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NATURAL HISTORY OF *MISUMENOPS ARGENTEUS* (THOMISIDAE): SEASONALITY AND DIET ON *TRICHOGONIOPSIS ADENANTHA* (ASTERACEAE)

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ABSTRACT. Seasonal fluctuations, phenology and diet of *Misumenops argenteus* (Araneae, Thomisidae) on *Trichogoniopsis adenantha* (Asteraceae) were investigated in the Serra do Japi, southeastern Brazil, over a 2 year period. This spider population increased at the beginning of the rainy season, reaching a peak in March, and decreased in May, reaching its lowest density in the cold/dry season. In the rainy season (December–May), most of the individuals were in the young or juvenile phase (3rd–6th instars). The spiders reached adulthood between the end of the cold/dry season and the beginning of the hot/rainy season. Analysis of temporal displacement (with up to a 3 month delay) detected a one month delay between the blooming period of *T. adenantha* and the beginning of the rainy season. The number of arthropods (potential prey of *M. argenteus*) on the plants increased concomitantly with the increase in the number of reproductive branches. The *M. argenteus* population also increased numerically 2 months after the rise in arthropod density. These results indicate that the spiders require time to respond to changes in environmental conditions. Of the 595 spiders examined, 76 (12.8%) had prey. Prey items included arthropods belonging to several guilds, but spiders showed a preference for wingless prey or prey that remained on the branches for longer periods of time.

Keywords: Prey, seasonal distribution, plant-animal interactions

A single plant species can serve as a food resource for several different organisms. However, this resource can vary seasonally in abundance and quality (Begon et al. 1996; Espírito-Santo & Fernandes 1998). Frequently, plant-consuming insects are synchronized with the abundance of food, as well as with environmental conditions such as temperature and humidity (Wolda 1988; Vasconcellos-Neto 1991; Bernays & Chapman 1994). Predators, such as spiders, can adjust their phenology in response to abiotic conditions (Crane 1949; Plagens 1983; Rinaldi & Forti 1997; Rossa-Feres et al. 2000; Arango et al. 2000) and the availability of prey (Riechert & Luczak 1982; Plagens 1983; Riechert & Harp 1987; Costello & Daane 1995; Arango et al. 2000) and foraging sites (Plagens 1983; Arango et al. 2000). The thomisid crab spiders are sit-and-wait predators that frequently forage on flowers and leaves (see Foelix 1996). These spiders tend to choose their foraging sites based on the availability of food items (Morse & Fritz 1982; Morse 1984) since, when in optimal sites, they prey indiscriminately on several groups of arthropods (Dean et al. 1987; Agnew & Smith 1989; Lockley et al. 1989; Nyffeler & Breene 1990).

Misumenops argenteus (Rinaldi) (Thomisidae) occurs on several plant species, but uses the reproductive branches of *Trichogoniopsis adenantha* (DC.) as foraging sites more frequently (Romero 2001). In this study, we examined the seasonal fluctuations and phenology of *M. argenteus* on *T. adenantha*, and assessed whether these phenomena were synchronized with the seasonality of biotic and abiotic factors such as the period of plant blooming (which corresponds to the availability of foraging sites), the availability of arthropods (potential prey) associated with this plant and rainfall. We also investigated whether *M. argenteus* captured its prey non-selectively relative to the potential prey available.

METHODS

Study site and organisms.—This work was done along the edges of the Mirante track (elevation 1170 m), in the Serra do Japi (23°11′S, 46°52′W), close to the city of Jundiaí, in southeastern Brazil. The climate is seasonal, with a mean monthly temperature varying from 13.5 °C in July to 20.3 °C in January. The driest months are from June–September (Pinto 1992). The local vegetation is characterized by high elevation semi-deciduous mesophile forest, with canopy height varying between 10–15 m, and very dense undergrowth containing specific plant species (Leitão-Filho 1992).

Trichogoniopsis adenantha is a perennial shrub species (0.2–1.8 m high) that occurs along the forest margins in the Serra do Japi. This species produces up to seven pink or lilac-colored flowerheads (yellowish in the predispersal phase) arranged in racemes, but with desynchronized development, such that given branch often has flowerheads in different phenophases. These flowerheads attract arthropods belonging to several guilds including pollinators, herbivores, parasitoids and predators (Romero 2001). *Trichogoniopsis adenantha* blooms throughout the year with peak flower production occurring in the hot/rainy season (Almeida 1997). Consequently, the availability of food resources and foraging sites for *M. argenteus* can vary seasonally. *Misumenops argenteus*, a small, yellowish crab spider, is the principal predator on *T. adenantha*, where it becomes cryptic. Romero (2001) showed that the frequency of this spider on reproductive branches of this plant is 2.6-fold higher than on vegetative ones.

Voucher specimens of the spiders collected (males and females) were deposited in the Arachnological Collection of the Laboratório de Artrópodes Peçonhentos, Instituto Butantan, São Paulo.

Population fluctuation and phenology of *M. argenteus*.—The seasonal fluctuation of *M. argenteus* was determined as the variation in spider density (number of individuals/500 branches) throughout the year. The population phenology was determined based on temporal variations in age structure over the same time period (e.g. Peck 1999). To determine age structure, each *M. argenteus* found was classified as 1) young [total body length (cephalothorax + abdomen) $\leq$ 3.0 mm; 3rd and 4th instars], 2) juvenile ($>$ 3.0 mm but $\leq$ 4.5 mm; 5th and 6th instars), 3) subadult ($>$ 4.5 mm but $\leq$ 5.0 mm, or when the male had a dilated palp; 7th instar), or 4) adult ($>$ 5.0 mm, and/or when there were sclerotized genitalia; 8th instar). These data were used to construct a phenogram of the maturation and recruitment of individuals during the life cycle of this species. To study the populational parameters of *M. argenteus*, between 17 and 26 individuals of *T. adenantha* (height from 0.2 m–1.8 m) per study day were sampled during biweekly visits along a 1 km transect of the Mirante track. The first plant found at the end of each 20 m interval was inspected to ensure random sampling. Each plant was inspected for 3–10 min, depending on its size. The population of *T. adenantha* along this 1 km transect consisted of at least 400 individuals.

Synchrony and displacement between events.—To study the synchrony between the phenologies of *M. argenteus* and *T. adenantha*, the number of vegetative branches ($\geq$ 5 cm long) and reproductive branches of all the plants inspected was scored. The branches were classified as reproductive when they had at least one flowerhead. Branches with flowerheads only in the seed-dispersal phase were excluded from the analysis because they do not attract floral visitors or *M. argenteus* (Romero 2001).

Prey.—The availability of potential prey for *M. argenteus* was assessed by recording of all arthropods occurring on *T. adenantha* during a one hour period, usually between 10:30 h and 13:30 h, in biweekly inspections from December 1998–March 2000. Arthropods were identified to the genus, family or superfamily level. Arthropods not identified in the field and the food items of *M. argenteus* were fixed in 70% ethanol and identified in the laboratory. Rainfall data were obtained from the experimental station at Jundiaí, located 8 km from the study area.

Statistical analysis.—Relationships between the density of *M. argenteus* and rainfall, phenology of *T. adenantha* (number of reproductive branches/plant) and prey density (number/hour) were examined using the Pearson correlation test (Zar 1996) with $\alpha = 0.05$. The same comparisons were done separately for the density of young, juvenile, subadult and adult spiders. The data, expressed as proportions, were normalized by log or log (n + 1) transformation. Since organisms generally need time to respond to environmental changes (e.g. Arango et al. 2000), the correlation between different variables and time was also examined. To verify whether *M. argenteus*

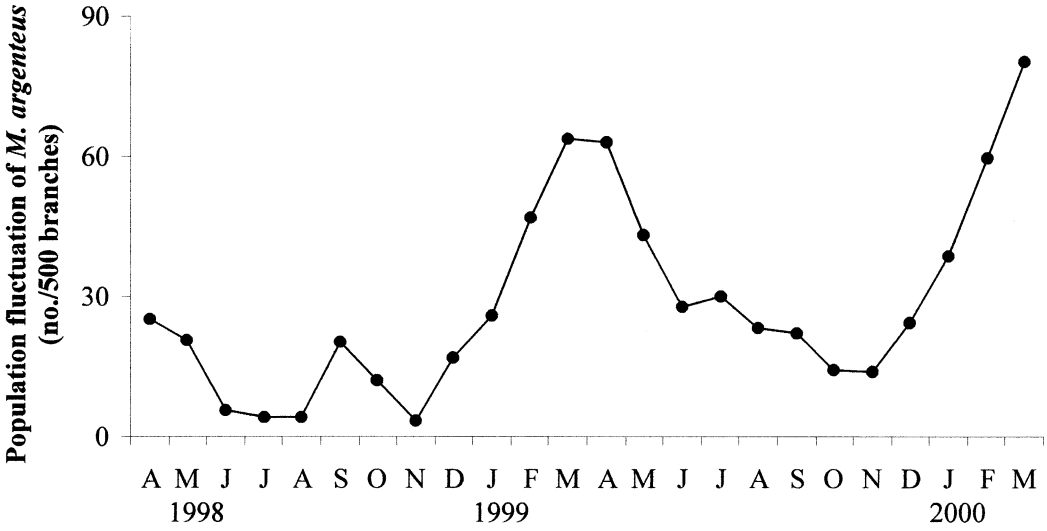

Figure 1.—Population fluctuation of *Misumenops argenteus* (Thomisidae) on *Trichogoniopsis adenantha*, from April 1998–March 2000, along the Mirante track, Serra do Japi. (*n* = 595 individuals).

chose prey at random, the range of prey used was compared with the distribution of available arthropods determined by the field observations using a G-test (Zar 1996). The preference and rejection of each prey item by *M. argenteus* was evaluated using Manly's α index of dietary preference for a constant prey population (Krebs 1999) based on the formula

$$\alpha_i = \frac{r_i}{n_i}\left[\frac{1}{\sum (r_j/n_j)}\right]$$

where α_i = Manly's index for prey type i, r_i and r_j = proportion of prey type i or j in the diet, and n_i and n_j = proportion of prey type i or j in the environment. A preference, detected as a deviation from the random sample of the prey, was indicated by values of $\alpha_i > 1/m$ (m = total number of prey types). In contrast, avoidance was indicated by values of $\alpha_i < 1/m$. This index is appropriate when the number of prey captured is much smaller than the total number of prey available (see Krebs 1999).

RESULTS

Population fluctuation and phenology of *M. argenteus*.—The population size of *Misumenops argenteus* started to increase at the beginning of the hot/rainy season (November) and reached a peak in March. The number of individuals decreased in May to reach the lowest density in the cold/dry season (July–September) (Fig. 1). In the rainy season, most individuals were in the young and juvenile phases (3^{rd}–6^{th} instars). Adulthood was reached between the end of the cold/dry season (June–July) and the beginning of the hot/rainy season (December–January) (Fig. 2).

Population recruitment occurred in November and December (Fig. 2). Young were present from October–April, with a peak in December–January. The proportion of juveniles started to increase in February and decreased between July and September. Subadults occurred in highest proportions in August and declined from November–December. The adult population was largest from July to November–December, with a peak in September 1998 and in October–November 1999 (Fig. 2). Young and juveniles together represented 70%−80% of the total number of *M. argenteus*, while subadults and adults were most frequent in the periods with a reduced population size (Figs. 1, 2).

Synchrony and displacement between events.—After the cold/dry season, the first rains occurred in September, but intensified from December–March (Fig. 3). The greatest abundance of reproductive branches in *T. adenantha* occurred from November–March, while that of arthropods occurred from March–May and in November and December; the number of *M. argenteus* peaked in March and April (Figs. 1, 3).

The numbers of flowering branches and rainfall were correlated in the same month ($r = 0.51$; $n = 16$; $P = 0.043$), or with the subsequent month, i.e., a temporal displacement of one month ($r = 0.85$; $n = 15$; $P < 0.001$). There was no correlation between arthropod density and rainfall in the same month, or after one, two or three months ($P = 0.66$; $P = 0.90$; $P = 0.54$ and $P = 0.44$, respectively), but there was a slight trend only between arthropod density and the density of reproductive branches in the same month ($r = 0.43$; $n = 16$; $P = 0.09$). The density of *Misumenops argenteus* correlated with rainfall only after three months ($r = 0.75$; $n = 13$; $P = 0.003$), with reproductive branches only after two months ($r = 0.79$; $n = 14$; $P < 0.001$), and with arthropod density only after two months (r = 0.57; $n = 14$; $P = 0.035$).

The density of young *M. argenteus* was positively correlated with rainfall in the same month ($r = 0.53$; $n = 24$; $P = 0.007$), and with arthropod density after three months ($r = 0.55$; $n = 13$; $P = 0{,}05$), but not with the number of reproductive branches for a time displacement of less than three months ($P \geq 0.08$). The density of juveniles was correlated with rainfall after two months ($r = 0.66$; $n = 22$; $P = 0.001$), but not with the number of reproductive branches, nor with arthropod density for a time displacement of less than three months ($P > 0.1$). The density of subadults and adults was not correlated with rainfall, with the number of reproductive branches, or with arthropod density for a time displacement of less than three months ($P > 0.1$).

Prey.—Of the 595 *M. argenteus* examined, 76 (12.8%) were feeding (Table 1). The prey consisted of herbivores (43.5%), pollinators (8%), parasitoids (12%), and predators (23%); 10.5% were eventuals (arthropods that occurred randomly on *T. adenantha*).

Misumenops argenteus fed mostly (84%) on the families (or genera) of arthropods that typically occurred on *T. adenantha* (Table 1). However, the use of arthropod prey was not random (Table 1; $G = 48.42$; 16 df; $P < 0.0001$) since there was a tendency to use more Grillidae sp., Ctenuchinae, Braconidae, ants and Chironomidae than predicted by Manly's index (Table 1). In contrast, *M. argenteus* used fewer Miridae sp. 1, Hoppers, Ithomiinae, Reduviidae sp. and Muscoidea than predicted by Manly's index (Table 1). There was no predation on *Melanagromyza* sp., Miridae sp. 2, Syrphidae spp. and Apoidea spp. (Table 1). Most of the ants and chironomid flies observed (≈ 90%) were glued in the glandular trichomes of *T. adenantha*.

DISCUSSION

Population fluctuation, phenology, synchrony and displacements.—There was a one month delay between the beginning of the rains and the increase in the number of reproductive branches in *T. adenantha*, as well as in the synchrony between the number of reproductive branches and the increase in arthropod density. In contrast, a displacement of two months occurred between the increase in arthropod density (potential prey for *M. argenteus*) and the increase in spider population size. Similar results were obtained by Arango et al. (2000) in a system involving *Cnidoscolus aconitifolius* (Mill.) I.M. Johnstone (Euphorbiaceae), floral visitors and *Peucetia viridans* Hentz (Araneae, Oxyopidae). Climatic changes were probably the primary factor molding *T. adenantha* phenology, as also observed for several other plant species in the study area (Morellato et al. 1990; Morellato & Leitão-Filho 1990, 1992). The reproductive branches and flowerheads used as foraging sites by *M. argenteus* (Romero 2001) supplied food for several herbivore and pollinator species. If this resource become scarce during some period of the year, the insects directly dependent on it also become scarce. Consequently, the carrying capacity of the habitat (*T. adenantha*) for *M. argenteus*, expressed as the availability of foraging sites and prey, diminishes, thereby reducing the spider population size.

The density of young increased in the same month as rainfall. It is probable that eggsacs, although not frequently observed, were deposited in September and October, the beginning of the rainy season. These results suggest that rainfall is a stimulus for mating and egg laying, as seen with other errant spiders (Crane 1949; Rossa-Feres et al. 2000).

Prey.—Thirteen percent of the *M. argenteus* found were feeding. The population studied showed the same rate of prey capture when compared with reports for other Thomisidae (Dean et al. 1987; Nyffeler & Breene 1990). *Misumenops argenteus* fed on a wide

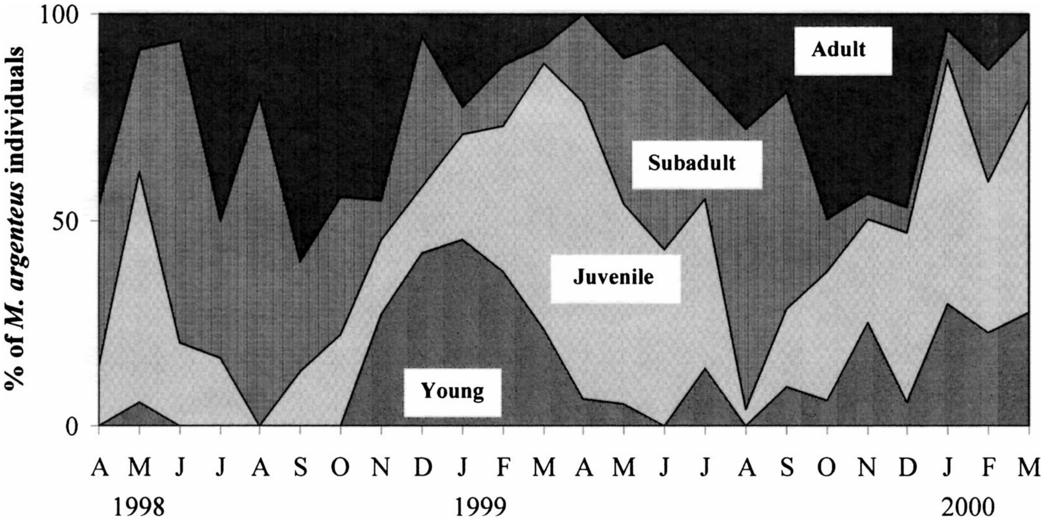

Figure 2.—Phenogram of the age structure of *Misumenops argenteus* (Thomisidae) population on *Trichogoniopsis adenantha* (Asteraceae), from April 1998–March 2000, along the Mirante track, Serra do Japi. (n = 595 individuals).

range of food items. Similar results have been described for other Thomisidae, including *Xysticus cristatus* (Clerck), *X. kochi* Thorell, *Misumenops celer* (Hentz) and *Misumena vatia* (Clerck) (Dean et al. 1987; Agnew & Smith 1989; Lockley et al. 1989; Nyffeler & Breene 1990). This polyphagy in *M. argenteus* may reflect the large variety of available prey, as described by Tanaka (1991) for *Agelena limbata* Thorell.

Despite the wide range of prey types captured, *M. argenteus* did not select prey randomly. In general, spiders avoid ants because of the potential damage that this prey can

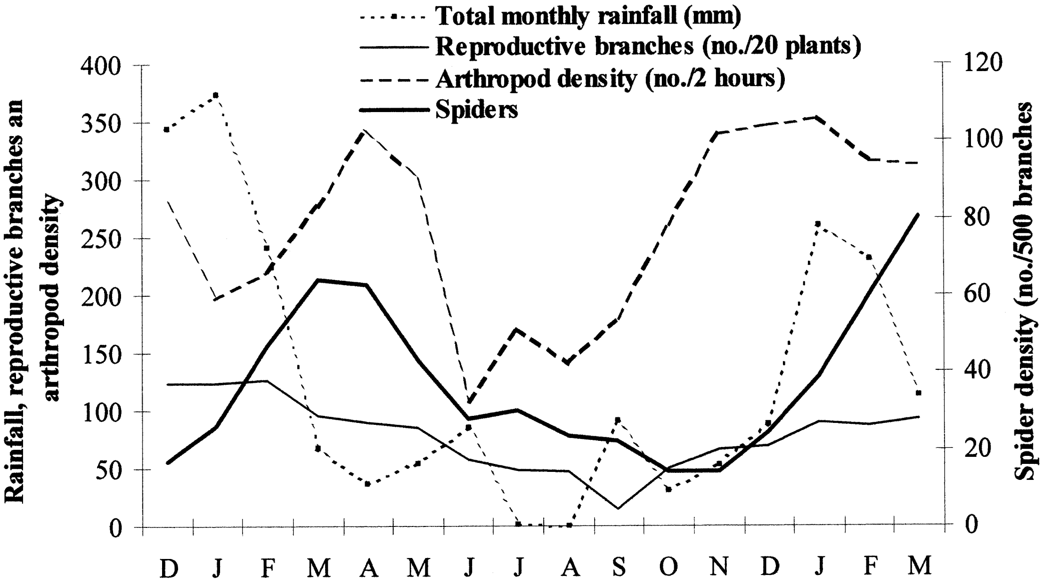

Figure 3.—Rainfall, number of reproductive branches (with flowerheads) per 20 *Trichogoniopsis adenantha* plants, arthropod density on the plants and *Misumenops argenteus* density (no./500 reproductive and vegetative branches), from December 1999–March 2000, along the Mirante track, Serra do Japi.

cause the predator (Riechert & Luczak 1982). However, *M. argenteus* captured more ants than the value expected (17% of all prey). Although ants occur only randomly on *T. adenantha*, the probability of spiders encountering ants is high because ants remain for longer periods and move around more on the plants than winged insects. Moreover, the glandular trichomes, which are very dense in *T. adenantha*, can reduce the velocity of the ants by sticking to these insects, making them easy for the spider to capture. Approximately 90% of the ants observed on the plants were stuck in the glandular trichomes and *M. argenteus* was seen preying on them ($n = 2$). In addition, almost all of the Chironomidae, also frequently used by *M. argenteus*, were stuck in the glandular trichomes. Like ants, Grillidae sp. and Braconidae also remain for longer periods on the plants. The Grillidae sp. lives amongst the leaves and flowerheads of *T. adenantha* and rarely flies, and the Braconidae spend a long time to laying eggs in endophagous insects in the flowerheads (G.Q. Romero, pers. obs.). Thus, insects that spent longer periods on the plants were more easily captured by the spiders.

In contrast, *M. argenteus* captured very few Miridae sp.1, hoppers and Reduviidae sp. relative to the expected value, and did not capture *Melanagromyza* sp., a small, very agile fly that can easily escape from the spiders (Romero 2001). Most of the hoppers on *T. adenantha* (≈ 60–70%) belonged to the family Membracidae, which is frequently tended by large ants of the genus *Camponotus*. These ants, which are not captured by the crab spider and are not affected by the glandular trichomes (G.Q. Romero, pers. obs.), may protect the membracid hoppers against the spiders. The Reduviidae sp. was probably not captured by the crab spider because the latter forages primarily on reproductive branches whereas the former forages primarily on vegetative branches. In addition, the Reduviidae sp. population peaked in the cold/dry season (Romero 2001).

Misumenops argenteus captured more Ctenuchinae (Arctiidae) and fewer Ithomiinae, both of which are lepidopteran floral visitors, even though the latter group was more abundant than the first. Insects of both groups are similar in size, and both sequester pyrrolizidine alkaloids from the host plant to use in their defense against predation by spiders (Trigo 2000). The legs of ithomiines are very long, compared to the ctenuchine, and this may help them escape the spiders when they land on the flowerheads. Whereas some errant spider species (*Lycosa ceratiola* Gertsch & Wallace and tarantulas) or orb-spiders (*Nephila clavipes* (Linnaeus)) avoid pyrrolizidine alkaloids (reviewed in Trigo 2000), *M. argenteus* captures and consumes ctenuchines that contain such alkaloids in their exoskeleton (J.R. Trigo, pers. comm.). In contrast to spiders which masticate their prey (including exoskeleton), thomisid spiders, such as *M. argenteus*, suck their prey dry, leaving the exoskeleton intact (Pollard 1993). This could explain why *M. argenteus* does not avoid prey with defensive chemicals confined to the exoskeleton compared to spiders which masticate their prey and avoid such insects.

In conclusion, rainfall was the principal abiotic factor that influenced the trophic interactions in the *T. adenantha*—arthropod–spider system. With increased rainfall, the plants increased their production of reproductive branches that subsequently attracted and supported populations of plant-dwelling arthropods which in turn supported the *M. argenteus* population. These results indicate that a strong bottom-up effect influences the system. However, experiments by Romero (2001) showed *M. argenteus* to be effective in diminishing herbivore density and in enhancing the fitness of *T. adenantha*, thus indicating that top-down effects also act to structure this system. These results show the importance of interactions between biotic and abiotic factors in determining the structure of arthropod community associated with *T. adenantha*.

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Table 1.—Prey available to and captured by *Misumenops argenteus* on *Trichogoniopsis adenantha* (Asteraceae), and the Manly's indices of dietary preference. Indices greater or smaller than 0.059 (1/total number of prey types) indicate preference or avoidance by the spider, respectively (see Methods). [a] = Insects consumed but not sampled in the biweekly observations. ''Eventuals'' = arthropods that occurred randomly on the plants.

	Prey				Manly's index
	Available	(%)	Captured	(%)	
Herbivores					
Endophages					
Melanagromyza sp. (Dip.)	136	8.5	0	0	—
Xantaciura sp. (Dip.)	26	1.6	2	2.6	0.053
Trupanea sp. (Dip.)	29	1.8	1	1.3	0.024
Cecidomyiidae spp. (Dip.)[a]	0	0	3	3.9	—
Suckers					
Miridae sp.1 (Het.)	345	21.6	7	9.2	0.014
Miridae sp.2 (Het.)	29	1.8	0	0	—
Aphididae spp. (Hom.)	86	5.4	6	7.9	0.048
Hoppers (Hom.)	73	4.6	2	2.6	0.019
Chewers					
Geometridae spp. (larvae) (Lep.)	131	8.2	7	9.2	0.037
Grillidae sp. (Ort.)	30	1.9	3	3.9	0.069
Chrysomelidae spp. (Col.)	47	2.9	2	2.6	0.029
Pollinators					
Ithomiinae spp. (Lep.)	79	4.9	2	2.6	0.017
Syrphidae spp. (Dip.)	13	0.8	0	0	—
Apoidea spp. (Hym.)	15	0.9	0	0	—
Ctenuchinae spp. (Lep.)	10	0.6	4	5.3	0.276
Parasitoids					
Braconidae spp. (Hym.)	52	3.2	5	6.6	0.066
Pteromalidae spp. (Hym.)	61	3.8	4	5.3	0.045
Predators					
Reduviidae sp.1 (Het.)	167	10.4	2	2.6	0.008
Araneae spp. (Arach.)	73	4.6	5	6.6	0.047
Formicidae spp. (Hym.)	87	5.4	13	17	0.103
Eventuals					
Chironomidae spp. (Dip.)	16	1.0	3	3.9	0.129
Muscoidea spp. (Dip.)	95	5.9	2	2.6	0.014
Coreidae sp. (Het.)[a]	0	0	1	1.3	—
Staphylinidae sp. (Col.)[a]	0	0	1	1.3	—
Carabidae sp. (Col.)[a]	0	0	1	1.3	—
Total	1600		76		

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