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Effects of male size on searching behaviors in the sun dance of *Bembix*

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EFFECTS OF MALE SIZE ON SEARCHING BEHAVIORS IN THE SUN DANCE OF *BEMBIX*

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ABSTRACT.—Males of solitary wasp species are faced with the task of locating potential mates, a task made more difficult by inconspicuous females and a landscape seemingly devoid of landmarks. Males may employ a variety of strategies to locate females. In this study, we test for variation among males within the sun dance of *Bembix.* We show that males of *Bembix americana spinolae* Lepeletier behave differently within the sun dance and that these differences can be predicted by the size of the male. We show that large males spend more time at "rest" and require a greater number of male–male contacts to be displaced from rest than small males. This difference in mate location strategy, however, appears to be density dependent, as large and small males in small aggregations exhibit no difference in the strategies they employ.

RESUMEN.—Los machos de la especie de avispa solitaria se enfrentan a la búsqueda de parejas potenciales, lo cual es difícil debido a que las hembras son apenas visibles y el paisaje parece estar desprovisto de puntos de referencia. Es posible que los machos utilicen una gran variedad de estrategias para encontrar hembras. En este estudio examinamos la variación entre la danza ritual del sol de los machos del género *Bembix.* Mostramos que los machos del género *Bembix americana spinolae* Lepeletier se comportan de manera diferente dentro del ritual de la danza del sol y que estas diferencias se pueden predecir según el tamaño del macho; encontramos que los machos de tamaño grande pasan más tiempo "en reposo" y necesitan una mayor cantidad de contacto macho-macho para ser desplazados del resto que los machos pequeños. Sin embargo, estas diferentes estrategias para hallar pareja aparentemente son dependientes de la densidad, ya que no se registraron diferencias entre las que emplean los machos grandes y los machos pequeños en los grupos pequeños.

The task of mate location among solitary- and aggregative-nesting Hymenoptera can be daunting. Potential mates may not advertise their location or their sexual receptivity (Evans 1970). In order to locate cryptic females, some males patrol resources that are intrinsically valuable to females or burrows from which females are emerging. In this latter example, males compete with one another for access to the emerging virgin females. This type of scramble competition is employed by species that vary greatly with respect to the distribution of females in the environment, though some argue that it evolves most commonly when females are broadly distributed (Thornhill and Alcock 1983).

Males in the genus *Bembix* Fabricius employ such a strategy; they form large aggregations in nesting areas that coincide with daily female emergences. This behavior is called the "sun dance" because it often occurs in the morning hours and because the males in the aggregation actively move and displace each other, giving the appearance of a highly choreographed dance (Rau and Rau 1918, Evans 1966, 1970, Alcock et al. 1978, Schöne and Tengö 1981). Males that engage in the sun dance often confine themselves to a small area within the aggregation (Tsuneki 1956) and may be attracted by female pheromones (Schöne and Tengö 1981), a phenomenon that has been documented in many other taxa (Jones 1930, Marikovskaya 1968, Lüps 1973, Alcock et al. 1976, Bergström and Tengö 1978). In *Bembix rostrata* Linnaeus, the male lands and "searches" briefly for a female by alternately touching the ground with the left and right antennae (Schöne and Tengö 1981). Time spent in contact with the ground, then, may have a positive relationship with reproductive success. When a female emerges, she is directly pursued and surrounded by many males that are presumably vying for position to mate with the female (personal observation 2008).

In other groups of solitary nesting Hymenoptera, it has been shown that male body

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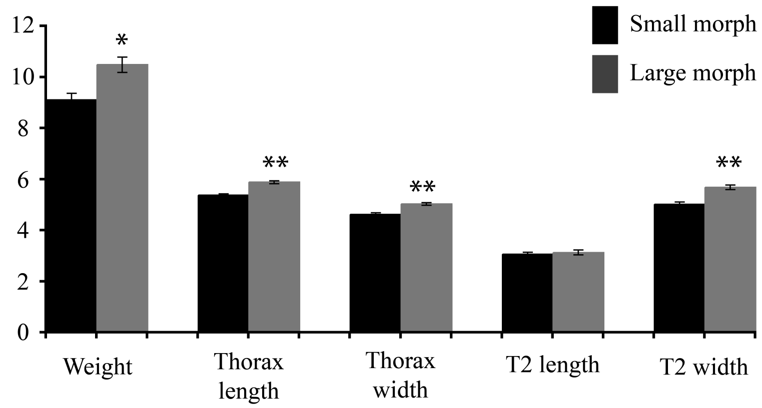

Fig. 1. Results of the morphometric analysis. Bins represent the mean measurement taken from the small (black) and large (gray) morph males. Error bars represent the standard error of the mean. The weight is expressed in centigrams, and the distance measures are expressed in millimeters. The number of asterisks above a bin represents the degree of significance. The lack of an asterisk denotes the lack of significance.

size may affect reproductive success, particularly for males that defend territories (O'Neill 1983, O'Neill and O'Neill 2003, 2007, 2009, O'Neill et al. 2010). The sun dance represents an interesting position among the mating systems employed by solitary Hymenoptera. While males that engage in the sun dance neither defend territories, nor form a traditional lek, the benefits derived from the sun dance are similar to both; namely, males that are the most fit acquire a proportionally larger percentage of the mating events (Bradbury 1985). Very little research on the sun dance has been done, so it is unclear if males of different sizes vary with respect to mate location strategy or reproductive success.

In connection with another experiment, we located 3 aggregations of male *Bembix americana spinolae* Lepeletier on the sand dunes of Ash Meadows National Wildlife Refuge. Ash Meadows is located in Nye County near Pahrump, Nevada, approximately 90 km west of Las Vegas. Two of these aggregations were large, consisting of more than 50 individuals, and the third was smaller, consisting of approximately 20 individuals. We noted that there were 2 distinct size classes of males, and we observed the behaviors performed by large and small males within each aggregation. We individually marked a subset of the males in the aggregations with acrylic paint, marking as many large males as small males, but these males did not return to the aggregation. We assume they landed on nearby vegetation to groom the paint off their bodies. Consequently, we visually divided the aggregation area into quarters and noted, for both large and small males, the time spent stationary and the number of male–male contacts required to displace a male from a stationary position.

Because we were not able to identify the males individually, and so that we could reduce the probability of counting the same individual multiple times, we collected data only from 5 small and 5 large wasps in a single quadrat. Once we had collected data from at most 5 wasps of both size classes, we moved either to a different quadrat of the same aggregation or to a different aggregation. We feel confident that this protocol minimized problems of pseudoreplication because previous evidence suggests that wasps remain localized within aggregations (Tsunecki 1956). We then collected small and large males for morphometric analyses. We performed a *t* test on the behavioral data to test for a significant difference between size morphs within the large and small aggregations in the time spent at rest and the number of male–male contacts required to displace a male from resting. We also performed a *t* test to test for differences between individuals we considered "large" and "small" in the following morphometrics: weight, distance between the anterior margin on the scutum to the posterior margin of the scutellum, width of the scutum just anterior to the tegulae, length of the second abdominal tergite (T2), and width of T2.

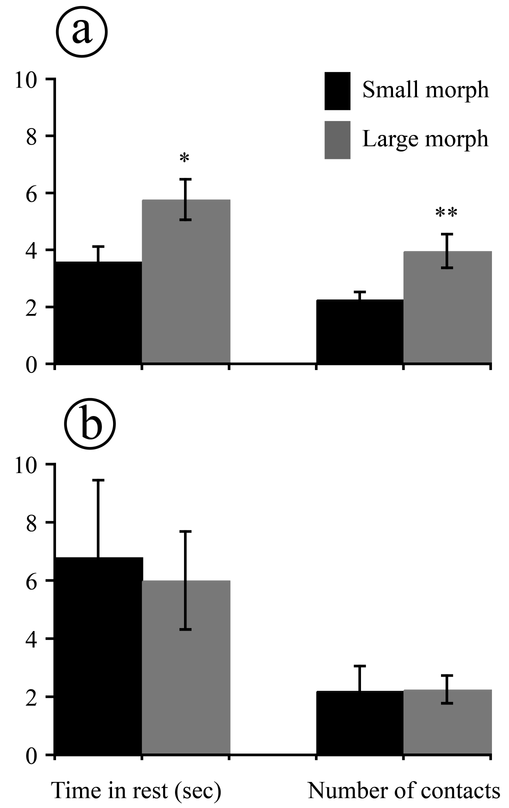

Fig. 2. Results of the behavioral analysis: **a,** comparison of the time spent at rest and the number of male–male contacts between small (black bins) and large (grey bins) males in large aggregations; **b,** same comparison for the small aggregation. Error bars represent the standard error of the mean. The number of asterisks above a bin represents the degree of significance. The lack of an asterisk denotes the lack of significance.

We found a significant difference between large and small males in weight ($t_{0.05(2),12}$ = –3.38, $P < 0.05$), mesosomal width ($t_{0.05(2),12}$ = –4.56, $P < 0.01$), mesosomal length ($t_{0.05(2),12}$ = –5.45, $P < 0.01$), and T2 width ($t_{0.05(2),12}$ = –5.06; Fig. 1), though there was no significant difference between male size morphs in the length of T2 ($t_{0.05(2),12}$ = –0.56, $P > 0.05$). We also found that large males in large aggregations spend significantly more time at rest ($|t|_{0.05(2),63}$ = –2.52, $P < 0.02$) and require more male–male contacts than small males to displace them from resting ($|t|_{0.05(2),63}$ = –2.94, $P < 0.005$; Fig. 2a). There does not, however, appear to be a difference between large and small males in small aggregations in the amount of time stationary and the number of male–male contacts required to displace a male($|t|_{0.05(2),7}$ = 0.77, $P > 0.05$; Fig. 2b).

These data strongly suggest that male size affects the tactics that males employ in the sun dance. Large males spend more time stationary and require more male–male contacts to displace them. Males land and remain stationary, presumably, to locate the burrows of emerging females (Schöne and Tengö 1981). The location of females may be revealed by pheromones released by an emerging female or by substrate-borne vibrations (Jones 1930, Marikovskaya 1968, Lüps 1973, Alcock et al. 1976, Bergström and Tengö 1978, Schöne and Tengö 1981). This longer stationary time exhibited by large males, then, will have a significant impact on their potential for reproductive success because more time may increase their probability of successfully mating.

Though our data strongly suggest that there is a significant difference in the size between males that spend relatively more or less time stationary, it is possible that male size in *B. americana* exists as a continuum or gradient of sizes, rather than as distinct classes. Our collections and observations, however, lead us to believe that this is not the case. Also, though we took measures to ensure that no pseudoreplication occurred within the aggregation, some wasps may have been counted more than once. We are confident, however, that our data set and statistical analysis are robust enough to not be affected by pseudoreplication, if it occurred.

The difference in tactics between males, however, is not found in small aggregations. We found no difference between the size classes in the amount of time spent stationary or the number of male–male contacts required to displace a male. This observation is not overly surprising because the size of male aggregations has been shown to impact the behaviors of individuals within the aggregation (Höglund et al. 1993, Höglund and Alatalo 1995, Weldon 2007). In some tephritid flies, for example, the size of the male aggregation affects the decision of individual males to release a pheromone and attract females (Weldon 2007). In other aggregations, the number of individuals is positively correlated to aggressive interactions between males (Höglund et al. 1993, reviewed in Höglund and Alatalo 1995). Our data, however, were collected from wasps within a single small aggregation. While these data suggest that the size of the male aggregation has a significant impact on the tactics that males employ during the dance, further work will be necessary to validate this claim.

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