

DIEL PATTERNS OF *LARRA BICOLOR* (HYMENOPTERA: SPHECIDAE) IN PUERTO RICO

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ABSTRACT

Behavioral observations of *Larra bicolor* F., a sphecid parasitoid of *Scapteriscus* mole crickets, made in Puerto Rico differed significantly from records made in Brazil. Foraging and host-searching occurred over a greater daily period and were less severely affected by climatic conditions. Foraging adults, previously recorded only on *Spermacoce verticillata* L. and species of *Hyptis*, were also frequently found on *Euphorbia heterophylla* L. and *Croton glandulosus* L. Mate-searching is described and appears to be based on the attraction of males to a female-produced pheromone.

Key Words: Parasitoid, behavior, Sphecidae, *Larra*, mole cricket, Gryllotalpidae, *Scapteriscus*.

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INTRODUCTION

The genus *Larra* (Hymenoptera: Sphecidae) contains over 60 species of parasitoid wasps that utilize mole crickets (Orthoptera: Gryllotalpidae) as hosts (Bohart and Menke 1976). *Larra bicolor* F. parasitizes and develops on at least five species of economically important mole crickets in the genus *Scapteriscus* (Castner 1984), three of which were introduced onto the island of Puerto Rico (Nickle and Castner 1984). Although the feeding habits of these species vary (Castner and Fowler 1984a), all species probably cause mechanical injury to turf and crops by underground tunneling. The absence of specialized natural enemies allowed mole crickets to become important pests of agriculture in Puerto Rico, causing extensive damage to tobacco, sugar cane, and vegetable crops (Barrett 1902; Van Zwaluwenberg 1918; Martorell 1939).

In the late 1930s a biological control program was initiated against *Scapteriscus didactylus* (Latreille) in Puerto Rico. Williams (1928) reported that *Larra bicolor* (= *Larra americana* Saussure) parasitized *S. didactylus* (mistakenly identified as *S. vicinus* Scudder). *Larra bicolor* wasps were collected from Brazil during 1936 to 1939 and released at seven sites in Puerto Rico (Wolcott 1938). Successful establishment was reported at three locations by 1941 (Wolcott 1941a). Castner and Fowler (1984b) surveyed the northern coast of Puerto Rico in 1983 for *L. bicolor* wasps and found them well established, although no more widespread than indicated in older reports (Wolcott 1950). The effect of *L. bicolor* on Puerto Rican mole cricket populations has not been evaluated.

MATERIALS AND METHODS

Nine weeks (May - June 1981 - 83) were spent in Puerto Rico making ecological observations and collecting *L. bicolor*. Field sites were sought near the town of

Isabela, where wasps were reported to be established since 1939 (Wolcott 1941a). Study locations were selected by surveying fields and pastures for *Spermacoce verticillata* L. (Rubiaceae), a native plant formerly classified in the genus *Borreria* (Wunderlin 1979). *Spermacoce verticillata* produces white, spherical inflorescences that are highly attractive to *Larra* spp. wasps (Williams 1928). The potential productivity of sites was judged by the number of *L. bicolor* observed foraging at *S. verticillata* blossoms during a 30 minute period. Based on these criteria, two adjacent fields were chosen. One was planted with cassava in 1981 and was reverting back to natural pasture in 1982 and 1983. The other was used as a pasture during all three years.

Observations on the daily habits of *L. bicolor* were made in 1981 and 1982 while collecting female wasps for releases in the state of Florida (Castner 1983). During 1983 population studies were conducted (Fowler and Castner, unpublished data), and wasps were monitored for 40 minutes of each hour throughout the photophase for 10 days. During the monitoring periods, foraging wasps were located by checking blooming clumps of *S. verticillata*. Hunting females and mate-seeking males were found by visually scanning the surface of the ground. The air temperature and soil surface temperature were measured every hour.

RESULTS AND DISCUSSION

Host Searching

Female wasps ($n > 100$) searched for mole crickets by walking along the ground. When a wasp encountered a surface gallery formed by the mole crickets' passage through the soil, it burrowed in and sought its prey underground. When a mole cricket was found, it usually tried to evade the wasp by surfacing ($n = 15$). Although wasps were only observed attacking and parasitizing mole crickets on the surface, it is possible that they were able to successfully subdue and parasitize hosts underground, when the tunnels were large enough. Wasps searching underground often came up periodically to survey the soil surface in the immediate area. Sometimes a wasp emerged from the same hole it made when going down, and other times it surfaced at a completely different point. One female entered the ground and surfaced 15 times from the same hole while under observation. Although it initially covered the soil surface only several centimeters from its entrance hole, the area checked was increased each time up to a distance of 35 cm from the hole. These surface forays lasted several seconds until the wasp entered the ground for another 10 to 30 second period of subterranean searching.

Mole crickets attempted to escape the wasps by burrowing up and out onto the soil surface. It is unknown if this evasive action resulted from actual physical contact between host and parasitoid, or if the mole cricket detected the danger in some other way. Although the female wasp's vision is acute, field observations of wasp/mole cricket encounters ($n = 15$) suggested that at least half of the potential hosts escaped in this manner. Captured mole crickets were immediately paralyzed and parasitized.

Figure 1a illustrates the daily host-searching behavior of female *L. bicolor*. Wasps searched for hosts from approximately 0640 to 1545 hr EDT (sunrise = 0545 hr). Two to three eggs per female per day were usually obtained under controlled conditions. The most eggs obtained in one day from a female wasp was five.

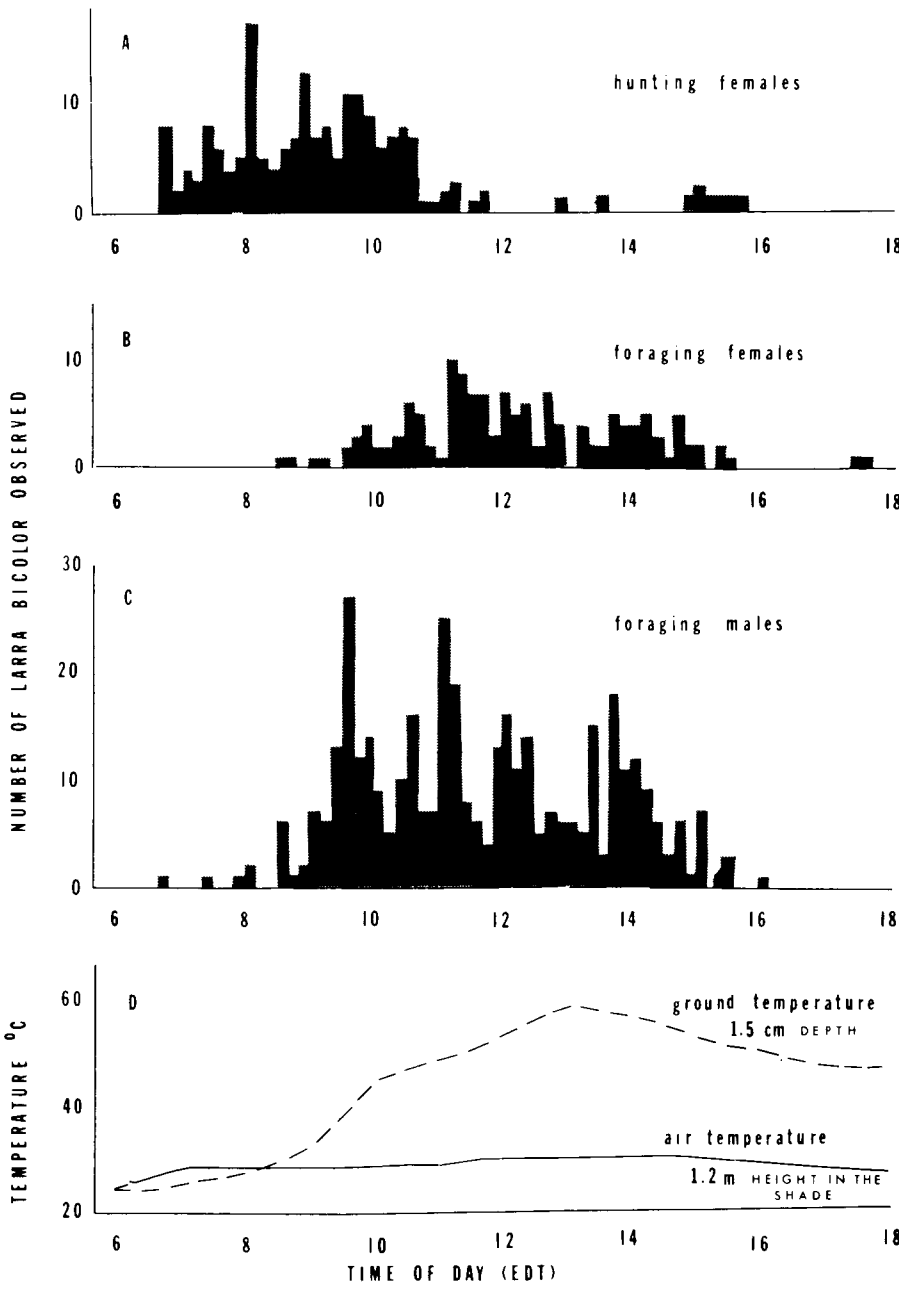


Fig. 1. Daily hunting and foraging patterns observed in a population of *Larra bicolor* wasps in Puerto Rico. Numbers represent total wasps observed during 10 days.

Host-searching behavior occurred both under clear, sunny conditions and during cloudy, overcast weather. No wasps were seen hunting during a rain. It is not known if females patrol a given territory in their search for mole crickets. The one observed encounter between hunting females resulted in aggressive actions, with one wasp charging the other and driving it away.

Field observations ($n = 15$) and lab experiments (Castner 1983) indicate that small nymphs are attacked by *L. bicolor* as readily as large adults. On one occasion, a female wasp successfully parasitized a mole cricket nymph that was smaller than itself.

Foraging

Male and female wasps concentrated their foraging efforts from approximately 0830 to 1530 hr (Fig. 1b, 1c). A proportionally higher number of males than females was observed at flowers early in the morning.

Larra bicolor was found most abundantly at the blossoms of *S. verticillata* and more than 200 were collected from these plants. Other plant species commonly utilized by the wasps were *Croton glandulosus* L. and *Euphorbia heterophylla* L. Both of these are members of the Euphorbiaceae and bear extra-floral nectaries that the wasps exploit. *Larra bicolor* was found so commonly on the species named that surveying and collecting this parasitoid was facilitated by locating and monitoring the nectar-producing individuals of these plants.

Foraging female wasps were wary and often exhibited quick and jerky motions, accented by short, rapid flights from one blossom to the next. On *S. verticillata*, which produces flower heads at different heights, females ($n > 50$) frequented the lower and inner-most blossoms. Any motion that disturbed a wasp resulted in an immediate evasive flight, or a complete cessation of movement. In the latter case, the wasp's head was oriented towards the disturbance. After several minutes of immobility the wasp either continued its foraging or flew away. Male wasps were generally much less easily disturbed while foraging.

Mate Searching

Male wasps ($n > 200$) were seen from 0630 to 1130 hr flying 6 to 12 cm above the ground in search of females. The restriction of mate-seeking behavior to a limited portion of the day was also reported by Lin (1963) in *Sphecius speciosus* (Drury) (Hymenoptera: Sphecidae), and is not uncommon in the aculeate Hymenoptera. This behavior in *L. bicolor* appears to be linked with adult female emergence, which occurs during early morning (Castner, unpublished data).

The distribution of *Larra* emergence sites is not known. Presumably the wasp grub pupates near the remains of its hosts in an underground tunnel or chamber. Laboratory observations support this, as larvae that successfully constructed cocoons did so within several centimeters of their hosts' remains (Castner 1983). Laboratory studies (Castner 1983) have shown that the ultimate larval instar is incapable of moving any great distance on its own, however, it is possible that the developing larva influences its host's burrowing movements for its own benefit.

Male *L. bicolor* ($n > 200$) patrolling areas of ground, flew in an erratic, roughly circular pattern. No territories appeared to be established, and no signs of aggression were observed between conspecific males, although as many as six would gather at one time in proximity to a female.

Both vision and chemoreception are apparently important in mate location. The production of a pheromone by the female is supported by observations of searching males ($n > 50$) landing within 15 - 25 cm of a single female on the ground, and on areas where female wasps had left or been collected from several minutes earlier. It therefore appears that a pheromone is used for long-distance (several meters) location, with vision being relied upon to recognize the female once within the approximate vicinity.

Female *L. bicolor* searching for hosts were continually harassed during the morning hours by mate-seeking males. Approaching the female from behind, a male would attempt to mate by running up or flying directly on her. A female was never observed to be receptive to these advances ($n = 20$). The usual reaction was to fly 15 to 20 cm away, or completely out of the area if the males persisted. Females foraging at blossoms were never approached. No mating was observed in the field or laboratory.

BEHAVIORAL DIFFERENCES IN POPULATIONS

The behavior of *L. bicolor* in Puerto Rico differs markedly in certain respects from observations made by Williams (1928), Wolcott (1938), and Martorell (1939) in Brazil. The female wasp's foraging activities were reportedly much more dependent on daily weather patterns in Brazil. Wolcott (1938), on the basis of several months of collecting *L. bicolor* near Belem, reported that females hunt only in early morning. He proposed that the ground was still damp then from the previous day's rain and mole cricket surface galleries were easier to find. *Larra bicolor* was abundant in Brazil only at the beginning (February) and end (May) of the rainy season (Williams 1928; Wolcott 1938; Martorell 1939), with numbers decreasing significantly for each day without rain. Females were reported to forage only during mid-day, and only if sunny, cloudless conditions prevailed. The passage of a cloud resulted in the wasps seeking cover in the foliage, very often that of the *S. verticillata* on which they were feeding (Wolcott 1938).

Wasps collected near Isabela, Puerto Rico, were seen both hunting and foraging over a much greater time period. Foraging was not restricted to mid-day and wasps did not remain in shelter during cloudy weather. However, the number of foraging females did increase during clear, sunny conditions. Observations on males agree with those of earlier authors in that foraging took place throughout the morning and afternoon. According to Wolcott (1938), the daily rains in Brazil seem to occur with more predictability and possibly with more violence than in Puerto Rico. Such rains may necessitate the wasp seeking shelter for self protection, thus justifying its immediate response to cloud cover. The daily division of early morning hunting and mid-afternoon foraging is also sensible where rains consistently occur in the afternoon or evening every day. In Puerto Rico, however, such environmental consistency was not observed. The ground or soil surface temperature appears to play a major role in restricting hunting behavior. Only sporadic host searching occurred after the ground temperature reached 50°C (Fig. 1d). During the 1981 collecting season (May 23 - June 16) near Isabela, the final nine days were without rain and no decrease in the number of *L. bicolor* was observed.

Wolcott (1941b) indicated that the presence of *S. verticillata*, was a major limiting factor of the establishment and spread of *L. bicolor* in Puerto Rico. While observations in Puerto Rico and Florida verify the attraction of *L. bicolor* to

S. verticillata, it should be noted that foraging occurs at many other plants. In Puerto Rico *L. bicolor* was also frequently seen feeding at the nectaries of *E. heterophylla* and *C. glandulosus*.

I hypothesize that the amount of time an individual female spends hunting is inversely proportional to her ovipositional success. Wasps that successfully oviposit early in the day need to mature additional eggs and/or replenish carbohydrate reserves, and spend the rest of the day foraging. Unsuccessful females continue to search for a host either until successful, or until physiological requirements force them to forage.

The results of a rearing experiment where all hosts were parasitized at approximately the same time, showed that 81% ($n = 13$) of the male *L. bicolor* emerged at least one day before the earliest emerging female (Castner 1983). Protandry is common among most bees and wasps (Alcock 1980; Alcock et al. 1978). In many species this affords the male an opportunity to locate the nesting or emergence site likely to be used by a female, or a landmark or other similar structure used in mate location.

The following hypothesis is presented to explain the observed behavior of male and female *L. bicolor* wasps, and assumes that females are monogamous. If upon emergence a female-produced sex pheromone is triggered, then mating should occur shortly after the female reaches the surface and becomes available to patrolling males. Since female emergences are probably randomly scattered, males increase their chances for mating by actively patrolling large areas rather than guarding and waiting at small ones. Males continue searching past the early morning period of female emergence in order to locate virgin females that have escaped detection. The pheromone persists for a period of time after mating has occurred, thus explaining the non-receptive attitude of the females observed being harassed.

Our knowledge of developmental time and longevity in the laboratory suggests that after several generations the emergence of females in the field may occur daily. The consistent collection of females with no signs of wear over several three-week periods in Puerto Rico, supports this. Males would therefore be expected to spend the morning hours of every day patrolling likely areas in order to maximize their chances of inseminating as many females as possible.

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