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OBSERVATIONS ON THE MATING BEHAVIOR OF
MALE *STICTIA HEROS* (HYMENOPTERA: SPHECIDAE)

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ABSTRACT

Males of the neotropical sand wasp *Stictia heros* (Fabr.) displayed territorial behavior in female nesting areas, presumably to gain access to newly eclosed virgin females. Males hovered above a fixed point of the beach and defended small areas (1 m²) with rapid flights at all intruders. Observations of marked individuals revealed that males defend the same site for at least several days. Unlike head and abdominal temperatures, the thoracic temperature of males varied independently of ambient temperature, indicating active thermoregulation of the flight muscles. Differences between our results and those of Larsson (1989) are discussed.

Key Words: Reproduction, wasps, territoriality.

RESUMEN

Los machos de la avispa perforadora del suelo neotropical *Stictia heros* (Fabr.) mostró comportamiento territorial en áreas de nidos de hembras, presumiblemente para lograr acceso a hembras virgenes nuevamente emergidas. Los machos revolotearon arriba de puntos fijos en la playa y defendieron areas pequenas (1 m²) con vuelos rápidos a todos los intrusos. Observaciones de individuos marcados revelaron que los machos defienden el mismo sitio por varios dias. Contrario a las temperaturas abdominales y de la cabeza, la temperatura toracica de los machos variaba independientemente de la temperatura ambiental, indicando termoregulación activa de los músculos de vuelo. Se discuten algunas diferencias entre nuestros resultados y los de Larsson (1989).

Sand wasps typically occupy hot, sunny habitats where thermoregulatory constraints might be expected to influence their activity pattern and behavior. Indeed, several studies (e.g., Willmer 1985, Larsson 1990) have described the effects of high ambient temperature (T_{am}) on the nesting and provisioning behavior of female sand wasps. In comparison, little attention has been given to body temperature regulation and its effects on behavior in male sand wasps. In one of the few studies addressing this subject, O'Neill & O'Neill (1988) found males of the beewolf *Philanthus psyche* Dunning modified their territorial behavior in response to high T_{am} by changing perch locations from the ground to plants and shortening perching duration at any one site.

Recently, Larsson (1989) described alternative mating tactics among males of the sand wasp *Stictia heros* (Fabr.) and proposed that changes in ambient temperature affected the display of these tactics. Specifically, Larsson (1989) reported that between approximately 0700-1045 hours *S. heros* males patrolled emergence and nesting areas by making looping, circular flights over large areas (75 m²) of the beach. While displaying patrolling behavior, males were apparently not aggressive at all or only weakly so. At about 1045 hours, however, males were observed to switch from patrolling to territorial behavior. When adopting territorial behavior, males hovered at fixed positions above the beach and vigorously defended areas of about 25 m² against all intruders. Males remained territorial until the end of their daily flight period at approximately 1145 hours.

Larsson (1989) proposed that by switching behaviors males were able to reduce their thoracic heat load and thereby remain active despite rising ambient temperatures. As support for this suggestion, Larsson (1989) measured thoracic temperatures (T_{th}) of patrolling and territorial males and found that the average thoracic temperature excess ($T_{th} - T_{am}$) did not differ significantly between these groups even though territoriality was exhibited under higher T_{am} (33-34 °C) than patrolling (28-32 °C).

Here, we provide some additional behavioral observations for *S. heros* males as well as more complete data on body temperature regulation. As will be shown, the information presented here does not support the notion that thermoregulatory constraints influence the mating tactics exhibited by *S. heros* males.

MATERIALS AND METHODS

Data were collected between 30 January to 4 February, 1987, at Playa Naranjo and between 26 February to 4 March, 1987, at Playa Tamarindo in Provincia Guanacaste, Costa Rica. Larsson (1989) also used Playa Naranjo for his study, which was conducted from 3-8 January, 1989. At Naranjo, we established a small plot (4 m x 4 m) on the beach, marked all males found within this area, and made hourly censuses of the plot between 0600-1800 hours on two different days. Males were uniquely marked with a small dot of enamel paint on thorax; marks were applied directly to unanesthetized males held in an aerial net. Using a mercury thermometer, we also measured T_{am} at 30 cm above the sand (the height at which males typically fly) at hourly intervals on the two census days. At Tamarindo, we established three plots (each 5 m x 5 m) and on one day censused males hourly between 0600-1800 hours. T_{am} was measured as described above.

At Tamarindo, we also obtained temperature measurements of the thorax, abdomen (T_{ab}), and head (T_{he}) for individual males. Temperatures were measured with a 0.03 mm copper-constantan thermocouple threaded into a 30-gauge (0.3 mm diam) hypodermic needle with the thermocouple junction mounted in the orifice. Temperatures were read to within 0.1 °C using a Bailey Bat-12 thermocouple thermometer. Males were captured in flight with an aerial net and then quickly positioned within the netting (without touching the wasp), and the needle probe was inserted into the center of the thorax and abdomen (the order was alternated between successive males). Head temperature was

then recorded for about half of the individuals. All 3 temperatures were read within 8-10 s of capture. T_{am} was then measured at the point of capture.

RESULTS

The timing of male activity differed slightly between the two study sites. At Naranjo, 4-5 males were always present in the plot during censuses conducted between 0900-1300 hours on both census days, while no males were seen at any other time of the day. T_{am} increased from approximately 33 °C to 38 °C during the period of male activity, and the maximum T_{am} recorded was 39.5 at 1400 hours. Males were active somewhat earlier at Tamarindo. An average of 5 males were present per plot during censuses conducted between 0800-1100 hours (range: 3-6 males per plot per census), and males were absent during all other censuses. T_{am} increased from approximately 31 °C to 38 °C during the period of male activity and peaked at 40.1 °C at 1400 hours. At both sites, females were engaged in nest building and provisioning throughout the day.

Though active at slightly different times, males at both localities exhibited territorial behavior exclusively. Males in both populations hovered about 30 cm above a fixed point of the beach and defended small areas (about 1 m²) via rapid flights at all intruders. Males were in nearly continuous flight and landed infrequently for brief (2-5 s) intervals. Casual observations also revealed that males periodically left their territory (and the beach) for periods of 10-30 min; these territories remained vacant during the owner's absence. Upon being chased, intruders invariably left the immediate area, and no instances of escalated aggression, such as grappling, were observed. At least over periods of several days, territory holders appeared to be highly site-faithful. At Naranjo, we marked a total of 5 males in the study plot (all on the first day of observations), and all of them defended their original territory for the remainder of the study period (i.e., for the next 4 days).

Males of *S. heros* appeared to maintain relatively constant T_{th} at different T_{am} . Simple linear regression revealed that T_{th} varied independently of T_{am} ($t=0.7$; $P < 0.5$; Fig. 1) and ranged only between 39.6 °C and 44.0 °C (mean=41.6 °C). In contrast, both T_{ab} ($t=13.6$; $P < 0.0001$) and T_{he} ($t=5.9$; $P < 0.0001$) increased with increasing T_{am} (Fig. 1) and did so at rates similar to one another ($t=0.9$; $P < 0.5$) and to unity ($T_{ab} - t=0.1$; $P < 0.9$; $T_{he} - t=0.6$; $P < 0.9$). As these results imply, $T_{th}-T_{am}$ was inversely related to T_{am} ($t=5.6$; $P < 0.001$, while both $T_{ab}-T_{am}$ ($t=1.2$; $P < 0.20$) and $T_{he}-T_{am}$ ($t=0.6$; $P < 0.90$) varied independently of T_{am} .

One mating was observed during our study at Tamarindo at 0830 hours. A tight cluster of 10-15 males formed quickly on the sand, and intense fighting continued for approximately 10 s. The mating pair then broke free from the group and immediately flew inland away from the beach. Several males pursued the mating pair for at least 30-40 m at which point they were lost from view.

DISCUSSION

The behavior of male *S. heros* in the populations we studied was similar to that described for males of *S. signata* (L.) (Post 1981) and *S. vivida* (Handlirsch) (Evans 1966). In all of these species, males hover over small areas (1-7 m²) in female nesting areas and defend their territory by chasing, butting, or grappling with intruders. Moreover, males of these species appear to exhibit high site fidelity and may defend the same territory for days or weeks. Alternate, non-territorial mating tactics have not been reported for either *S. signata* or *S. vivida*. In contrast, *S. carolina* (Fabr.) males patrol large areas within nesting aggregations and do not exhibit aggressive behavior (Evans 1966, Evans & O'Neill 1988).

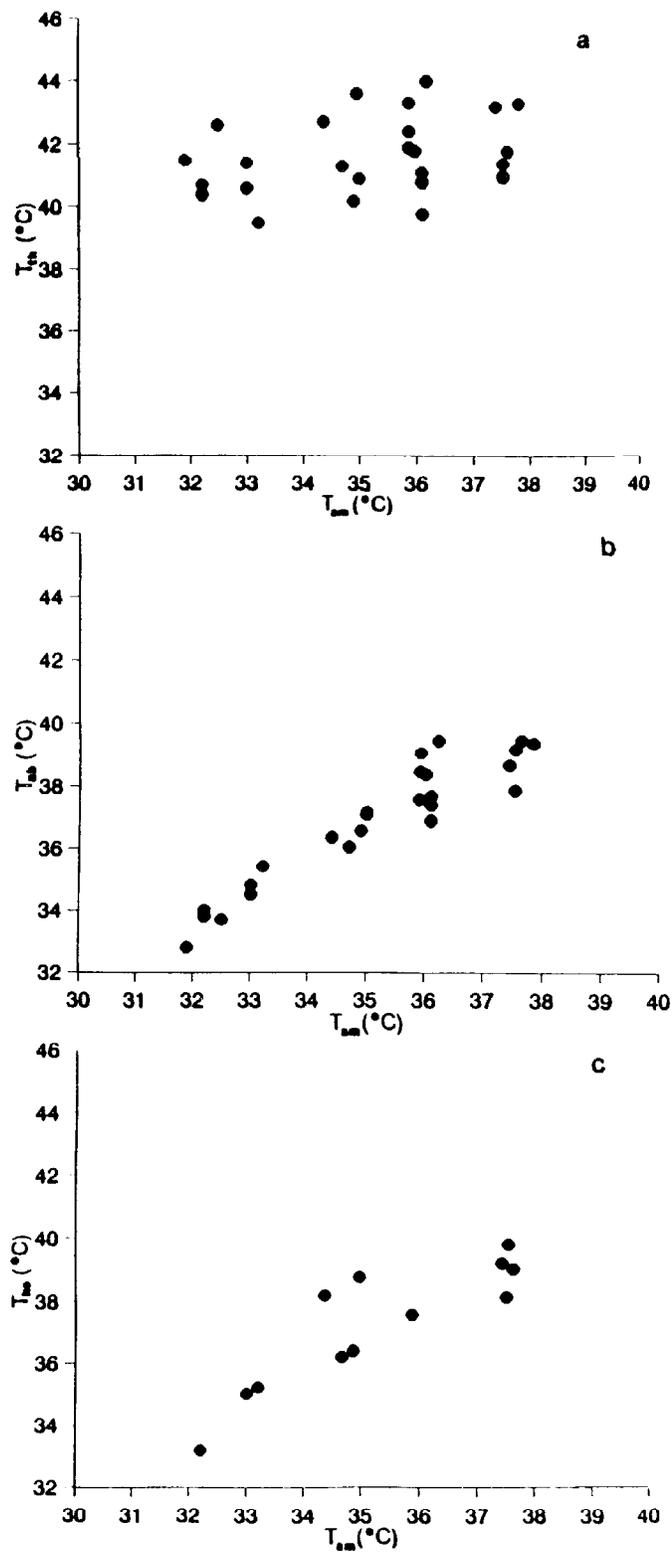


Fig. 1. Relationships between T_{am} and T_{th} (a), T_{ab} (b), and T_{he} (c) per male of *S. heros*. Regression equations: $T_{th} - Y = 38.1 + 0.10(X)$, $r^2 = 0.05$, $n = 25$; $T_{ab} - Y = 1.6 + 1.0(X)$, $r^2 = 0.89$, $n = 25$; $T_{he} - Y = 6.3 + 0.87(X)$, $r^2 = 0.59$, $n = 14$.

The observation by Larsson (1989) that *S. heros* males in his study population displayed both territorial and patrolling tactics indicates greater plasticity in male behavior than previously recognized for the genus. At present, however, it is not known what factors affect the expression of non-territorial behavior in *S. heros*. However, two results from our study call into question Larsson's (1989) proposal that thermoregulatory constraints were responsible for the behavioral shift he noted from patrolling in the early morning to territoriality near the end of the activity period. Most importantly, we observed male territoriality over a wide range of T_{am} , including early morning when thermoregulatory constraints were probably negligible. It thus appears unlikely that territoriality represents a temperature-specific mating tactic. In addition, unlike Larsson (1989), who found that T_{th} of males increased with increasing T_{am} , we observed that T_{th} was relatively constant over a wide range of T_{am} . Therefore, at least over the thermal range considered, our data do not indicate that *S. heros* males encountered serious difficulty in regulating T_{th} . Though T_{ab} and T_{he} both increased with increasing T_{am} , they were lower than T_{th} over all T_{am} and presumably did not constrain male behavior.

Alternatively, it is possible that male density affects the expression of non-territorial mating tactics, such as patrolling, in *S. heros*. Male density was approximately five times higher in the populations we studied than in Larsson's (1989) population (20 males per 100 m² vs. 4 males per 100 m², respectively). Perhaps when population size is low, males increase their searching areas to compensate for the low density of emerging females; in this situation, the defense of a small area may result in extremely low encounter rates with receptive females. Note this scenario differs from that described for other insects (e.g., Alexander 1961, Borgia 1980), where the expression of territorial behavior is inversely related to male density.

In conclusion, insufficient data for *Stictia* species exist to characterize intrapopulation variation in male mating behavior. Larsson's (1989) observations on *S. heros* are intriguing, since they reveal previously undetected plasticity in mate searching tactics. However, additional data are required to describe more completely the nature and occurrence of different mating tactics and to identify the factors underlying their expression.

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RESISTANCE OF SELECTED INTERSPECIFIC
LYCOPERSICON HYBRIDS TO GREENHOUSE WHITEFLY
(HOMOPTERA: ALEURODIDAE)

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ABSTRACT

Lycopersicon interspecific hybrids and species inbreds were examined for resistance to the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleurodidae), in four separate greenhouse studies. The two *L. pennellii* Correll interspecific hybrids (ICR.13 X LA1735 and ICR.13 X LA716) were the most toxic and/or repellent to adult whiteflies. ICR.13 X LA1735 exhibited the most adult and nymphal antibiosis and adult antixenosis, supported the lowest number of eggs and nymphs and developed the smallest second generation of adults. The *L. esculentum* Miller entry (ICR.13) was usually intermediate in all characteristics examined. All the entries in the study were able to support all the whitefly developmental stages which suggests selective pressure could possibly overcome a resistance mechanism based solely on adult antibiosis. This study provides evidence for adult and nymphal antibiosis mediated by trichome exudates and the possibility that a second nymphal antibiosis mechanism is present within the leaves of LA1735.

Key Words: Insecta, *Trialeurodes vaporariorum* spp., tomato.

RESUMEN

En cuatro estudios separados, se examinaron híbridos inter-específicos y líneas endogámicas de *Lycopersicon* para resistencia a la mosca blanca de los invernaderos, *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleurodidae). Dos híbridos inter-específicos de *L. pennellii* Correll (ICR.13 X LA1735 y ICR.13 X LA716) fueron los más tóxicos o más repelentes a los aleyrodidos adultos. ICR.13 x LA1735 mostró el máximo de antibiósis a los adultos y ninfas a antixenosis de los adultos, sostenía el mínimo número de huevos y ninfas, y desarrolló la más pequeña generación segunda de adultos. La partida *L. esculentum* Miller (ICR.13) usualmente fue intermedia en todas características examinadas. Todas las plantas en el estudio fueron capaces de sostener todos los estados de desarrollo de la mosca blanca, lo cual sugiere que presiones selectivas posib-