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### Population dynamics, age structure and sex ratio of the bromeliad-dwelling jumping spider, *Psecus chapoda* (Salticidae)

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## Population dynamics, age structure and sex ratio of the bromeliad-dwelling jumping spider, *Psecas chapoda* (Salticidae)

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### Abstract

In this study, the population fluctuations, phenology and sex ratio of the bromeliad-dwelling jumping spider *Psecas chapoda* were investigated in an area of semi-deciduous forest in south-eastern Brazil. *Psecas chapoda* occurred and reproduced on *Bromelia balansae* (Bromeliaceae) throughout the year. The number of egg sacs increased at the beginning of the rainy season (September to December), but the population size and phenology were stable over time and correlated weakly with rainfall and temperature. The principal factor affecting the dynamics of *P. chapoda* was the blooming of *B. balansae*, which expelled spiders because of the drastic change in plant architecture. Male spiders were more frequent than females during the juvenile phase, whereas females were more frequent than males during the subadult and adult phases, suggesting a sex ratio that favoured males. The biotic and abiotic factors that influence the population dynamics and sex-dependent vulnerability determination are discussed.

**Keywords:** Animal–plant interactions, seasonal fluctuation, age structure, sex ratio, *Psecas*, *Bromelia*, Brazil

### Introduction

The phenology of an organism, seen as temporal variations in its life cycle, can be affected by several biotic and abiotic factors. A knowledge of these factors is crucial for understanding a species' population dynamics and community structure (Wolda 1988). Spiders can adjust their phenology and reproductive periods in response to biotic and abiotic conditions (Reiskind 1981; Plagens 1983; Rinaldi and Forti 1997; Arango et al. 2000; Crouch and Lubin 2000; Rossa-Feres et al. 2000; Romero 2001), to prey availability (Riechert and Luczak 1982; Riechert and Harp 1987; Arango et al. 2000; Crouch and Lubin 2000; Romero and Vasconcellos-Neto 2003) and the availability of foraging sites (Nentwig 1993; Arango et al. 2000; Romero and Vasconcellos-Neto 2004).

The jumping spider *Psecas chapoda* (Peckham and Peckham 1894), previously identified as *P. viridipurpureus* (Simon 1901) in Rossa-Feres et al. (2000), inhabits *Bromelia balansae* Mez. (Bromeliaceae), a bromeliad that does not accumulate rain water. The entire life cycle, including courtship behaviour, mating, egg laying and population recruitment of

young occur on the bromeliad. Females make up to two egg sacs in the middle region on the concave upper surface of the leaf. These sacs are then covered by a ceiling of silk anchored to the edges of the leaf, with females remaining under this ceiling and above the egg mass (Rossa-Feres et al. 2000). During blooming, *B. balansae* folds its leaves to the ground to expose its inflorescence to pollinators. Flowering plants are not occupied by *P. chapoda*, probably because the change in plant architecture does not favour the occupation by the spiders (Romero and Vasconcellos-Neto, unpublished data). Rossa-Feres et al. (2000) showed that the phenology of a population of *P. chapoda* occurred in synchrony with the rainy season, in a region with a strongly seasonal climate and a pronounced dry season.

The aims of this study were: (1) to describe the population fluctuations and phenology (seasonal variations in age structure) of *P. chapoda*; (2) to assess whether abiotic factors, such as rainfall and temperature, and biotic factors, such as the blooming periods of *B. balansae* affect the population dynamics of *P. chapoda*; and (3) to determine the sex ratio of this spider population.

## Material and methods

### Study area

This work was done in a grassland area, between a river and a 1.5 ha fragment of semi-deciduous forest, close to the city of Dois Córregos (22°21'S, 48°22'W), São Paulo state (south-eastern Brazil). Only one terrestrial bromeliad species, *Bromelia balansae*, occurs in this region. *B. balansae* is a large bromeliad, with a leaf length reaching 2.5 m in the forest and ~1.2 m in open areas (grasslands). The leaves have large, curved spines spaced 2.5–3.5 cm apart. This perennial bromeliad lives ~3–5 years (G. Q. Romero, personal observation), does not accumulate rain water in its rosette and blooming occurs at the beginning of rainfall (Rossa-Feres et al. 2000).

### Population dynamics of *P. chapoda*

The population dynamics of *P. chapoda* were assessed between May 1998 and May 2000 by monthly inspections of 23–145 *B. balansae* plants that were previously marked in grassland (open area), along a 250-m transect 15 m from the forest edge. When young individuals of *B. balansae* appeared, they were also marked. The number of *P. chapoda* individuals and egg sacs was recorded for each plant inspected. Plants that had mature fruits or fruits already dispersed were not inspected since in these phenophases the plants showed traces of senility (wilted or dried leaves) or had already died.

The seasonal fluctuations were determined by the spider density (individual number per bromeliad) over time. The phenology was represented by the temporal variation in spider age structure (e.g. Peck 1999). To determine the age structure, the spiders were classified as young (spiderlings, instar 3), juveniles (instars 4 and 5), juvenile males and females (instar 6), subadult males and females (instar 7) and adult males and females (instar 8). Each instar and sex of *P. chapoda* had a specific spot and colour pattern (Rossa-Feres et al. 2000; G. Q. Romero, personal observation) that facilitated identification of the individuals. However, juvenile, subadult and adult females had the same spot and colour pattern. Juvenile females were small and about the same size as juvenile males (up to 1.1 cm in length), and were easily distinguished from other females. Subadult and adult females were the same size (up to 1.6 cm in length), which made the identification of these age classes

difficult. Because of the difficulty in capturing these females to determine their sex, adult and subadult females were grouped for subsequent analysis.

#### *Synchrony and displacement between events*

Linear regression analysis (Zar 1996) was used to assess whether climatic factors (rainfall and temperature) affect the seasonal fluctuations in *P. chapoda* (number of spiders per bromeliad), with up to 3 months of displacement from the dependent variable. The dependent variable was spider fluctuation and the independent variables were climatic factors, with all variables (dependent and independent) being obtained monthly. The temperature and rainfall data were obtained from the experimental station at Itauna farm, 5 km from the study area. The data representing densities were normalized by log or log ( $n+1$ ) transformations.

#### *Blooming of B. balansae and the dynamics of P. chapoda*

To verify whether the blooming of *B. balansae* affects the occurrence and population dynamics of *P. chapoda*, 116 and 74 bromeliads were randomly selected in August 1998 and 1999, respectively, and then monitored monthly for flowering and for the number of spiders. These inspections were done up to December of the respective years, since by this time all of the bromeliads had flowered (G. Q. Romero, personal observation). Two groups of bromeliads were thus identified, one which flowered between August and December and one that did not flower until December of 1998 or 1999. The spider densities in these two groups of bromeliads were compared using repeated measures ANOVA (Zar 1996), in which the months were considered as the repeated factor.

The size (surface area) of the bromeliads belonging to these sets was estimated in August 1998 and 1999 by measuring the length (L) and breadth (B) of a leaf from the middle layer. The product of  $L \times B$  was multiplied by 0.5 to estimate the leaf area, since the leaf shape resembled an isosceles triangle. The resulting area was multiplied by the total number of green leaves of the bromeliad to estimate the surface area of the plant.

#### *Sex ratio*

The sex ratio of *P. chapoda* was monitored monthly throughout the study and was calculated for juvenile males versus females (antipenultimate instar) and for adult+subadult males versus adult+subadult females. Adult and subadult instars were grouped because of difficulties in determining the age of adult and subadult females. The sex ratios of each instar in each month were compared using the *G*-test (Zar 1996).

Voucher specimens of *P. chapoda* were deposited at the Coleção Aracnológica do Laboratório de Artrópodes Peçonhentos do Instituto Butantan under the accession number IBSP 16242.

## **Results**

#### *Population dynamics, synchrony and displacement between events*

*Psecas chapoda* occurred on *B. balansae* throughout the year during the 2 years of observation (Figures 1, 2), and also produced egg sacs throughout the year (Figure 1). The

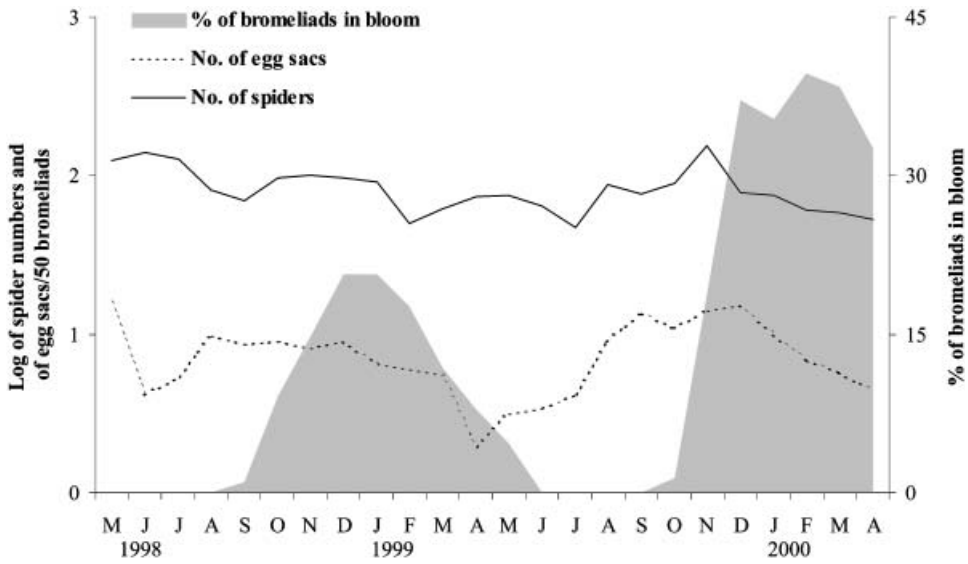


Figure 1. Fluctuations in the number of *Psecas chapoda* and egg sacs (log) on bromeliads with and without inflorescence, and the frequency (%) of bromeliads in bloom (with inflorescence or infrutescence) between May 1998 and April 2000 ( $N=3516$  spiders and 314 egg sacs).

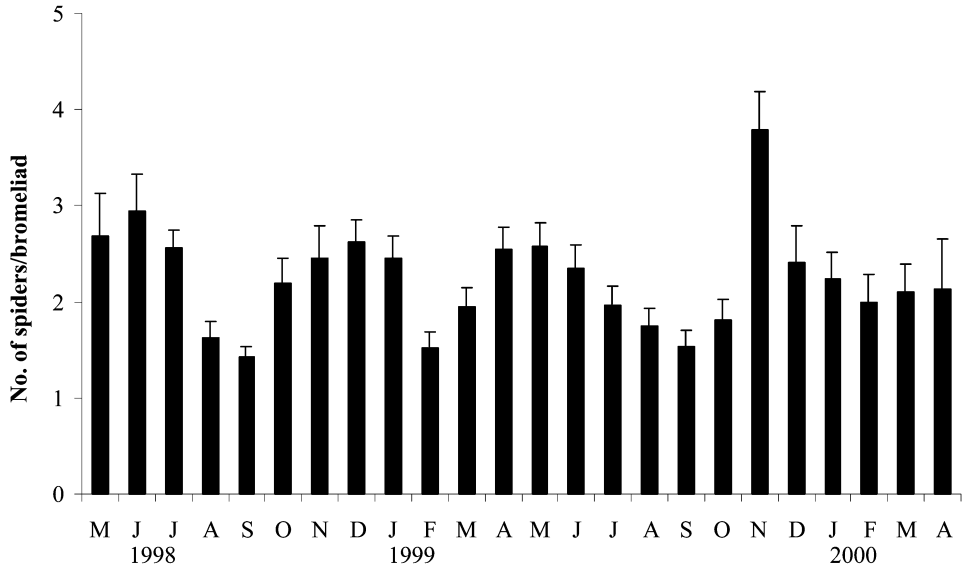


Figure 2. Mean number ( $\pm$  SE) of *Psecas chapoda* per *Bromelia balansae* with no inflorescence, from May 1998 to April 2000 ( $N=3516$  spiders).

size of the *P. chapoda* population varied little over time (Figure 1). However, the mean number of individuals per bromeliad (spider density) varied between the months of 1998 (ANOVA;  $F_{7,629}=4.53$ ;  $P<0.001$ ) and 1999 (ANOVA;  $F_{11,843}=6.35$ ;  $P<0.001$ ), and was lower in August and September in 1998, and in February and March, and from August to October in 1999 (Figure 2). The number of egg sacs varied seasonally and was higher in

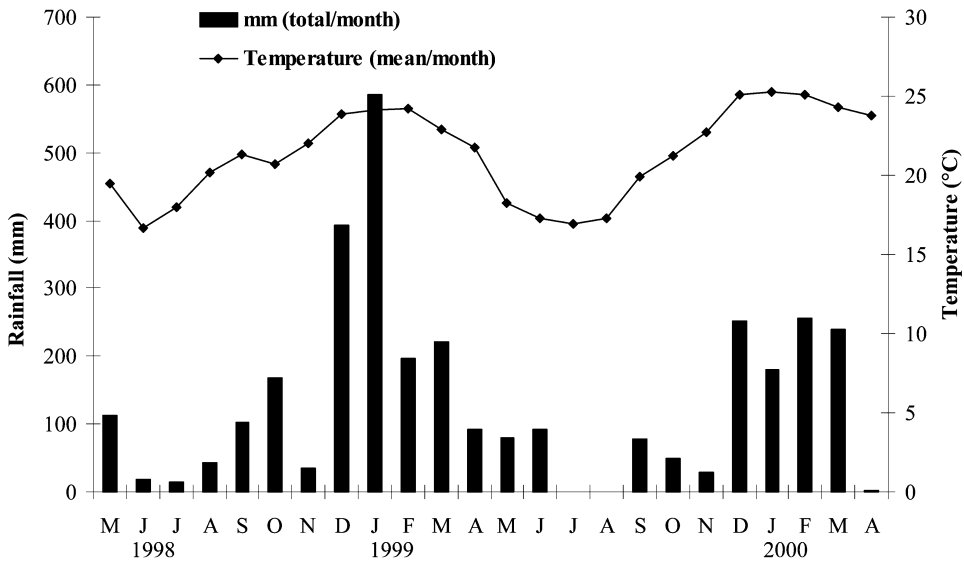


Figure 3. Climatic data from Itauna farm (5 km from the study site), from May 1998 to April 2000.

May and from August to December in 1998 and from September to December in 1999 (Figure 1), the latter two periods corresponding to the beginning of rainfall (Figure 3). Like the spiders, the bromeliads also reproduced at the beginning of rainfall (Figures 1, 3).

The *P. chapoda* density correlated positively, but slightly, with rainfall 1–2 months after the beginning of rainfall, but correlated positively with temperature only after 3 months of increased temperature (Table I; Figures 1–3). The females produced more egg sacs 2–3 months after the beginning of rainfall and increased temperature (Table I; Figures 1, 3). *Bromelia balansae* flowered from September to December, 1 month after the beginning of rainfall ( $r^2=0.29$ ;  $P=0.008$ ; Figures 1, 3).

Table I. Regression analysis examining the effects of rainfall and temperature on the density of *Psecas chapoda*, displaced 1, 2 and 3 months relative to the dependent variable (spider density).

	Displacement (in months)	$r^2$	$F$	$P$
Rainfall versus number of spiders	0	0.01	0.23	0.630
	1	0.17	4.31	0.050
	2	0.18	4.36	0.050
	3	0.07	1.51	0.230
Temperature versus number of spiders	0	0.06	1.45	0.242
	1	0.10	2.43	0.134
	2	0.16	3.75	0.067
	3	0.36	10.77	0.004
Rainfall versus number of egg sacs	0	0.01	0.28	0.602
	1	0.09	2.09	0.163
	2	0.19	4.70	0.042
	3	0.53	21.86	<0.001
Temperature versus number of egg sacs	0	0.07	1.73	0.202
	1	0.01	0.15	0.702
	2	0.23	5.73	0.027
	3	0.57	23.98	<0.001

The phenogram (Figure 4) shows that the age structure of *P. chapoda* varied little during the 2 years of the study. Although instars occurred in all seasons because the females produced egg sacs throughout the year, there was an increase in spiderling frequency in September (Figure 4) at the beginning of the rain season (Figure 3). In 1998, the number of spiderlings peaked in October and continued elevated until April 1999. In September and December 1999, the frequency of spiderlings was high, but with no well-defined peak. In contrast, the other age classes were structurally very stable over time (Figure 4).

#### Blooming of *B. balansae* and the dynamics of *P. chapoda*

In the period that preceded the reproduction of *B. balansae* (August), the group of plants that had not yet flowered between August and December had a higher number of spiders compared to those that did not flower until December. This phenomenon was observed in 1998 ( $F_{1,101}=25.40$ ;  $P<0.001$ ; Figure 5A) and 1999 ( $F_{1,70}=4.93$ ;  $P=0.030$ ; Figure 5B). The size of plants ready to reproduce was greater than those not ready to reproduce in 1998 (mean  $\pm$  SE in  $\text{cm}^2$ ; to reproduce:  $8595.34 \pm 1084.78$ ; others:  $3418.13 \pm 442.84$ ; Mann-Whitney *U*-test;  $T=1860$ ;  $P<0.001$ ) and 1999 (to reproduce:  $6269.05 \pm 817.22$ ; others:  $3791.64 \pm 400.61$ ; Mann-Whitney *U*-test;  $T=931$ ,  $P=0.002$ ). The population size of *P. chapoda* seems not to be affected by *B. balansae* blooming (Figure 1). However, the number of spiders in the group of bromeliads that flowered decreased as the proportion of these bromeliads increased (Figure 5A, B). In contrast, the number of spiders in the group of plants that did not flower until December increased (Figure 5A, B). The interactive effect of the bromeliad groups (with versus without inflorescence) and time was significant in both years (Table II).

#### Sex ratio

Throughout the year, adult and subadult females were more frequent relative to males of the same age. In contrast, juvenile males belonging to the antipenultimate instar were more frequent compared to females of the same age (Table III).

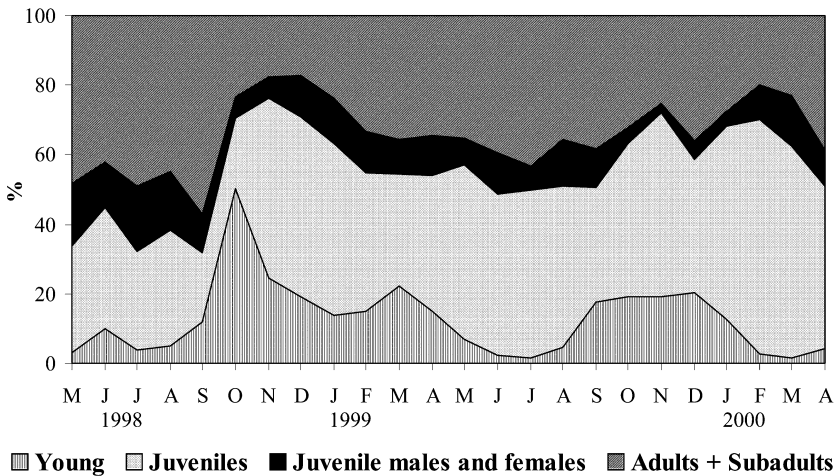


Figure 4. Phenogram of the *Psecas chapoda* population on plants of *Bromelia balansae* without inflorescence, from May 1998 to April 2000 ( $N=3516$  spiders).



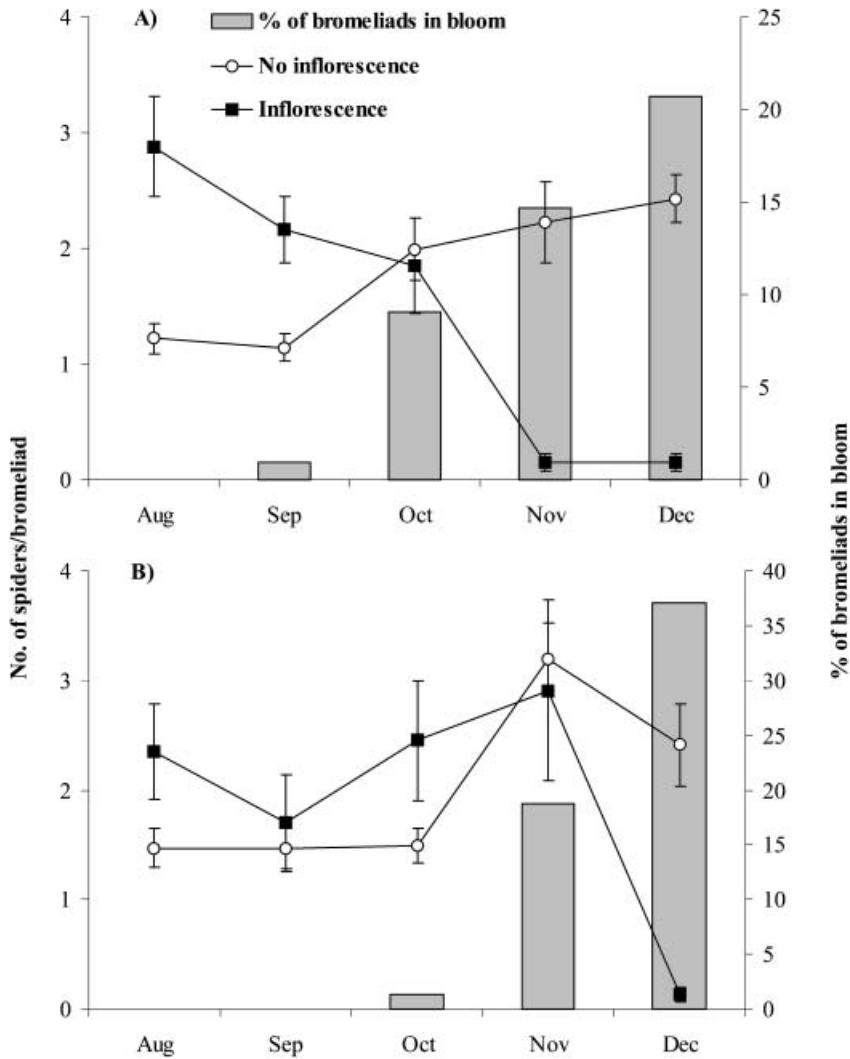


Figure 5. Mean number ( $\pm$ SE) of spiders *Psecas chapoda* on bromeliads that produced inflorescence between August and December and on bromeliads that did not produce inflorescence until December, in 1998 (A) and 1999 (B). The frequency (%) of bromeliads that bloomed up to December is also shown.

## Discussion

*Psecas chapoda* inhabited *B. balansae* throughout the year, suggesting a strong association of the spider with this plant. In addition, males were frequently seen displaying courtship behaviour throughout the year (G. Q. Romero, personal observation) and females also produced egg sacs in all months, thus reinforcing the hypothesis of a high level of spider-plant association. Females generally tend to maximize their offspring survivorship by choosing suitable, safe sites to oviposit (Morse 1990, 1992, 1993; Harvey 1994). *Bromelia balansae* must be an excellent site for reproduction and spiderling survival, since its leaves have a large surface area that facilitates the courtship behaviour of males, and the rosette of this plant has microhabitats and small spaces that shelter spiderlings against desiccation

Table II. Repeated measures ANOVA examining the variation in the density of *Psecas chapoda* on *Bromelia balansae* that bloomed versus those that did not bloom (bromeliad groups).

Source of variation	df	MS	F	P	G-G
1998					
Bromeliad groups	1	19.42	2.14	0.147	
Error	100	9.08			
Time	4	9.32	2.78	0.027	0.046
Bromeliad groups $\times$ Time	4	66.29	19.78	<0.001	<0.001
Error	400	3.35			
1999					
Bromeliad groups	1	4.04	0.75	0.389	
Error	58	5.36			
Time	4	19.39	5.44	<0.001	0.002
Bromeliad groups $\times$ Time	4	24.49	6.87	<0.001	<0.001
Error	232	3.56			

Time was treated as the repeated factor. The probabilities were corrected against sphericity using the Greenhouse-Geisser (*G-G*).

Table III. Sex ratios of adult + subadult males and females (Ad+Subad, ultimate and penultimate instars) and of juvenile males and females (antepenultimate instar) of *Psecas chapoda*, between May 1998 and April 2000.

Month	Individuals	Males (N)	Females (N)	Sex ratio (M:F)	G-test	P
January	Ad+Subad	12	64	1:5.33	37.41	<0.001
	Juveniles	20	0	1:0.00	—	—
February	Ad+Subad	17	39	1:2.29	4.04	0.044
	Juveniles	15	7	1:0.47	2.25	0.134
March	Ad+Subad	18	52	1:2.89	8.09	0.004
	Juveniles	20	5	1:0.25	8.31	0.004
April	Ad+Subad	27	57	1:2.11	10.23	0.001
	Juveniles	16	11	1:0.69	0.59	0.442
May	Ad+Subad	38	59	1:1.55	4.15	0.041
	Juveniles	14	12	1:0.86	0.04	0.841
June	Ad+Subad	41	67	1:1.63	5.89	0.015
	Juveniles	23	10	1:0.43	4.47	0.034
July	Ad+Subad	74	120	1:1.62	10.54	0.001
	Juveniles	52	9	1:0.17	31.80	<0.001
August	Ad+Subad	35	85	1:2.43	20.60	<0.001
	Juveniles	34	11	1:0.32	11.22	<0.001
September	Ad+Subad	51	71	1:1.39	2.97	0.084
	Juveniles	17	11	1:0.65	0.89	0.345
October	Ad+Subad	32	60	1:1.87	8.04	0.004
	Juveniles	14	5	1:0.36	2.93	0.086
November	Ad+Subad	31	60	1:1.93	8.76	0.003
	Juveniles	9	10	1:1.11	0.00	—
December	Ad+Subad	22	50	1:2.27	10.39	0.001
	Juveniles	23	8	1:0.34	6.55	0.010

The *G*-tests were calculated using Yate's correction.

and predation. The leaves also have large spines that can protect adult and immature spiders against vertebrate predators.

The high stability of the seasonal fluctuations and age structure over time indicated that there was generation overlap in this population of *P. chapoda*. In contrast, Rossa-Feres et al. (2000) reported that another population of *P. chapoda* studied 200 km from our site

showed strong population recruitment characterized by the sequential appearance of spiderlings, juveniles, subadults and adults throughout the seasons. These authors also reported that mating in this population of *P. chapoda* occurred only between August and March, with egg sacs appearing only from November to March, and in July. Rain was suggested to be influential in moulding the phenological patterns of the population since the climate was strongly seasonal (Rossa-Feres et al. 2000). However, the climate at our site was also strongly seasonal (Figure 3). The proximity of the bromeliads to the river could have provided this spider population with allochthonous resources. Throughout the year, dipterans of the family Chironomidae emerge from this river and are captured by the spiders (G. Q. Romero, personal observations). This additional food source has probably helped to maintain the dynamics of this spider population stable. Polis and Hurd (1995) showed that the density of spiders on some plant species was low when distant from the sea coast, but high when close to sea level, because the high density of detritivorous insects (allochthonous input) coming from organic matter deposited by the sea enhanced the carrying capacity of the spider population.

In contrast to the low variation in the number of individuals, the number of egg sacs increased 2–3 months after the beginning of the rain. This finding was similar to that of Rossa-Feres et al. (2000). Rain was probably a stimulus for adult spiders to begin mating and laying eggs.

The blooming of *B. balansae* clearly affected the density of *P. chapoda* because the altered architecture of the plant, with the folding of its leaves to the ground, expelled the spiders (G. Q. Romero and J. Vasconcellos-Neto, unpublished data). However, this effect must be cryptic in the population since the spider population fluctuated very little. This limited fluctuation probably reflected the fact that the frequency of bromeliads in bloom in the population was not very high (21–37%), and that the spiders may have migrated to neighbouring bromeliads when expelled by the blooming bromeliad. The large variation in the density of spiders per bromeliad and the increasing number of spiders on plants that lacked inflorescence could reflect this migration of *P. chapoda* from plants with inflorescence to those without. These results suggest that the blooming of *B. balansae* can influence the size and growth of the *P. chapoda* population and the spider population dynamics. Theoretically, if all of the bromeliads of the population bloomed at the same period, the spider population could be driven to local extinction. This system thus provides good conditions for studying population dynamics in metapopulations (see Hanski and Gilpin 1991).

Whereas females were more frequent in the adult and subadult phases compared to males, in the antipenultimate instar (juvenile males and females), the frequency of males was higher than females, suggesting that this *P. chapoda* population has a sex ratio skewed towards males. During courtship display, the males always maintain a higher position on the leaf, while the female is lower down, close to the bromeliad base, where it is protected against predators. In this courtship behaviour, the males move a lot and can easily be detected by a predator (Rossa-Feres et al. 2000). Moreover, males must spend more energy on courtship, and hence they probably die faster than females. Males also move among bromeliads more often than females (G. Q. Romero, personal observations), with the latter remaining for a long time below the ceiling of silk built to protect themselves and the egg sacs (Rossa-Feres et al. 2000). In their migrations out of the plant, the males become more vulnerable to attack by natural enemies. Hence, natural selection may have skewed the sex ratio to males since the rate of mortality among males must be higher than for females, as also occurs in several other organisms (see Halliday 1994).

In conclusion, *P. chapoda* was strongly associated with *B. balansae* since the spider inhabited and reproduced on the plant throughout the year. Abiotic factors (e.g. rainfall) appear to stimulate mating and the laying of eggs, but do not affect the spider population dynamics. However, the blooming of *B. balansae* results in a dramatic change in plant architecture that expels *P. chapoda* and affects the spider population dynamics. More males than females are born in this population, possibly because the mortality rate of males is higher than for females. This higher mortality may reflect the greater energy spent in courtship behaviour and the vulnerability of males to predation.

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