Nectar-Seeking and Host-Seeking by *Larra bicolor* (Hymenoptera: Crabronidae), a Parasitoid of *Scapteriscus* Mole Crickets (Orthoptera: Gryllotalpidae)

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ABSTRACT *Larra bicolor* F. (Hymenoptera: Crabronidae) is a specialist parasitoid of *Scapteriscus* (Orthoptera: Gryllotalpidae) mole crickets, attacking adults and medium to large nymphs of the hosts. Adult wasps derive energy from plant nectars. In replicated trials in pastures in northern Florida, many more wasps fed on nectar of *Spermacoce verticillata* F. (Rubiaceae), a non-native plant, than on nectar of the native plants *Spermacoce prostrata* Aubl. or *Spermacoce remota* Lamarck. Few of them fed on the native plant *Solidago fistulosa* Michx. (Asteraceae). About as many fed on the native plant *Chamaecrista fasciculata* (Michx) Greene as on *S. verticillata* in the autumn months until the native plant ceased flowering by October. In contrast, *S. verticillata* continues flowering until the first hard freeze, which typically occurs in December, so overall, it is a more reliable nectar source in northern Florida and may be still more reliable in frost-free areas of southern Florida where it may flower year-round. The number of immature wasps (eggs and larvae) parasitizing mole crickets was positively related to host density but also declined with distance from a plot of *S. verticillata* out to 200 m, based on samples of pitfall trap–collected mole crickets. The occurrence of parasitized mole crickets at a 200-m distance suggests that female wasps recruited to a plot of *S. verticillata* forage for hosts out to at least 200 m. This in turn suggests that mole cricket populations might be diminished by planting plots of *S. verticillata* at least 400 m apart when *L. bicolor* wasps are present.

KEY WORDS nectar source, conservation biocontrol, manipulative biocontrol

Larra bicolor (F.) (Hymenoptera: Crabronidae) is a widely distributed South American solitary parasitoid wasp using various species of *Scapteriscus* (Orthoptera: Gryllotalpidae) mole crickets as hosts (Menke 1992). Stock from Amazonian Brazil (via Puerto Rico) was introduced in 1981 into southern Florida, and stock from Bolivia was introduced in 1988 into northern Florida (Frank et al. 1995) to combat invasive mole crickets, which are the worst pest insects of pasture and turf grasses in Florida (Frank and Walker 2006). By 2005, progeny of the Bolivian stock had become widely distributed, whereas the Brazilian stock occupied a very restricted area (Frank et al. 2009).

Adult wasps derive most of their energy from the nutrients contained in plant nectars. A neotropical plant, *Spermacoce verticillata* F. (Rubiaceae), has long been recognized as a favored food source in the native and introduced range of the wasp (Wolcott 1941, Castner 1988), although neither of these authors quantified observations of feeding on plants. Arévalo and Frank (2005) quantified feeding by *L. bicolor* at *S. verticillata* compared with four other plants in northern Florida, but *S. verticillata* proved to be the most visited. Advocacy of *S. verticillata* for use to attract *L. bicolor* in Florida has been questioned because of concerns regarding the economic and ecological costs associated with introduction and propagation of nonindigenous plant species. We describe tests of *S. verticillata* versus two native *Spermacoce* species and two other native plants in hope of finding a native plant that will outperform *S. verticillata.*

Attraction of *L. bicolor* adults to nectar source plants, in the manner of butterfly gardening, is a useful technique to show their presence at any locality. We successfully used plots of *S. verticillata* at many localities in Florida to do this. The question is whether such plots, which attract and provide nutrients to adult parasitoids, help to diminish pest populations in the surrounding area, and if so, to what distance outward from the plot? Evidence from the literature for other host–parasitoid systems (Baggen and Gurr 1998, Rogers and Potter 2004) suggests that they can, but we sought evidence for the *Larra*--*Scapteriscus* interaction.

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Materials and Methods

Choice of Nectar Source Plants. Four experimental native plant species were selected for evaluation and comparison to the non-native control species *S. verticillata:* partridge pea, *Chamaecrista fasciculata* (Michx.) Greene (Fabaceae); goldenrod, *Solidago fistulosa* Michx. (Asteraceae); woodland false buttonweed, *Spermacoce remota* Lamarck (Rubiaceae); and prostrate false buttonweed, *Spermacoce prostrata* Aubl. (Rubiaceae) (Wunderlin 1998). *C. fasciculata* and *S. fistulosa* were chosen on the basis of historical observations of *Larra* spp. feeding from these plants in the field (Smith 1935, Arévalo and Frank 2005). *S. remota* and *S. prostrata* were included because both are indigenous *Spermacoce* species that occur throughout Florida (Wunderlin 1998).

In December 2005, >40 specimens of each plant species were potted in commercial potting soil and maintained in a greenhouse located adjacent to the University of Florida's Entomology and Nematology building in Gainesville, FL. Seedlings were watered daily and fertilized once per month with a solution of "Peter's All Purpose Plant Food" 20–20-20 (N-P_2O_5-K_2O) (United Industries, St. Louis, MO). In March 2006, all plants were removed from the greenhouse, transported into the field, and planted in the ground at two field sites located at The University of Florida's Beef Research Unit (BRU) and Horse Teaching Unit (HTU) in Alachua County, FL. Immediately after planting, each plant was generously watered. To keep the plants healthy and flowering throughout the experiment, the plants were watered periodically during dry periods.

Each field site contained a total of 15 treatment plots ≈1 by 0.5 m in size. Treatment plots were arranged in three randomized complete blocks at each site. Blocks were spaced >30 m apart. Treatment plots within blocks were laid out in a side-by-side parallel array with 4 m of spacing between each plot. Plots were covered with a 50 by 100-cm sheet of black polyethylene plastic sheeting to prevent other weeds and grasses from growing in the plots. Treatment plants grew through four evenly spaced 15-cm-diameter holes in the plastic sheet. Each plot was visibly marked by a border of 1.0-cm-diameter yellow, nylon rope, supported by wooden stakes positioned at the plot corners.

Recorded observations of adult wasps began in July 2006 and continued through November 2006. Wasp counts were conducted semiweekly around 1300 hours at the HTU and 1400 hours at the BRU (peak activity time). Both male and female wasps observed visiting the plants in each individual plot were counted for 1 min. A timer was used to standardize the amount of time spent at each plot. Local temperature and basic weather conditions (sunny, partly cloudy, overcast, or rainy) were also recorded.

Data were analyzed by multilevel analysis of variance (ANOVA) to determine main effects from site, month, treatment, and their interactions using Proc GLM of the SAS 9.1 (SAS Institute, Cary, NC). Count values were transformed by $\log_{10}(x + 1)$ to achieve normality for ANOVA. Female wasps are typically larger, and their abdomen is darker red and glossier than in males, making separation in the field easy. Means and SEs for numbers of males, females, and total wasps observed on each plant were calculated for each month. Within each month, data were pooled across farms, and treatment effects were analyzed by one-way ANOVA followed by mean comparisons using Duncan's multiple range tests (MRT). Analysis was performed on log-transformed data, but untransformed means and SEs are presented in the tables.

Host-Seeking Distance. In August 2005, a plot of 16 *S. verticillata* plants, ≈3 by 1 m in size, was established in a large grass pasture at a private horse farm (Duncan Farm) located ≈10 km southeast of the town of Hampton in Bradford County, FL. To prevent other weeds and grasses from crowding the plants, the surface of the plot was covered with a 3 by 1-m sheet of black polyethylene plastic. Plants grew through two rows of evenly spaced 15-cm-diameter holes in the plastic. The plot was surrounded with barbed wire to discourage the horses from destroying the plants.

A line of 10 pitfall traps, spaced at 20-m intervals, extended out from the long edge of the plot. Each trap was constructed as described by Lawrence (1982): the center of the trap is an 18.9-liter (5 gal) plastic bucket with lid, sunken into the ground to just below the lid; holes in the wall of the bucket just below the lid allow insertion of four gutters, one pointing in each cardinal direction and capped at its distal end; the gutters are fashioned from 3-m lengths of thick-walled PVC pipe, 7.6 cm in diameter. These gutters are sunken into the ground to the level of a longitudinal slit, 2.5 cm wide, in each; the catchment edge on the soil surface is thus ≈2 by 3 by 4 (=24) m as contrasted with the circumference of a simple pitfall trap area on the soil surface. Traps were monitored approximately once per week from October to December 2005 and from August to December 2006. Mole crickets caught in the traps were transported to the University of Florida's Entomology and Nematology building in Gainesville, FL, and inspected under a stereomicroscope for the presence of *L. bicolor* larvae or eggs. Numbers of *S. borellii* Giglio-Tos and *S. vicinus* Scudder captured, each cricket's relative size (pronotal length), and presence of parasitoids were recorded for each trap. Parasitoid instars were also noted.

Average monthly means and SEs were calculated for total cricket numbers and percent parasitism. Yearly means and SEs for numbers of mole crickets, parasites, and percent parasitism were calculated for all distances from the *S. verticillata* plot using SAS 9.1 (SAS Institute). Correlation coefficients (r) were calculated between all variables to determine any linking relationships. Using the Proc Reg procedure of SAS 9.1, regression analysis was used to compute the linear function of each significant ($P < 0.05$) relationship.

Results

Choice of Nectar Source Plants. Multilevel ANOVA indicated significant ($P < 0.05$) effects on males, females, and total wasps from treatment, month, and treatment × month interactions, but not from farm ($P < 0.01$). During July, August, and September, sig-

Table 1. Number (mean ± SEM) of total wasps (females + males; females, males) observed on each plant species

Plant species	July	Aug.	Sept.	Oct.	Nov.
Males and females					
Spermacoce verticillata	17.2 ± 6.5A	31.5 ± 14.6A	25.7 ± 7.9A	40.7 ± 23.6A	31.2 ± 23.5A
Chamaecrista fasciculata	37.5 ± 19.3A	47.8 ± 23.6A	21.5 ± 12.4A	0.0B	2.4 ± 2.4B
Solidago fistulosa	0.5 ± 0.5B	1.2 ± 1.2B	0.0B	0.8 ± 0.7B	2.4 ± 1.5B
Spermacoce prostrata	0.0B	0.3 ± 0.2B	0.5 ± 0.5B	0.0B	0.0B
Spermacoce remota	0.0B	0.0B	0.0B	0.0B	0.1 ± 0.1B
Females					
Spermacoce verticillata	2.2 ± 1.3B	1.3 ± 0.8B	2.2 ± 1.2A	1.7 ± 1.1A	1.0 ± 0.6A
Chamaecrista fasciculata	14.8 ± 8.5A	10.5 ± 5.5A	2.8 ± 1.1A	0.0A	0.4 ± 0.4AB
Solidago fistulosa	0.5 ± 0.5B	0.5 ± 0.5B	0.0B	0.0B	0.4 ± 0.2AB
Spermacoce prostrata	0.0B	0.0B	0.0B	0.0B	0.0B
Spermacoce remota	0.0B	0.0B	0.0B	0.0B	0.0B
Males					
Spermacoce verticillata	15.0 ± 5.6A	30.2 ± 14.0A	23.5 ± 6.9A	39.0 ± 22.5A	30.2 ± 23.2A
Chamaecrista fasciculata	22.7 ± 11.1A	37.3 ± 18.2A	18.7 ± 11.6B	0.0B	2.0 ± 2.0B
Solidago fistulosa	0.0B	0.7 ± 0.7B	0.0C	0.8 ± 0.7B	2.0 ± 1.3B
Spermacoce prostrata	0.0B	0.3 ± 0.2B	0.5 ± 0.5C	0.0B	0.0B
Spermacoce remota	0.0B	0.0B	0.0C	0.0B	0.1 ± 0.1B

Values represent counts from all plots (2 locations × 3 replications). Means with same letters are not significantly different ($P < 0.05$) according to Duncan's MRT on log-transformed data).

nificantly more wasps (male + female) were observed on the native *C. fasciculata* and the control plant, *S. verticillata,* than on *S. fistulosa, S. prostrata,* or *S. remota.* However, during October and November, the control plants outperformed all four native species at attracting wasps (Table 1).

During July and August, more female wasps were attracted to *C. fasciculata* than to *S. verticillata. C. fasciculata* attracted an average ± SEM of 14.8 ± 8.5 and 10.5 ± 5.5 female wasps in July and August, respectively, compared with an average of 2.2 ± 1.3 and 1.3 ± 0.8 females observed on *S. verticillata* (Table 1). The abundance of male wasps and total wasps (males + females) observed for both *C. fasciculata* and *S. verticillata* during July and August was similar (Table 1).

Comparable numbers of female wasps and total wasps (males + females) were observed visiting the control plant, *S. verticillata,* and the native plant, *C. fasciculata,* in September. However, the control plant attracted significantly more male wasps than the native plant during this period. In September, an average of 23.5 ± 6.9 male wasps was observed at *S. verticillata* plots compared with an average of 18.7 ± 11.6 male wasps found at *C. fasciculata* plots. November was the only month that wasps were seen on *S. remota* (Table 1).

Host-Seeking Distance. Average monthly mole cricket catch increased by 42% from 2005 to 2006. Approximately 90% of all mole crickets trapped were *S. vicinus.* Because the seasonality of the two *Scapteriscus* species is very similar and because we have not noted a differential response to them by *L. bicolor,* we pooled the data for the two species. Because of wide variation among samples, the numbers of mole crickets and parasitoids recorded from each trap were averaged over yearly periods. Average numbers of mole crickets and parasitoids recorded for each of the 10 traps, in 2005, ranged from 2.6 ± 1.2 to 7.7 ± 2.0 crickets and 0.1 ± 0.1 to 2.0 ± 0.9 parasitoids. In 2006, the average numbers ranged from 4.4 ± 0.9 to 20.6 ± 4.8 crickets and 0.5 ± 0.2 to 2.6 ± 0.6 parasitoids for each trap. The highest levels of parasitism for both years were observed in November and December (Table 2).

Correlations between the number of crickets caught in the traps and the number of associated parasitoids were highly significant ($r = 0.84, P < 0.003, N = 10$) for 2005 and ($r = 0.84, P = 0.002, N = 10$) for 2006. Numbers of parasitized mole crickets (y) captured at a particular location increased positively with the total numbers of mole crickets (x) captured in 2005 ($y = 0.29x - 0.16$) and in 2006 ($y = 0.11x + 0.27$) (Fig. 1). The relationship was highly significant for 2005 ($R^2 = 0.71, P < 0.003$) and 2006 ($R2 = 0.72, P < 0.003$). In fact, the relationship was nearly identical for both years. These results suggest that the probability of finding parasitized mole crickets increases as local cricket abundance increases. The regression lines (Fig. 1) give no indication of curvilinearity and thus no reason to think that percent parasitism increased superproportionately to host density; we verified this by finding a nonsignificant correlation of percent parasitism on host density.

Parasitized mole crickets were found at every sampled distance from the nectar source (Table 3). These

Table 2. Number (mean ± SEM) of mole crickets caught in pitfall traps and percent parasitized by *L. bicolor*

Month	2005		2006	
	Total crickets	% parasitism	Total crickets	% parasitism
Aug.	—	—	57.0	5.3
Sept.	—	—	48.3 ± 7.4	5.8 ± 2.2
Oct.	35.0 ± 13.0	6.4 ± 1.9	92.5 ± 53.8	9.8 ± 4.0
Nov.	42.8 ± 10.1	31.5 ± 6.4	118.8 ± 31.8	18.7 ± 1.5
Dec.	57.0 ± 44.0	26.9 ± 6.4	70.0	17.1

Values represent monthly sampling means (2005: Oct. $N = 2$, Nov. $N = 5$, Dec. $N = 2$; 2006: Aug. $N = 1$, Sept. $N = 4$, Oct. $N = 4$, Nov. $N = 6$, Dec. $N = 1$).

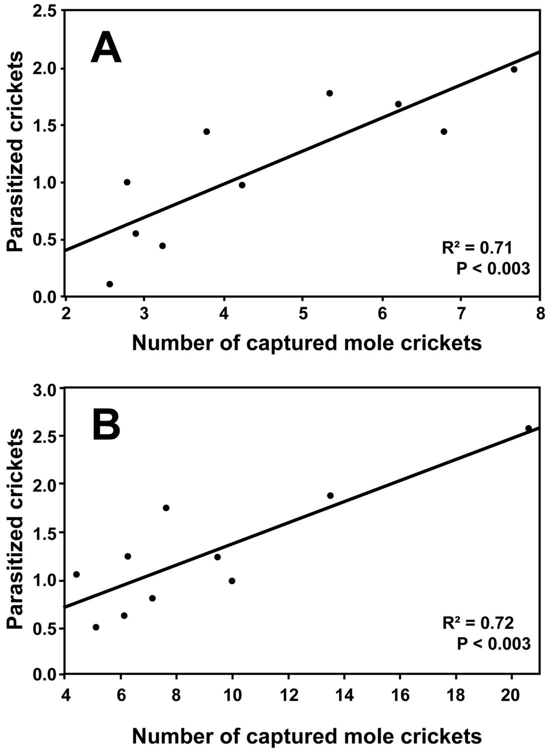

Fig. 1. Average number of parasitized mole crickets captured in pitfall traps as a function of the average mole cricket catch per trap. (A) Numbers recorded for 2005. (B) Numbers recorded for 2006.

preliminary data suggest a trend of higher levels of parasitism near to the nectar source, although parasitized crickets were found at all distances, even at 200 m.

Discussion

Spermacoce verticillata has been judged nontoxic to cattle (Francis 2000) and not invasive of native ecosystems (Anonymous 2007). However, many turf growers and farmers are still reluctant to grow *S. verticillata* despite the fact that it readily attracts beneficial insects such as *L. bicolor*. Its common name in Puerto Rico is botón blanco (Francis 2000), meaning "white button." Unfortunately, U.S. botanists dubbed it with the long and unappealing name, "shrubby false buttonweed" (Wunderlin 1998). We have tried to promote its use by gardeners and ranchers with the name Southern Larraflower, which audiences simplified to "Larraflower," and that name seems to be gaining circulation.

Table 3. Average no. of parasitized mole crickets (±SEM) per sampling occasion, trapped at each distance from the plot of wildflowers, in 2005 and 2006

Distance (m)	2005	2006
20	1.7 ± 0.6	1.8 ± 0.4
40	1.8 ± 0.6	1.9 ± 0.6
60	1.4 ± 0.5	2.6 ± 0.6
80	0.4 ± 0.2	1.3 ± 0.3
100	2.0 ± 0.9	1.0 ± 0.3
120	0.6 ± 0.3	0.5 ± 0.2
140	1.0 ± 0.4	0.8 ± 0.3
160	1.0 ± 0.4	0.6 ± 0.2
180	1.4 ± 0.6	1.3 ± 0.4
200	0.1 ± 0.1	1.1 ± 0.4

We observed many wasps on *S. verticillata* during the final 2 mo of the study because this plant continued to produce flower blossoms, whereas *C. fasciculata* began to display signs of senescence in early October.

For those growers who have misgivings in promoting use of a non-native plant (*S. verticillata*) to assist a non-native wasp to control non-native mole crickets damaging non-native commodities, the native plant *C. fasciculata* should provide an alternative. It may be a better nectar source in the summer. Perhaps mixed plots of the two plants would be even better. In frost-free areas of Florida, *S. verticillata* should provide nectar year-round. Herbarium collection data for *C. fasciculata* in southern Florida suggest that its flowering period there, too, is summer but with a few records for November and January (Fairchild Tropical Garden Herbarium 2007). Thus, in southern Florida also, there may be an advantage to mixed plots of the two plants.

Previous studies found strong correlations between nearby flowering vegetation and greater percentage parasitism (Lewis et al. 1998, Rogers and Potter 2004). In the case of the mole cricket parasitoid, *L. bicolor*, it was not known how a nearby nectar source would affect local parasitism levels or the wasp's distribution patterns. We examined these effects by measuring the proportion of captured mole crickets that were parasitized by *L. bicolor* at regular distance intervals.

The native *Larra analis* F. attacks the native mole cricket *Neocurtilla hexadactyla* (Perty), and its adults have been reported feeding at nectar of *C. fasciculata* (Smith 1935). We found it and its host *N. hexadactyla* rarely during this study and did not record either. We have seen *L. analis* adults feeding at nectar of *S. verticillata.* We have never reared *L. analis* adults from *Scapteriscus* mole crickets nor *L. bicolor* adults from *Neocurtilla* mole crickets. This may be related to the distant association (separate tribes) of these two genera.

Our data indicate that the mole cricket population at our field site was not evenly distributed. The number of wasp eggs and larvae found on mole crickets also exhibited a clumped distribution that correlated with the distribution of mole crickets. These results show a strong positive relationship between the total number of mole crickets caught and the number of associated parasites. However, percent parasitism did not significantly correlate with cricket abundance. These findings suggest that *L. bicolor* females are not concentrating their efforts in areas where mole crickets are more prevalent; rather, their foraging patterns are more random. For a randomly foraging parasitoid, the probability of encountering suitable hosts is dependent on the density of hosts inhabiting the foraging area. Consequently, more individuals will be parasitized in high-density host patches, but the percentage of parasitized hosts in each patch will be variable.

Our results also suggest that the number of parasitized mole crickets declines as their distance from the wasp's host plants increases. Therefore, we conclude that any decline in parasitized cricket number, relative to distance, was caused by females spending substantially more time searching for hosts close to a familiar nectar source. It is worth noting that all of these traps were contained within a very large grassy pasture that seemed to offer few if any alternative sources of nectar.

These findings suggest that *Scapteriscus* parasitism level, by the hymenopteran parasitoid *L. bicolor*, is influenced by two aspects of the mole cricket's population demographics: the population's local density and its proximity to high-quality nectar sources, with the former being more clearly shown important. By integrating the interpretations from both sets of results, we conclude that the highest levels of parasitism should be found in host patches that have high mole cricket population densities and are close to (<200 m) a plentiful nectar source. This conclusion has important implications for habitat management and biological control of pest mole crickets. We propose that establishing patches of *S. verticillata* and *C. fasciculata* roughly 400 m apart would increase and enhance the resident *L. bicolor* population, thereby maximizing the number of mole crickets encountered by female wasps in these areas. This should result in a rise in parasitism levels and a proportional reduction in the local mole cricket population.

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