of these genera in our study area probably have to search a great deal to find a receptive female. Selection for high mobility may be the reason for adult males with longer legs (shorter legs of juveniles and females may be more efficient for prey capture). Furthermore, high mobility in the leaf litter is probably more complicated for the smaller species, due to the relative size of the obstacles, which could cause a higher dimorphism in the relative size of the legs. Further studies will be necessary to verify if the pattern found for these species applies to other hunting spiders, specially for those foraging on the ground of forests, and to evaluate which are the selective pressures that determine different degrees of sexual dimorphism in hunting spiders.

ACKNOWLEDGMENTS

This paper is part of the thesis of the three first authors, all in the post-graduation program of the convenio between INPA and the University of Amazonas. We thank Gary Polis (*in memoriam*), Lucille Anthony, Friedrich Barth, Antônio Brescovit, Harold Fowler, Pe-

dro Gnaspini, Hilton Japyassú, Christopher Martius, Gilson Moreira, Eduardo Venticinque and David Wise for suggestions on the thesis, and Rudy Jocqué, Petra Sierwald, James Berry, Gustavo Hormiga, and anonymous reviewers for commenting on the manuscript. We are indebted to the workers of the "Reserva Florestal Adolpho Ducke" for their hospitality and help. We thank Luis Macedo Mestre for the unpublished data on *C. villasboasi*. Financial support came from fellowships from the Brazilian institutions CAPES (for Gasnier and Azevedo) and CNPq (for Torres-Sanchez) and field support grants from CNPq (project 400023/98) and from the German institutions DFG (proj. Prof. Dr. L. Beck) and GTZ (project BE 281).

LITERATURE CITED

- Azevedo, C.S. 2000. Ecologia de *Ancylometes gigas* (Pickard-Cambridge, 1897) (Araneae: Pisauridae), uma aranha errante que vive próximo a corpos de água em uma floresta tropical úmida. Master's thesis, UA/INPA/CAPES. Manaus, Brazil. 56 p.
- Coddington, J.A., G. Hormiga & N. Sharff. 1997. Giant female or dwarf male spiders? *Nature* 385: 687–688.
- Elgar, M.A. 1991. Sexual cannibalism, size dimorphism, and courtship behavior in orb-weaving spiders (Araneidae). *Evolution* 45:444–448.
- Gasnier, T.R. 1996. Ecologia comparada de quatro espécies de aranhas errantes do gênero *Ctenus* (Walckenaer) (Araneae, Ctenidae) em uma floresta na Amazônia Central: Bases para um modelo integrado de coexistência. Dr. Thesis, UA/INPA/CAPES. Manaus, Brazil. 77pp.
- Gasnier, T.R. & H. Höfer. 2001. Patterns of abundance of four species of wandering spiders (Ctenidae, *Ctenus*) in a forest in central Amazonia. *Journal of Arachnology* 29:95–103.
- Guillaumet, J.L. 1987. Some structural and floristic aspects of the forest. *Experientia*, 43:241–251.
- Head, G. 1995. Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (Class Araneae). *Evolution* 49: 776–781.
- Hedrick, A.V. & E. Temeles. 1989. The evolution of sexual dimorphism in animals: hypothesis and tests. *Trends in Ecology and Evolution* 4:136–138.
- Höfer, H. & A.D. Brescovit. 2000. A revision of the Neotropical spider genus *Ancylometes* Bertkau (Araneae: Pisauridae). *Insect Systematics and Evolution* 31:323–360.
- Höfer, H., A.D. Brescovit & T. Gasnier. 1994. The wandering spiders of the genus *Ctenus* (Cteni-

- dae: Araneae) of Reserva Ducke, a rainforest reserve in central Amazonia. *Andrias* 13:81–98.
- Hormiga, G., N. Scharff, & J. Coddington. 2000. The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). *Systematic Biology* 49:435–462.
- Huber, K. C., T.S. Haider, M.W. Müller, B.A. Huber, R.J. Schweyen, & F. Barth. 1993. DNA sequence data indicates the polyphyly of the family Ctenidae (Araneae). *Journal of Arachnology*. 21: 194–201.
- Kotiaho, J., R.V. Alatalo, J. Mappes & S. Parri. 1999. Sexual signalling and viability in a wolf spider (*Hydrolycosa rubrofasciata*): measurements under laboratory and field conditions. *Behavioral Ecology and Sociobiology* 46:123–128.
- Legrand, R.S. & D.H. Morse. 2000. Factors driving extreme size dimorphism of a sit-and-wait predator under low density. *Biological Journal of the Linnean Society* 71:643–664.
- Luizão, R.C.C. & F.J. Luizão. 1991. Liteira e biomassa microbiana do solo no ciclo de matéria orgânica e nutrientes em terra firme na Amazônia Central. Pp. 65–75, *In Bases Científicas para Estratégias de Preservação e Desenvolvimento da Amazônia: Fatos e Perspectivas*, Vol 1. (A. L. Val, R. Figliuolo & E. Feldberg, eds). Instituto Nacional de Pesquisas da Amazônia, Manaus.
- Jocqué, R. 1981a. On reduced size in spiders from marginal habitats. *Oecologia* 49:404–408.
- Jocqué, R. 1981b. Size and weight variations in spiders and their ecological significance. *Biologisch Jaarboek Dodonaea* 49:155–165.
- Jocqué, R. 1983. A mechanism explaining sexual size dimorphism in spiders. *Biologisch Jaarboek Dodonaea* 51:104–115.
- Marques-Filho, A.O., M.N.G. Ribeiro, H.M. dos Santos, J.M. dos Santos. 1981. Estudos climatológicos da Reserva Florestal Ducke. IV. Precipitação. *Acta Amazônica* 11:759–768. Manaus.
- Nakamura, K. 1987. Hunger and starvation. Pp. 287–295, *in Ecophysiology of Spiders*. (W. Nentwig, ed.). Springer-Verlag, Berlin.
- Olive, C.W. 1981. Optimal phenology and body-size of orb-weaving spiders: foraging constraints. *Oecologia* 49:83–87.
- Petersen, B. 1950. The relation between size of mother and number of eggs and young in some spiders and its significance for the evolution of size. *Experientia* 6:516–518.
- Prenter, J., W.I. Montgomery & R.W. Elwood. 1995. Multivariate morphometrics and sexual dimorphism in the orb-web spider *Metellina Segmentata* (Clerck, 1757) (Araneae, Metidae). *Biological Journal of the Linnean Society* 55:345–354.
- Prenter, J., Elwood, R.W. & W.I. Montgomery. 1999. Sexual size dimorphism and reproductive investment by female spiders: A comparative analysis. *Evolution* 53:1987–1994.
- Prenter, J. Montgomery, W.I. & R.W. Elwood. 1997. Sexual dimorphism in northern temperate spiders: implications for the differential mortality model. *Journal of Zoology* 243:341–349.
- Ridley, M. 1989. Why not to use species in comparative tests? *Journal of Theoretical Biology* 136:361–364.
- Salvestrini, F.M.D. & T.R. Gasnier. 2001. Differences in the activity of juveniles, females and males of two hunting spiders of the genus *Ctenus* (Araneae, Ctenidae): active males or inactive females? *Journal of Arachnology* 29:276–278.
- Schmitt, A., M. Schuster, & F.G. Barth. 1990. Daily locomotor activity patterns in three species of *Cupiennius* (Araneae, Ctenidae): The males are the wandering spiders. *Journal of Arachnology* 18:249–255.
- Schneider, J.M. 1997. Timing and the mating system of the spider, *Stegodyphus lineatus* (Eresidae): how important is body size? *Biological Journal of the Linnean Society* 60:517–525.
- Schneider, J. M., M.E. Herberstein, F.C. de Crespigny & S. Ramamurthy. 2000. Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. *Journal of Evolutionary Biology* 13:939–946.
- Torres-Sanchez, M.P. 2000. Padrões espaciais de abundância, ciclo reprodutivo e variação de tamanho de adultos de *Phoneutria fera* Perty e *Phoneutria reidy* F.O. Pickard-Cambridge (Araneae, Ctenidae) na Reserva Florestal Adolpho Ducke, Amazonas, Brasil. Master's thesis, UA/INPA/CNPq. Manaus, Brazil. 86pp.
- Vertainen, L., R.V. Alatalo, J. Mappes & S. Parri. 2000. Sexual differences in growth strategies of the wolf spider *Hydrolycosa rubrofasciata*. *Evolutionary Ecology* 14:595–610.
- Vollrath, F. 1988. Spider growth as an indicator of habitat quality. *Bulletin of the British Arachnological Society* 7:217–219.
- Vollrath, F. & G.A. Parker. 1992. Sexual dimorphism and distorted sex ratios in spiders. *Nature* 360:156–159.
- Wise, D.H. 1993. *Spiders in Ecological Webs*. Cambridge Univ., Cambridge.
- Zar, J. 1984. *Biostatistical Analysis*. Prentice Hall. New Jersey. 718 p.

Manuscript received 27 December 2000, revised 3 November 2001.