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MALE MATE-LOCATING BEHAVIOR AND YEARLY POPULATION CYCLES IN THE SNOUT BUTTERFLY, *LIBYTHEANA BACHMANII* (LIBYTHEIDAE)

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ABSTRACT. This paper describes mating behavior and seasonal changes in population size in the snout butterfly, *Libytheana bachmanii.* At a central Arizona study site, we found a dramatic peak in the abundance of snout butterflies in late May and early June, with a smaller peak in the fall. Both peaks lasted several weeks and were separated by periods when few or no adult butterflies were found. Males are classic patrollers and search for females in and around the larval foodplant, desert hackberry (*Celtis pallida*). Courtship is like that of many other butterflies, with no distinctive displays by the male or female. We compare these results to those for the desert hackberry butterfly, *Asterocampa leilia*, which uses the same larval foodplant but has very different mate-locating tactics and, as some hypotheses predict, relatively stable and medium density populations from season to season.

Additional key words: desert hackberry, central Arizona, courtship.

The behavior of male insects at mate encounter sites varies along several axes. These include the time of day males visit sites, the duration of visits to a site, and whether males defend sites (Thornhill & Alcock 1983). Ultimate explanations for differences within and among species in these components of male behavior at encounter sites invoke ecological variables such as population density and encounter site size and distribution (Thornhill & Alcock 1983, Bradbury 1985). A special opportunity to study the ecological correlates and causes of mating systems arises when two or more species of similar size use the same encounter sites but differ in mate-locating tactics. In these situations, certain features of habitat and scale are naturally controlled, which permits a focus on differences in other factors such as population density that may have influenced the evolution of male mate-locating behavior.

In the upper Sonoran Desert of western North America, two butterfly species similar in size occupy the same locale and use the same larval food plant, desert hackberry (*Celtis pallida* Torrey; Ulmaceae). These butterflies appear to exhibit striking interspecific differences in male mate-locating behavior and in population dynamics. In one of the species, the desert hackberry butterfly, *Asterocampa leilia* (Edwards) (Nymphalidae), males are classic "perchers" (Scott 1974) that occupy and defend perch sites on or next to the larval food plant (Austin 1977, Rutowski & Gilchrist 1988, Rutowski et al. 1991). A male may occupy the same site for several mornings. In contrast, males of the other species, the snout butterfly, *Libytheana bachmanii* Strecker (Libytheidae) have been described as perchers by some (Scott 1986) and "patrollers," that conduct aerial searches within hackberry trees but do not occupy or defend perches, by others (Rutowski 1991).

Selection should favor males that patrol when the costs of site tenacity and defense outweigh the benefits (Brown & Orians 1970, Rutowski 1991). This should occur when population densities are extremely high or low. At high population densities the rate of interactions with intruders should place a high cost on site defense; at low population densities, the low rate of female arrival will yield low returns from site defense. Intraspecific switches from perching to patrolling have been related to increases (Alcock & O'Neill 1986, Wickman 1988) and decreases (Wickman & Wiklund 1983) in population density in other butterflies. The snout butterfly is notorious for undergoing large population explosions ("usually in late summer" Bailowitz & Brock 1991; "emigratory flights of millions of butterflies" Pyle 1981; Scott 1986), but the timing and duration of these events and population sizes between outbreaks have not been quantitatively documented. Populations of *A. leilia* are apparently subject to much less fluctuation (Rutowski et al., 1996).

To determine if an association exists between population characteristics and male behavior, we quantified population dynamics and features of the male and female behavior in *L. bachmanii*. Here we address the following questions: (1) what annual changes occur in the population size of this species; (2) what search tactics do males employ, and how do they differ from those of *A. leilia*; (3) what is the nature of courtship in this species; and (4) what is the mating history of individual females? Finally, we compare our profile of *L. bachmanii* with previous data on *A. leilia* and relate this information to hypotheses about the role of population density in the evolution of male behavior at mate encounter sites.

METHODS

Study site. We studied *L. bachmanii* at Round Valley in the Sycamore Creek flood plain, approximately 70 km NW of Phoenix, Arizona. The primary vegetation at this site includes shrubs and low trees, such as desert hackberry, mesquite (*Prosopis* spp.), catclaw (*Acacia greggii* Gray; Leguminosae), and paloverde (*Cercidium* spp.). The observations reported here were made from 1987 to 1995.

Census techniques. To assess yearly and daily changes in population size of *L. bachmanii*, we selected and mapped a 270 m census trail in the study site. The trail ran through a stand of hackberry trees and was used previously to census *A. leilia* populations (Rutowski et al., 1996). On each census, an observer walked the entire length of the route and recorded the location and behavior (perched or flying) of each *L. bachmanii* individual (males and females) seen on the census route. We tried to complete each census within 10 to 15 min to avoid counting moving individuals more than once; the cost of this approach was that we could not reliably distinguish males and females on the wing, so they were not scored separately. We censused the population in this way on sunny days every seven to 14 days during the flight season and once a month at other times, for a total of 40 days, from March 1993 to October 1994. On 35 of these days we ran four hourly censuses, from 0900–1200 h (MST). The other five days were during periods when no butterflies were found, so we ran only two or three censuses. At the end of each census, we measured the air temperature in the shade at 1 m above the ground.

Behavioral observations. Intrasexual and intersexual interactions were described from field observations. All interactions began when a male approached a conspecific. We recorded the durations of interactions from when an approaching male arrived within a few cm of the other individual until the interacting pair separated for the last time. Also, for a sample of perched males, we measured the height of each occupied perch. Observations and video records of field interactions between males and virgin females (reared from larvae collected in the field) of *L. bachmanii* were used to develop the description of courtship. To estimate mating frequencies of females, we dissected the females that had been collected at random and freeze killed during May, June, and July 1994. The abdomen of each was opened under insect Ringer's solution, and the number of spermatophores in the bursa copulatrix counted.

Tenure in hackberry trees. We attempted to determine if males behave differently in hackberry trees than they do in other trees. We selected a hackberry tree and a mesquite tree of similar size (about 3 m high and wide) that were representative of trees within the study site. An observer was stationed at each tree. At the same time, each observer

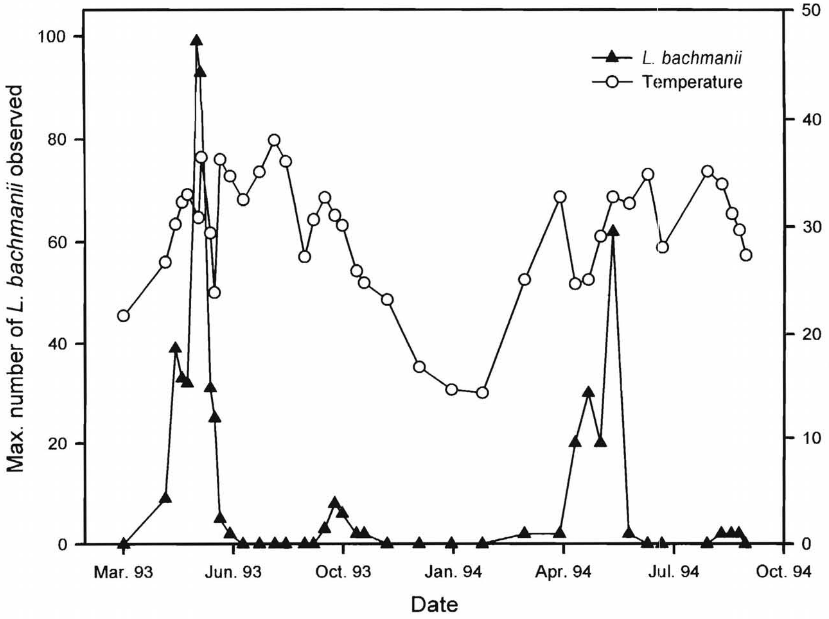

FIG. 1. Variation in the size of the *L. bachmanii* population and in the air temperature at 1 m with time of year. For each day on which we censused the population, the graph shows the maximum number of individuals observed on a single census and the temperature at the time of that census. *L. bachmanii* abundance is dependent on season but not on temperature (see text for details). This figure includes data from five days in which only two or three censuses were run and no butterflies were seen.

recorded the total time spent within the tree's perimeter for each male *L. bachmanii* that arrived at the tree. The data were collected on two sunny days in May 1986, using two different pairs of trees.

RESULTS

Population dynamics. The number of *L. bachmanii* seen along the census route on any given day fluctuated dramatically within each year (Fig. 1). On most days the maximum number of butterflies seen on any given census did not exceed 10 individuals; however, on three out of 40 census days we counted more than 60 individuals in at least one census. Flight seasons occurred at the study site twice each year: over six to eight weeks during May and June, and from four to six weeks during September and October. Peak population density was much greater during the spring flight season than in the fall. The average number of individuals observed on a day varied significantly with time of year (Kruskal Wallis test, n = 40 days, P = 0.006; Fig. 1). However, the average number seen on a day when the butterflies were active did not covary with air temperature at 1 m at noon on that day (Kruskal Wallis test, n = 35

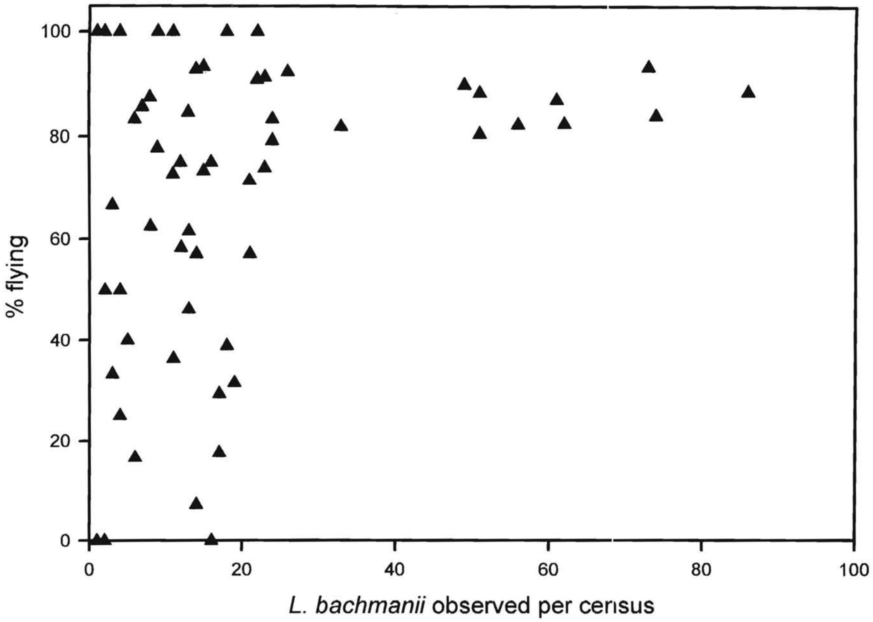

FIG. 2. The proportion of individuals seen in flight (rather than perched) as a function of population density (n = 1222). Butterflies that changed from flying to perching (or vice versa) while being censused not included.

days, P = 0.437). Although *L. bachmanii* are most abundant when ambient temperature is between 30 and 40°C, there were days on which these temperatures occurred but no butterflies were seen (Fig. 1).

Whether *L. bachmanii* were seen perched or flying during a census was related to the density of butterflies (Fig. 2). When we counted more than 20 butterflies along the census trail, at least 80% of them were flying. However, when counts were 20 or lower, the proportion of individuals in flight was variable, ranging from 0 to 100% of butterflies observed.

No consistent pattern of daily activity was found in the mornings (between 0900–1200 h). Time of day did not explain at all the number of adults seen on a census on days when the butterflies were active (ANOVA with time nested in date on log transformed counts during flight seasons, df = 75, P = 0.999). Moreover, we saw no consistent movement patterns that would lead us to describe these populations as migratory, as previous accounts have done (e.g., Pyle 1981).

Along the census route, snout butterflies were most commonly found near hackberry trees, their larval foodplant. When we divided the census route into 5 m segments and totaled butterfly sightings for each segment, we found that butterflies were not uniformly distributed along the trail (Fig. 3; $c^2 = 1034$, df = 53, $P < 0.0001$). Similarly, we found a non-

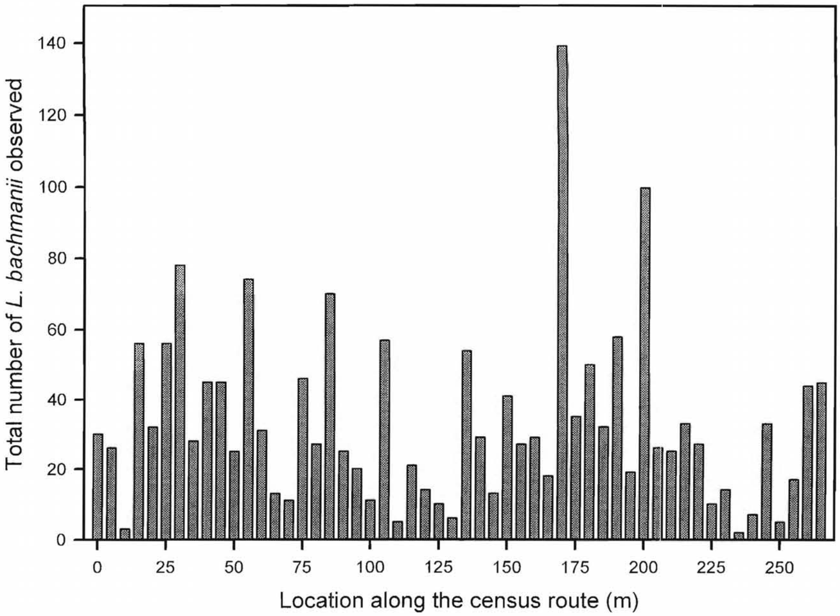

FIG. 3. Spatial distribution of *L. bachmanii* sightings (n = 1797) along the census route. The number observed on each 5 m segment is the total observed over 140 censuses on 35 days.

uniform distribution of hackberry trees along the trail ($c^2 = 36.9$, df = 53, $P < 0.05$). However, there was a significant, positive correlation between the number of *L. bachmanii* observed in each 5 m section of the census route and the number of hackberry trees in a section (Fig. 4; r = 0.56, df = 53, $P < 0.0001$).

Male searching behavior. Males were seen flying and perched in the study area, and flying males moved both within and among hackberry trees. Within hackberry trees, males moved slowly up and down close to branches and leaves. Perched butterflies were approached and inspected. Both flying and perching males approached and chased other butterflies (both conspecific and heterospecific) that flew nearby; however, at times two or three butterflies perched within a few centimeters of each other. Interactions with conspecific males in the spring flight period lasted an average of 14.6 ± 13.5 sec (median = 9.7 sec, range = 3.9–43 sec, n = 8). Males inspected heterospecifics for an average of 12.7 ± 10.3 sec (median = 7.3 sec, range = 2.8–36.2 sec, n = 16). The interaction durations were not significantly different (Mann-Whitney *U* test, $P > 0.9$).

Flying males spent significantly more time in hackberry trees than they did in mesquite (Fig. 5; Wilcoxon rank sum test, n = 22, P = 0.001).

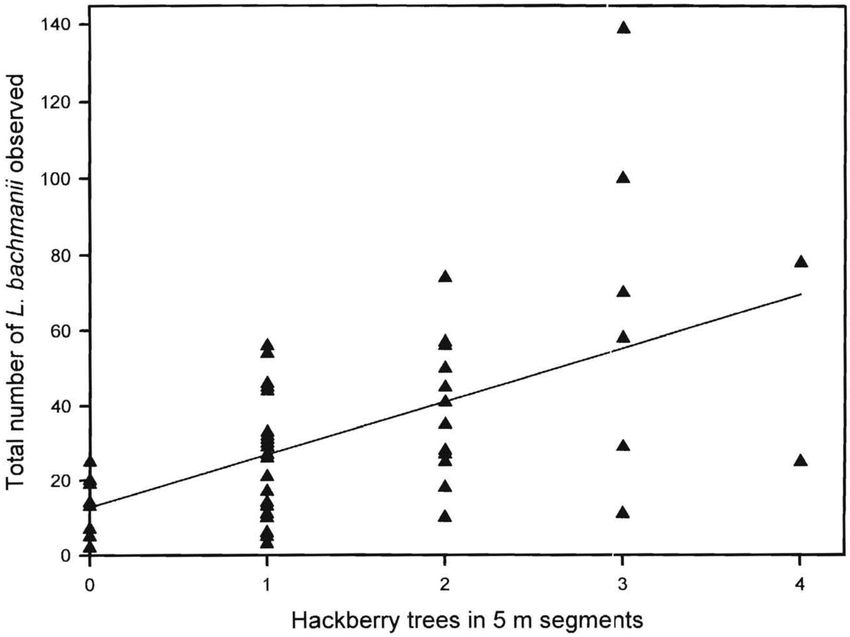

FIG. 4. The relationship between the number of hackberry trees and the number of *L. bachmanii* sightings in 5 m segments along the census route. There is a significant positive correlation between these variables (n = 1797, r = 0.56, df = 53, P < 0.0001).

Males moved through hackberry trees in an erratic, zigzag fashion. In contrast, their flight through mesquite trees was more direct, causing them to pass through the tree more quickly.

Males perched on exposed twigs and branches. Average perch height was 1.92 ± 0.31 m (median = 1.87 m, range = 1.5–2.5 m, n = 17) above the ground. The body of a perched male was oriented upwards with the wings closed or partially opened. The average time a male spent at a perch on a typical summer day was 77 ± 90.6 sec (range 3.4–430.3 sec, n = 55).

Courtship and mating behavior. Courtship leading to copulation began when a male approached a perched or flying female. A flying female was chased by a male until she alit on vegetation. A perched receptive female usually remained still with her wings folded as a male approached. The male then alit behind the female and moved alongside her with his head oriented in the same direction as hers. He then curled his abdomen toward the female, probing between her hindwings until he attained genital contact. After coupling, the male turned to face away from the female. During copulation, some females took flight, carrying the male with his wings closed, suspended head-down from her abdomen.

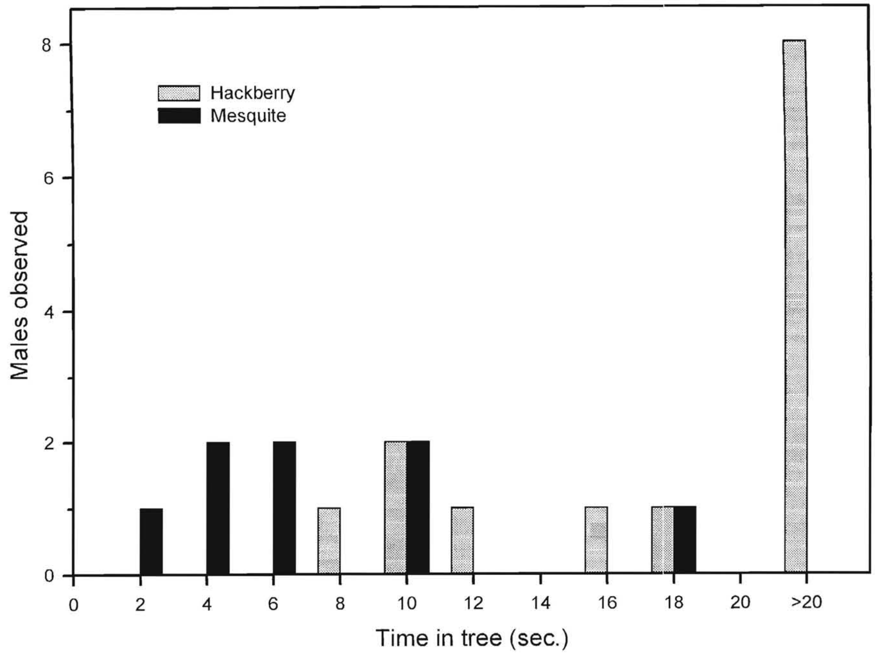

FIG. 5. Time spent by males in hackberry trees versus mesquite trees. See text for details.

Copulation ended when the pair uncoupled. Four pairs were found in copula, and the average time until they separated was 88.5 ± 40 min (range = 45–140 min, n = 4). During copulation the male passed a spermatophore to the female. The females collected for spermatophore counts were fresh to slightly worn in condition and carried an average of 1.28 ± 0.66 spermatophores (n = 28, range = 1–4 spermatophores). When females carried more than one spermatophore, one was roughly teardrop shaped, approximately twice as long as wide, and all others were partially or completely flattened and depleted. This suggests that matings do not occur in rapid succession. After copulation females flew about searching for oviposition sites. Eggs were laid singly, often on the end of sprigs of new hackberry growth.

Unsuccessful courtships lasted an average of 44.6 ± 79.7 sec (median = 42.3 sec, range = 23–78 sec, n = 6). In these interactions, flying females either did not alight, alit and fluttered their wings, or suddenly dropped toward the ground and alit. In the latter case, the male might search for the female, but he left after a brief time if he did not relocate her. Perched females may hinder males by spreading their wings and elevating their abdomens or by taking flight. On one occasion a male pursued a female in direct upward flight for about 5 m. The chase lasted for less than one minute, until one of the butterflies was captured by a cliff swallow (*Hirundo pyrrhonota* Vieillot).

DISCUSSION

The major results of this study are as follows. First, the *L. bachmanii* population that we studied in central Arizona displays an explosive increase in numbers twice a year, especially in the late spring. The reasons for these dramatic changes are not known. Apparently the snout butterflies diapause once or twice a year, but the stage in the life history at which this occurs or why it occurs at these times are not known. One possible answer is that population cycles are tied to the phenology of the desert hackberry. Hackberry trees produce new vegetation after the rainy periods that occur regularly each winter and mid to late summer. The new vegetation may foster the development of the larvae.

Second, both males and females are found primarily in or near the larval foodplant. Females are seeking oviposition sites; males are seeking females. Our observations show that males entering hackberry trees change their behavior from direct flight to a zigzag searching of the vegetation. We conclude that males are seeking both newly emerged virgin females and previously mated females. Newly-emerged females are likely to be common in hackberry trees because the larvae pupate on the larval foodplant (pers. obs.). In addition, we have in several instances seen a male mated with a newly emerged female (wings still flexible) next to a pupal exuvium on hackberry. Males are also probably looking for previously mated females who are ovipositing but are ready to mate again. Spermatophore counts show that females will mate more than once. Use of the larval foodplant as the mate encounter site has been reported for other butterflies (Lederhouse et al. 1992, Rutowski & Gilchrist 1988).

Third, at the larval foodplant, males use primarily a patrolling strategy to locate females. Figure 2 suggests the incidence of a territorial strategy at low population densities; however, several observations argue against this. Males always show low interest in other males and little site tenacity. In addition, we never saw any male-male contacts that led to the spiraling aggressive interactions described for some territorial species (e.g., Baker 1972). Finally, males and females are not distinguished in Fig. 2, and temperature, which could also play a role, is not controlled. Even if we ignore these confounding variables, most individuals at all population densities are on the wing.

Fourth, although the snout butterflies are a worldwide family of only nine species reported to have diverged from other butterfly lineages at least 35 million years ago (Emmel et al. 1992) and have unique palpal and wing morphologies, their courtship and mating behavior are very much typical of that reported generally for butterflies (Scott 1973, Silberglied 1978, Drummond 1984, Rutowski 1984).

Relationship between population density and male behavior at encounter sites. The documentation of the dramatic seasonal changes in population density in *L. bachmanii* provided here supports the hypothesis that population density is an important determinant of male tactics. Because population densities are usually extremely low or, for a brief period, extremely high, the costs of site tenacity and defense should outweigh the benefits. Patrolling has then evolved as the primary mate-locating tactic in this species.

The idea that population density is an important determinant of male behavior at encounter sites is further supported by comparing the results reported here for *L. bachmanii* with what is known of *Asterocampa leilia*, the desert hackberry butterfly. Males in this species also use desert hackberry as the mate encounter site. However, they occupy and vigorously defend perching sites on or next to hackberry trees where they sit and wait for females to fly by. In contrast to *L. bachmanii* and in support of the population density hypothesis, the population of *A. leilia* at the Round Valley site is relatively stable for a long period each year. On the same census route used in this study, we found an average of about 10 perching males from April to November (Rutowski et al., 1996). Compared with *L. bachmanii* their populations are at an intermediate level and relatively stable, which has, in our view, favored the evolution site tenacity and defense.

Meteorological variables have also been proposed to explain intra- and interspecific differences in whether males patrol or perch at encounter sites (Dennis 1982, Wickman 1985, 1988, Alcock 1994). However, in neither *L. bachmanii* (this study) nor *A. leilia* (Rutowski et al. 1994) have we seen any evidence that males switch from patrolling to perching or vice versa with changes in season, temperature, or time of day. Also, both species engage in their respective mate locating activities at the same time of the day. In summary, while this study implicates differences in population density to explain interspecific differences in male behavior, other nonmutually exclusive explanations such as temperature and predation will also need to be examined.

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