

SPATIAL DISTRIBUTION AND MICROHABITAT PREFERENCE OF *PSECAS CHAPODA* (PECKHAM & PECKHAM) (ARANEAE, SALTICIDAE)

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ABSTRACT. Although spiders generally do not have a strong association with the plants on which they live, the jumping spider *Psecas chapoda* inhabits and breeds on *Bromelia balansae* (Bromeliaceae). To understand the relationship between *Psecas chapoda* and *Bromelia balansae*, we investigated whether the type of habitat (forest or grassland), the size of the bromeliad and the inflorescence of the host plants affected the preference and/or density of *P. chapoda*. We also examined how spiders of different ages and their eggsacs were distributed on the leaf layers of the rosette of host plants and whether *P. chapoda* used other plants in addition to *B. balansae*. *Psecas chapoda* occurred with higher frequency on bromeliads in grasslands to those in forest. In grassland, larger bromeliads had more spiders, but this was not true of bromeliads in the forest. This spider avoided bromeliads with inflorescence. Most of the spiderlings (70%) occurred in the central layer of the rosette leaves, and their distribution pattern suggested that they sought shelter to protect themselves from desiccation or cannibalism, both of which are commonly observed in this species. Older spiders, as well as females without eggsacs, occurred in the external layers whereas 90% of the females with eggsacs occurred close to the central layers. Deposition of the eggsacs near the center of the rosette can allow the spiderlings to reach their shelter rapidly and to be less exposed to desiccation and cannibalism. The non-detection of *P. chapoda* on non-bromeliad plants, and the stereotyped behaviors on the host-plant suggest that this jumping spider was strongly associated with *B. balansae*.

Keywords: Animal-plant interaction, habitat selection, microhabitat, plant architecture, Salticidae

In contrast to host-specific herbivorous insects (Schoonhoven et al. 1998), spiders generally do not have a strong association with the plants on which they occur. However, some spider species inhabit and breed on specific plants and interact indirectly with their hosts (Louda 1982; Figueira & Vasconcellos-Neto 1991, 1993; Rossa-Feres et al. 2000; Romero & Vasconcellos-Neto 2004). Why some spiders choose specific plants and how the occurrence of such spiders affects the organization of spider communities are important aspects in understanding the community structure on a given host plant and in elucidating the direct and indirect interactions within and among species (Abraham 1983; Uetz 1991). The components of habitat reported to influence the numbers and types of spiders include the abundance and richness of prey (Riechert & Tracy 1975; Waldorf 1976; Rypstra 1983; Miller & Drawer 1984; Schmalhofer 2001), the availability of extra-

floral nectarines as a food source and as foraging sites (Ruhren & Handel 1999), the availability or density of sites for constructing webs (Lubin 1978; Rypstra 1983; Greenstone 1984; Herberstein 1997; Figueira & Vasconcellos-Neto 1991), the availability of foraging sites (Scheidler 1990; Romero 2001; Schmalhofer 2001; Romero & Vasconcellos-Neto 2003), the spatial distribution of web and foraging sites (Greenquist & Rovner 1976; Robinson 1981; Louda 1982) and the availability of sites for shelter (Riechert & Tracy 1975; Gunnarsson 1990, 1996) and breeding (Smith 2000).

The jumping spider *Psecas chapoda* (Peckham & Peckham 1894) (Salticidae), previously identified as *P. viridipurpureus* Simon 1901 by Rossa-Feres et al. (2000), is commonly found on *Bromelia balansae* Mez. (Bromeliaceae) and has an apparently host-specific distribution. This plant does not store rainwater in its rosette. *Psecas chapoda* spends its entire

reproductive cycle: courtship, mating, ovisac formation and populational recruitment of the young spiders on this plant (Rossa-Feres et al. 2000). Females produce 1–3 eggsacs on the concave side of the central region of the leaves. The eggsacs are enveloped with a plain silk cover and are spun at the edge of each leaf. Since females remain under this cover and on the eggsacs (Fig. 1) (Rossa-Feres et al. 2000), there may be maternal care of the offspring.

In this study, we examined the spatial and microspatial patterns of *P. chapoda* on *B. balansae* and investigated the factors affecting this distribution. Specifically, we assessed whether the type of habitat (forest or grassland) and the size and architecture (absence vs. presence of inflorescences) of the bromeliad affected the density of *P. chapoda*. We also determined whether spiders of different ages and the eggsacs were randomly distributed among the leaf layers of the rosette, and whether *P. chapoda* was associated exclusively with *B. balansae*.

METHODS

This work was done in a fragment of semideciduous forest (250 m x 60 m) and in an adjacent grassland area along the margin of a river, in the city of Dois Córregos (22° 21' S, 48° 22' W), São Paulo state, southwestern Brazil, from July 1998–May 2000 and in March and April 2002. Only *Bromelia balansae*, a ground-dwelling bromeliad (Figs. 2–4), occurs in the study area.

Habitat preference.—Habitat preference was determined by recording the number of *P. chapoda* on *B. balansae* growing in the forest and in the grassland. Observations were made in the cold-dry season (July 1998), at the beginning of the rainy season (October 1998), in the hot-rainy season (February 1999) and at the end of the rainy season (April 1999), along two parallel 250 m transects in the forest and grassland (one each). The two transects were at least 20–30 m apart, and 37–53 stalks of *B. balansae* in the forest and 75–103 stalks in the grassland were randomly chosen in each season. The spider density per bromeliad stalk was compared between the forest and grassland transects and among the four seasons using two-way ANOVA. Since the occurrence of the spiders may be skewed by the density of bromeliads, the number of

plants growing at 10 m intervals in 100 m x 6 m transects of forest and grassland was estimated to determine if there were variations in density between sites. Since the preference for bromeliads was affected by the presence of inflorescence, only bromeliads without inflorescence were included in the analysis (see below).

Influence of host plant size on the microhabitat preference.—To examine the preference of spiders for host plants of different sizes, the relationship between the bromeliad surface area and the number of *P. chapoda* was examined for bromeliads in grassland, at the forest margin and within the forest. The bromeliads (50–82 in grassland, 16–27 at the forest margin and 31–53 within the forest) were observed bimonthly from July 1998–July 1999. The bromeliads were randomly chosen in each sample period. Bromeliads growing under tree branches but which received incident solar light at any time of the day were considered to occur in the forest margin. The total surface area was estimated by multiplying the surface area of one leaf by the total number of green leaves on each bromeliad. The leaf surface area was estimated using the formula: length (L) x breadth (B) of a leaf from the middle layer of the rosette, chosen at random, x 1/2. Linear regression analysis was used to assess the relationship between surface area and the number of spiders. Student t-test was used to compare the bromeliad surface area between grassland and forest.

Influence of inflorescence on spider density.—The relationship between *B. balansae* inflorescence and spider density was examined by comparing the density of spiders on grassland *B. balansae* with and without inflorescence (Figs. 2–4). The observations were made in December 1998 and 1999 because almost all of the *B. balansae* at the study sites bloomed in this season. The results were analyzed using the G-test.

Preference for leaf layers.—*Bromelia balansae* has several leaf layers in the rosette (Figs. 2, 3). Since preliminary observations showed that *P. chapoda* was distributed in different layers of the rosette according to the spiders' age, the distribution patterns of spiders of different ages were determined by examining 24–64 grassland bromeliads with at least five leaf layers. The observations were



made bimonthly, from November 1999–May 2000. The bimonthly interval of observations was determined to avoid data dependence (i.e., temporal pseudoreplication, Hurlbert 1984), since spiders change instars by molting and the eggsacs are constructed and abandoned in approximately one month (Rossa-Feres et al. 2000; G.Q. Romero pers. obs.). Age-specific patterns of spots and coloration were used to classify *P. chapoda* as spiderlings (3rd instar), young (4th and 5th instars), and juvenile males (up to 1.1 cm in body length) or females (6th instar). Although sex-specific patterns of spots and coloration are also useful for discriminating subadult and adult stages, subadult and adult females with the same spot and coloration patterns and of similar size (up to 1.6 cm in body length) are difficult to distinguish in the field. In addition, the number of subadult males is extremely small. For these reasons, we created two additional groups, namely subadult (7th instar) + adult females (8th instar) and adult males (8th instar) (Rossa-Feres et al. 2000; G.Q. Romero pers. obs.). In the subadult and adult female class, the adult females with eggsacs were distinguished from subadult and adult females without eggsacs. The distributions of the five developmental stages above and those of subadult and adult females with and without eggsacs were analyzed using the G-test.

Selectivity of *P. chapoda* for the host plant.—The selectivity of *P. chapoda* for *B. balansae* was examined in March and April 2002, a period of high spider density, by the following three methods: 1) Direct observation; searching for spiders, silk shelters and abandoned eggsacs on 590 non-bromeliad plants belonging to the families Asteraceae, Fabaceae, Solanaceae, Asclepiadaceae, Lauraceae and several grasses. The plants examined were 10–170 cm tall and grew at least 3 m away from *B. balansae*. At each observation, we examined the abaxial and adaxial sides of leaves and branches. 2) Beating or shaking the plants with a stick. The spiders were collected on a beating tray, essentially a

cloth-covered frame that sloped slightly towards the center (Southwood 1978). All of the spiders dropping off non-bromeliad plants (up to 170 cm tall) were collected. Fifty plants were sampled in grassland, 50 at the forest margin and 50 within the forest. Five beats per sample (plant) were done between 1:00–4:00 p.m. 3) Pitfall traps; 30 pitfall traps (10 cm in diameter and 15 cm deep) containing 75% ethanol were placed among individuals (0.4–1.5 cm) of *B. balansae*. The spiders were collected five days after the traps were placed. Voucher specimens of *P. chapoda* were deposited in the Laboratório de Artrópodes Peçonhentos, Instituto Butantan, São Paulo.

RESULTS

Habitat preference.—The average number of *P. chapoda* on *B. balansae* was significantly greater in grassland than in forest (two-way ANOVA, $F_{1,534} = 123.67$, $P < 0.0001$, Fig. 5). The average number of *P. chapoda* on *B. balansae* also changed seasonally (two-way ANOVA, $F_{3,534} = 2.89$, $P = 0.035$) and was lower in the hot, rainy season (Fig. 5). The interaction between the factors habitat and seasonality was significant ($F_{3,534} = 2.82$, $P = 0.038$). There was no difference between the density of bromeliads in grassland and forest (T-test, $t = -0.46$, 18 df, $P = 0.648$).

Influence of host plant size on the microhabitat preference.—There were positive, significant relationships between bromeliad surface area (size) and number of spiders inhabiting the plant, in the grassland and forest margins (Table 1). Despite the bromeliads in the forest being bigger than the bromeliads in the grassland (data from July 1998; forest: $9649.0 \text{ cm}^2 \pm 1256.2$ (SE), grassland: 4609.5 ± 470.6 (SE); $t = -4.53$, 154 df, $P < 0.001$), there were no relationships between plant size and number of spiders in the forest (Table 1). Up to 21 spiders were seen on a single plant in the grassland area, whereas a maximum of 3 spiders was seen on bromeliads in the forest.

Influence of inflorescence on spider density.—Among bromeliads with no inflores-

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Figures 1–4.—1. Female of *P. chapoda* (arrowhead) under the plain silk cover and on the eggsac produced on a leaf of *B. balansae*. 2. Individual of *B. balansae* in vegetative phenophase in the grassland. 3. In the beginning of inflorescence release (note the central leaves folding back). 3. with presence of infrutescence. (Photos: G.Q. Romero).

Table 1.—Linear regressions of the relationship between the bromeliad size (surface area) and individuals number of *Psecas chapoda* in the grassland, forest margins and into the forest, in different seasons.

	Places	Equations	n	r ²	F	P
1998						
Jul	Grassland	$Y = 0.00033X + 1.44$	82	0.51	84.67	<0.001
	Margin	$Y = 0.000102X + 0.94$	21	0.27	7.06	0.016
	Forest	$Y = 0.0000013X + 0.63$	53	0.0003	0.02	0.899
Sep	Grassland	$Y = 0.00011X + 1.11$	76	0.09	7.22	0.009
	Margin	$Y = 0.000031X + 0.86$	22	0.04	0.77	0.390
	Forest	$Y = 0.0000006X + 0.28$	53	0.0001	0.001	0.932
Nov	Grassland	$Y = 0.00045X + 1.27$	74	0.08	6.70	0.012
	Margin	$Y = 0.000084X + 0.74$	27	0.06	1.51	0.231
	Forest	$Y = 0.000002X + 0.31$	48	0.001	0.06	0.806
1999						
Jan	Grassland	$Y = 0.00055X + 0.89$	67	0.22	18.64	<0.001
	Margin	$Y = 0.000047X + 1.92$	18	0.01	0.25	0.623
	Forest	$Y = 0.000002X - 0.56$	43	0.0009	0.04	0.849
Mar	Grassland	$Y = 0.00021X + 1.40$	62	0.07	4.28	0.043
	Margin	$Y = 0.00024X + 0.34$	20	0.28	7.07	0.016
	Forest	$Y = 0.000013X + 0.33$	36	0.04	1.29	0.264
May	Grassland	$Y = 0.00067X + 0.38$	50	0.47	43.05	<0.001
	Margin	$Y = 0.00021X + 0.19$	24	0.37	12.77	0.002
	Forest	$Y = 0.000029X + 0.20$	36	0.11	4.22	0.048
Jul	Grassland	$Y = 0.00017X + 1.50$	53	0.08	4.16	0.047
	Margin	$Y = 0.00011X + 0.25$	16	0.31	6.17	0.026
	Forest	$Y = 0.000005X + 0.35$	31	0.003	0.08	0.783

cence, 79% and 90% were occupied by *P. chapoda* in 1998 and 1999, respectively. In contrast, for bromeliads with inflorescences, only 17% and 13% were used by *P. chapoda* in 1998 and 1999, respectively. The percentage of bromeliads used by *P. chapoda* was significantly different between stalks with and without inflorescences (Fig. 6).

Preference for leaf layers.—Spiderlings occurred only in the first three central layers of the rosettes of *B. balansae*. Their distribution among the three layers was not random ($G = 30.60$, 2 df, $P < 0.0001$), and most spiderlings (70%) occupied the first layer in the center of the plant (Fig. 7). Although young spiders occurred on plants with five or more layers, 50% of this age interval was observed in the second layer ($G = 114.90$, 4 df, $P < 0.0001$, Fig. 8). Juvenile males and females were not found in the first layer and used the other layers randomly ($G = 5.03$, 3 df, $P = 0.170$, Fig. 9). The random use of all layers except for the first one was also observed for adult males ($G = 1.80$, 3 df, $P = 0.615$, Fig. 10). In the case of subadult and adult females, more than 40% occurred in the third layer (G

$= 43.20$, 4 df, $P < 0.0001$, Fig. 11). The distribution patterns of spiders among the leaf layers was different between adult females with eggsacs and subadult and adult females without eggsacs. More than 90% of the females with eggsacs occupied the second and the third layers ($G = 18.70$, 2 df, $P < 0.0001$), while the subadult and adult females without eggsacs occurred in the third, fourth and fifth layers with higher frequencies ($G = 22.65$, 4 df, $P = 0.0001$, Fig. 12). Only one adult or subadult female occupied the first layer.

Selectivity of *P. chapoda* for the host plant.—No individuals of *P. chapoda* or their vestiges (silk shelters and abandoned eggsacs) were found on 590 non-bromeliad plants close to *B. balansae* individuals. Although many spiders (~400 individuals) belonging to several families, including 6–7 Salticidae species, were collected by beating non-bromeliad plants and in pitfall traps on the ground between the stalks of *B. balansae*, no *P. chapoda* were found. In three years of observations, only three adult *P. chapoda* males were observed on the ground and one young was

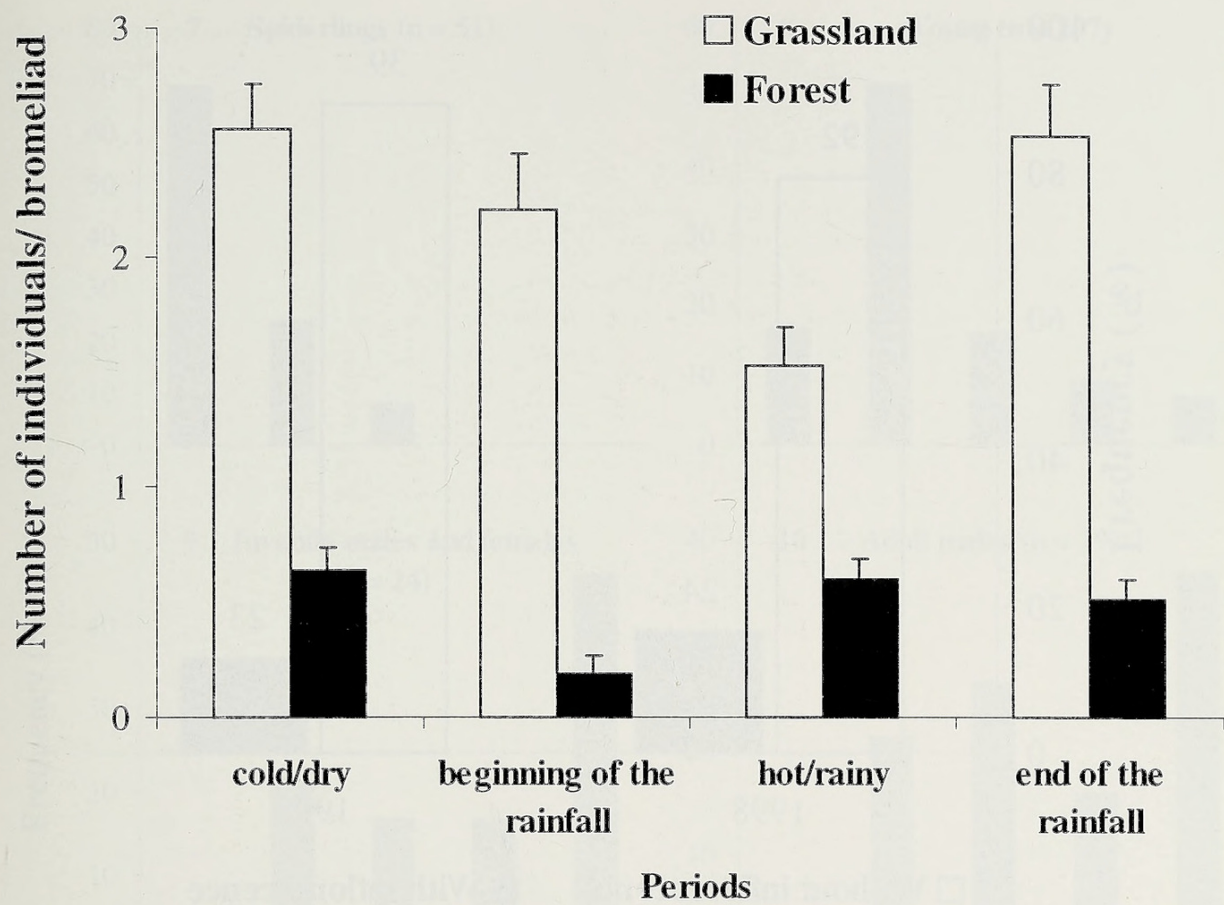


Figure 5.—Seasonal variation in the mean density of *Psecas chapoda* individuals on *Bromelia balansae* in grassland (open bars) and in forest (black bars). The sampled periods were: cold/dry = July 98, beginning of the rainfall = October 98, hot/rainy = February 99, end of the rainfall = April 99. Error bars are ± 1 SE.

seen on a gramineous leaf close to *B. balansae* in grassland.

DISCUSSION

Although several studies have shown that spiders of the family Salticidae may select certain microhabitats (Crane 1949; Richman & Whitcomb 1980; Jackson 1986; Cutler 1992; Cutler & Jennings 1992; Johnson 1995; Jackson & Li 1997; Taylor 1998), the distribution of *P. chapoda* on *B. balansae* and the absence of this species on non-bromeliad plants and in pitfall traps around bromeliads suggested a strong relationship between *P. chapoda* and *B. balansae*. The courtship, mating, deposition of eggsacs and populational recruitment of *P. chapoda* occur on *B. balansae*. *Psecas chapoda* also used *B. balansae* throughout the year at Sao José do Rio Preto (SP), about 200 km from the present study site (Rossa-Feres et al. 2000). Moreover, this spider species was collected and photographed (female) on *B. balansae* in Beni, Bolivia (Höf-

er & Brescovit 1994: picture 2a; H. Höfer, pers. comm.). In addition, *P. chapoda* was observed on *B. balansae* in 26 cities of three Brazilian states and in one locality of Paraguay (G.Q. Romero, unpubl. data). Thus, *P. chapoda* seems to be strictly associated with *B. balansae* in a large geographic range.

Our results show that *P. chapoda* preferred bromeliads in grassland to those in forest, and that bigger bromeliads were preferred more in grassland, whereas such a relationship between plant size and the average number of spiders was not observed in forest bromeliads. When the bromeliads are approached by an observer, *P. chapoda* on the leaf layers quickly jump towards the bottom of the rosette in a stereotyped jumping behaviour (G. Q. Romero, personal observation). The internal base of the rosette of bromeliads serves as a refuge and shelter from desiccation, as well as a resting place (G.Q. Romero, pers. obs.). In the forest, the bromeliads receive a large number of dry leaves from trees growing nearby and

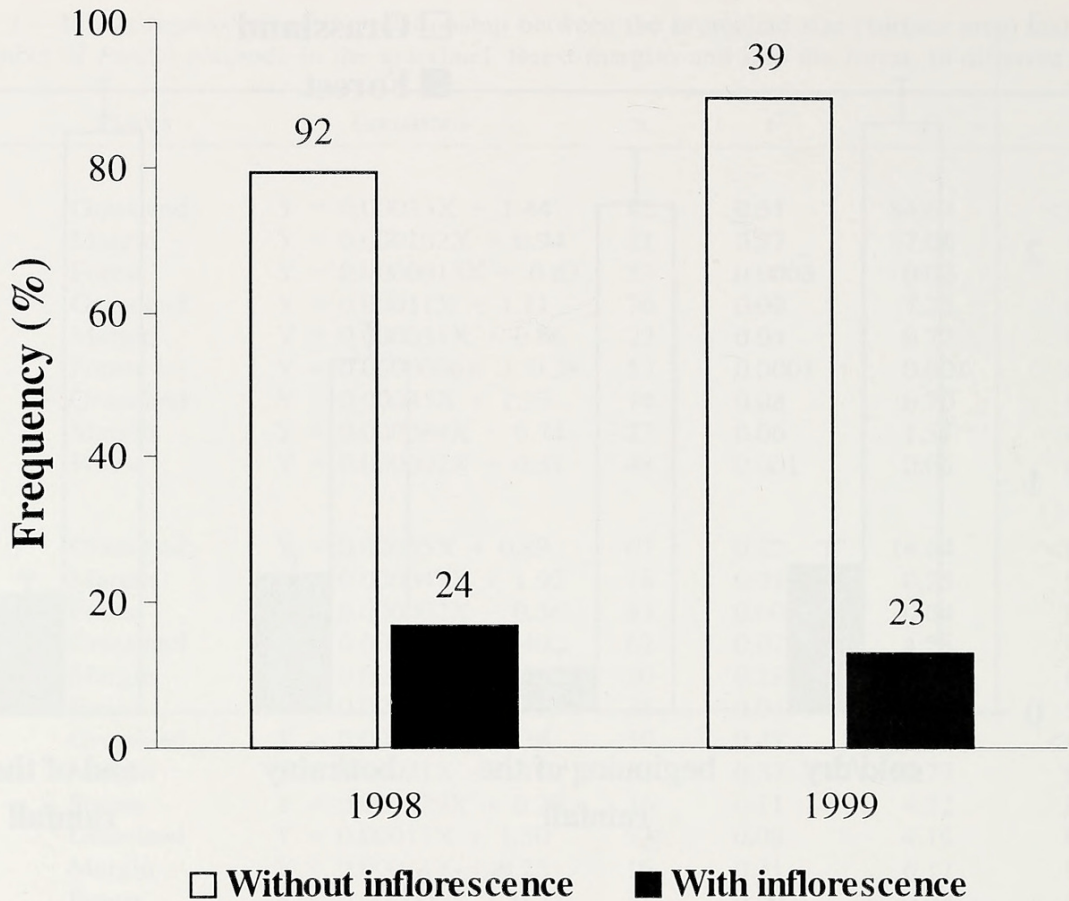


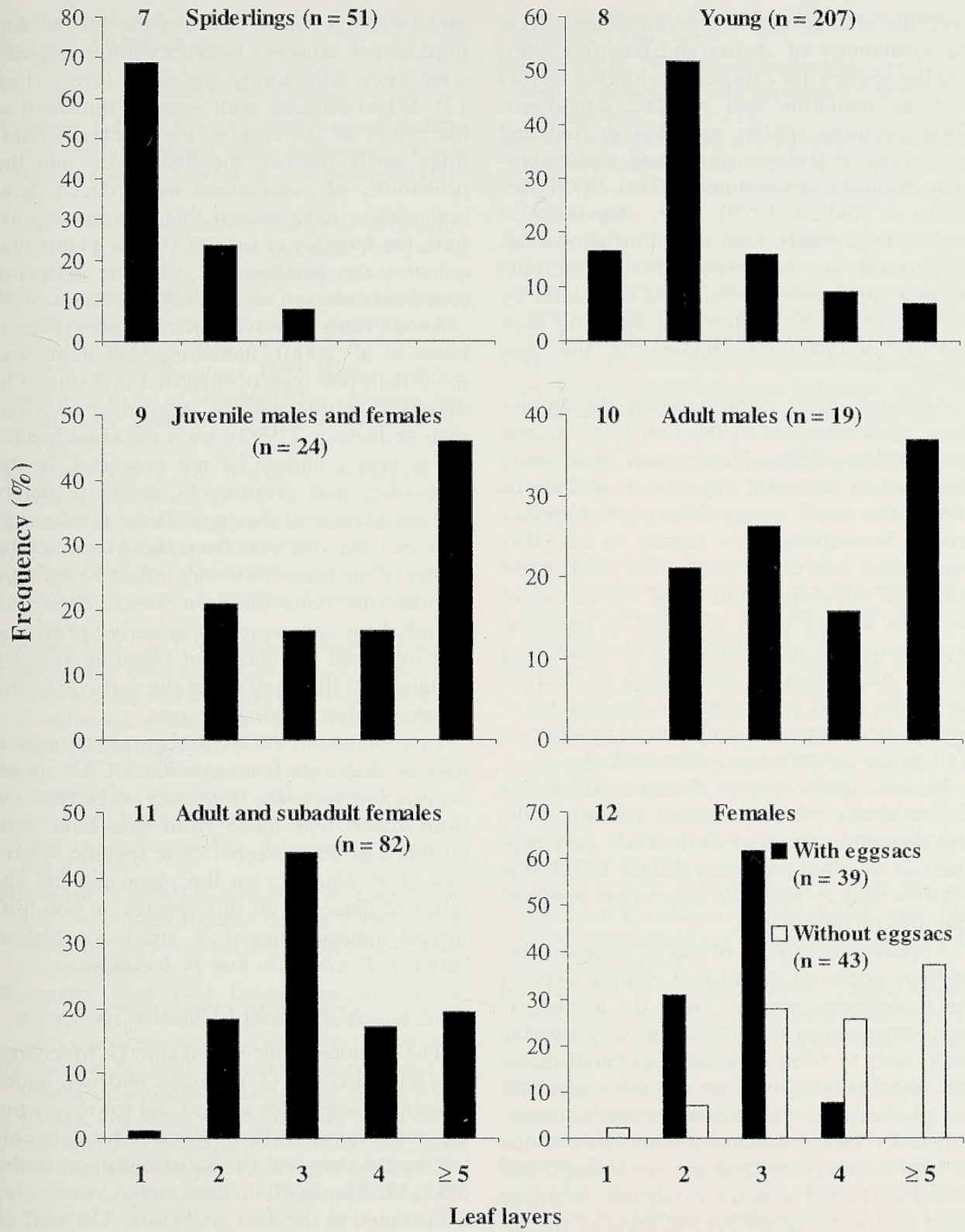
Figure 6.—Frequency of bromeliads with and without inflorescence occupied by *Psecas chapoda*, in December 1998 and 1999. The values above the bars indicate number of bromeliads examined. G-test with Yates' correction ($G_{1998} = 13.6$, 1 df, $P < 0.001$; $G_{1999} = 15.6$, 1 df, $P < 0.001$).

these leaves form a compact humic mass that fills completely the internal base of the bromeliad rosettes, regardless of the difference in size. Since a large quantity of dry leaves at the bottom of the rosette hampers the use of this microhabitat, *P. chapoda* appears to prefer grassland bromeliads which gather few or no dry leaves compared to forest bromeliads.

Larger bromeliads had more individuals of *P. chapoda*. Larger plants have a larger surface area available for foraging and many leaf layers in their rosettes for shelter, which can support more spiders. Generally, spiders that inhabit larger bromeliads consist of one adult male, one or two adult females frequently with eggsacs and several young and spiderlings, probably offspring of these resident females. In contrast, little, peripheral bromeliads are frequently occupied by young, juveniles and subadult spiders (G.Q. Romero, pers. obs.). Adult females probably choose larger bromeliads to obtain more food and shelter for their offspring, decreasing the probability of intraspecific competition and/or cannibalism.

Since salticids have good eyesight (Foelix 1982; Foster 1982), they can obtain more food on larger leaves. Figueira & Vasconcellos-Neto (1993) showed a strong relationship between the size of the *Paepalanthus bromelioides* (Eriocaulaceae) rosette and prey availability, and between the size of the *P. bromelioides* rosette and the weight and/or reproductive success of *Latrodectus geometricus* Koch 1841 (Theridiidae). According to these authors, larger plants offered a larger number of prey for *Latrodectus* females so that females grew rapidly and produced more eggs.

In addition to the size of *B. balansae*, the presence of inflorescence also affected the abundance of *P. chapoda* since almost all spiders occurred on bromeliads without inflorescence. During the reproductive period of *B. balansae*, the green color of the central parts (leaves) of the rosette changes to red prior to inflorescence blooming. At the same time, the leaves fold back and extend parallel to the ground (Fig. 4) probably to expose the flowers



Figures 7-12.—Distribution of *Psecas chapoda* individuals with different age class (7-11) and of adult females with eggsacs vs. adult + subadult females without eggsacs (12) in the leaf layers of the *Bromelia balansae* rosette (see text for the definitions of layers).

to pollinators. These changes alter the plant architecture from a conical tridimensional configuration to a flattened, almost bidimensional one. Since the leaves do not touch each

other even at this time because of the geometric conformation of the plant, the surface area of the leaves of bromeliads remains constant, even after the blooming season. How-

ever, the change in plant architecture affects the availability of shelter and breeding sites, and the spiders are exposed to external factors such as predation and climatic conditions. Some jumping spiders are able to find and catch prey in tridimensional and topographically complex environments (Hill 1979; Tarsitano & Andrew 1999). If *P. chapoda* also prefers bromeliads with a tridimensional arrangement, the preference for bromeliads without inflorescence could be explained by differences in the shelter and breeding sites and by architectural changes in the host plants.

Although most arthropods in the tropics show peak numbers in the hot, rainy season (see Wolda 1988), *P. chapoda* was more abundant in the cold, dry season and at the end of the rainy season. Many grass species around bromeliads grow rapidly in the rainy season and may cover part of the bromeliads. Although additional studies on the causes of the high density of *P. chapoda* in the cold, dry season are necessary, the abundance of grasses may affect the availability of food for the spiders, and may influence the amount of contact between male and female spiders, as well as the colonization of bromeliads.

In some spider species there are differences in the choice of microhabitat among adults and immatures in order to facilitate prey capture and to avoid predation (Edgar 1971). It is possible that *P. chapoda* may show age-specific use of bromeliads.

Approximately 70% of the *P. chapoda* spiderlings occurred in the first central layer of the *B. balansae* rosette. Since the leaves extend vertically in the first layer, they overlap each other to form a cylinder of small diameter. Small spiderlings can use this microhabitat to shelter from desiccation and/or cannibalism by larger spiders. Young spiders, one or two instars older than the spiderlings, and which still need a place to shelter, occurred more frequently in the second layer of the rosette because of the difficulty in reaching the first layer, that has very narrow and clumped leaves. Juvenile males and females of a similar size to the adults were generally restricted to outer layers.

The value of the central rosette as a nursery for spiderlings was also suggested by the different distribution of females with and without eggsacs. Almost all of the females with egg-

sacs (90%) occurred between the second and third layers, whereas females without eggsacs were more common in the outer layers (Fig. 12). When females with eggsacs remained at the center of the rosette, the hatched spiderlings easily reached the first layers and the probability of cannibalism was reduced. Several studies have shown that during oviposition, the females of insects choose plants that enhance the performance of their offspring (see Schoonhoven et al. 1998). Females of *P. chapoda* remained over their eggsacs (Rossa-Feres et al. 2000), indicating that there was more than one type of maternal investment in offspring in this species. According to Richman & Jackson (1992), such maternal behavior is very common, if not universal, in the Salticidae, and presumably deters predators and parasitoids of the eggs. These results suggest that the distance from the ovisac to the center of the bromeliad may influence the type of maternal behavior seen. Desiccation and cannibalism can represent selective pressures that influence the choice of breeding sites by females and this may affect the survival of the offspring after leaving the nest.

In conclusion, *P. chapoda* was associated with *B. balansae* from grassland. This spider occurred in very low frequency on bromeliads from forest and those from grassland with presence of inflorescence. The specific behaviors of *P. chapoda* on the plant and the absence of detection of this species on non-bromeliad plants suggest a strict association between *P. chapoda* and *B. balansae*.

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