

Research article

Social interactions and behavioral context in a largely solitary bee, *Lasioglossum (Dialictus) figueresi* (Hymenoptera, Halictidae)

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Summary

Understanding the development of behavioral differences among group members is a key to understanding social evolution or its loss. Social sweat bees (Halictinae) show distinct behaviors related to social competition and cooperation, and the frequencies of these behaviors differ for different functional groups (workers, guards, queens). These behaviors occur in solitary halictine bees under artificial conditions in a circular arena involving pairs of interacting bees. Reproductively active bees were tested, as were reproductively inactive bees, both from different nests and the same nests within a nesting aggregation. Among reproductively active bees, the first bee to display aggressive behavior more frequently had larger ovaries, and the first bee to withdraw from a social encounter more frequently had smaller ovaries. Body size did not influence these outcomes. The first bee placed in the arena was more likely to adopt an aggressive posture when bees first met, and the second bee placed in the arena was more likely to withdraw. Among reproductively inactive bees, females paired with a bee taken from the same nest were less likely to be aggressive than a bee paired with one from a different nest, suggesting familiarity (possibly kinship) can modulate aggressive behavior.

Introduction

Social relationships develop from behavioral differences among group members (e.g., Allee, 1938; Rowell, 1991; Fogel, 1995). Familiar examples include castes of social insects (e.g., Ants: Bourke and Franks, 1995. Bees: Seeley, 1995; Schwarz et al., 1997; Duchateau, 1989. Wasps: Ross and Matthews, 1991). An understanding of how such differences evolve requires information on social interactions among solitary individuals or individuals within groups in which social roles are not well-differentiated (e.g., Sakagami and Maeta, 1987; West-Eberhard, 1987; Wcislo et al., 1988; Kukuk and Crozier, 1990). This paper reports on social encounters between individuals of a primarily solitary sweat bee, *Lasioglossum (Dialictus) figueresi* Wcislo (Hymenoptera, Halictidae), and assesses whether females have the capacity to express behavioral components similar to those used during social interactions among individuals of social species.

For comparisons, caste-related behavioral differences have been studied for several social sweat bees, which nest in an underground tunnel system. Social interactions are comprised of the following components (Batra, 1964; Brothers and Michener, 1974; Bell et al., 1974; Breed et al., 1978; Smith and Weller, 1989; Plateaux-Quénu, 1978; reviewed in Michener, 1990; Plateaux-Quénu, 1993a, b; Wcislo, 1997):

1. *Withdraw*. One bee is approached from the front by the other, and one (or both) turn(s) around and walk(s) away. Withdrawing bees are neutral or intolerant of social interactions.
2. *Aggression*. One or both bees adopt an aggressive posture, in which the metasoma (abdomen) is curled forward, giving the entire body a “C” shape with mandibles and sting pointed at the other bee. Aggressive bees are intolerant of social interactions.
3. *Passing*. One bee walks past the other in the tube, ventral surfaces together. Passing is a normal social behavior within social groups. Within a nest, workers are frequent passers, while queens rarely pass; guards sometimes pass but are most frequently passed at the nest entrance (see Brothers and Michener, 1974). Bees that pass are tolerant of social interactions.
4. *Backing and following*. Bees contact or nearly contact each other in a frontal encounter, and then one bee walks backward while the other follows it walking forward. Backing-following behavior is apparently related to ways by which queens control workers (see Michener, 1990). Bees which back and follow are tolerant of social interactions.

Based on studies of the social bee, *L. (D.) zephyrum*, each female in a colony can express the full repertoire of social behavior, but workers, guards and queens differ in the relative frequencies of these behaviors (e.g., Breed et al., 1978; Michener, 1990). Sweat bee social interactions can be observed under extremely artificial conditions in which two bees are placed in a plastic tube with the ends connected to form a circle (Breed et al., 1978). For social halictines, behavior under these conditions is not different from the behavior of females in laboratory nests (e.g., Brothers and Michener, 1974; Bell et al., 1974; Bell and Hawkins, 1974; pers. obs.).

The evolutionary precursors of the behavioral components involved in sweat bee social interactions are not known, although they are hypothetically derived from aggressive behavior in solitary ancestors (e.g., Michener, 1977; reviewed in Wcislo, in press). Available data are equivocal with respect to this hypothesis because solitary behavior can represent the ancestral condition or can be evolutionarily derived from a social ancestor in some lineages of Halictinae (see Eickwort et al., 1996; Wcislo, 1996; reviewed in Wcislo, 1997). Several morphological traits suggest that solitary behavior in *L. (D.) figueresi* may be secondarily derived (W. T. Wcislo, unpubl.).

Materials and methods

Female *L. (D.) figueresi* were collected from nests in aggregations in the mountains above San Antonio de Escazú, San José Province, Costa Rica. Details of the habitat and natural history are given in Weislo et al. (1993). Most ($\geq 80\%$) active nests contain a single female from December to March, while the remaining nests contain 2 or rarely 3 females. Adult females provision a number of cells with pollen and nectar from December to March. These females are termed *reproductively active* bees. In March they cease activity and eventually die. The immature offspring of these females develop and eclose as adults in late April and early May. Adult males and females co-exist within the natal nest throughout May, but they do not excavate and provision cells at this time. Females collected at this time are termed *reproductively inactive* bees.

Preliminary studies on reproductively active bees were made with bees collected from nests at "Near site" of Weislo et al. (1993) in January 1988. Reproductively active bees for this study were collected at an aggregation ("Up-hill site") approximately 200 m up-hill from "Near site" in January, 1995. Reproductively active bees were collected as they returned to their nests carrying pollen. Nests were excavated to insure that all active females were solitary; no bees from multi-female nests were used in this study. Reproductively inactive females were collected by excavating a nest and capturing the first female I encountered. One or two reproductively inactive females from each nest were collected from the Up-hill site in May 1996.

Bees were uniquely marked on the thoracic nota with a single dot of Testor's paint. Each member of a dyad was placed in a clean glass vial until a second bee was collected and marked. Bees were placed into a 20 cm length of clear polyethylene tubing (inner diameter = 8 mm), and the ends of the tubing were joined to form a circle. Bees were not simultaneously placed in the tube, and there was a time lag of about 1 min between placing the first and second bee in the tube. Each member of a dyad experienced a different effective environment: the first bee (hereafter "occupant") initially experienced an empty tube, while the second bee experienced an already occupied tube. I tested for occupancy effects by comparing which bee first displayed aggressive or withdrawal behavior.

Observations were made outdoors under natural illumination. Bees usually walked around the circle and encountered one another repeatedly, and social interactions were recorded for 10 minutes. At the end of the observations, bees were removed from the tube, placed in Kahle's preservative and later dissected to measure ovarian development and body size, using a dissecting microscope fitted with an ocular micrometer.

This study involved three comparisons: (1) a reproductively active bee from one nest was paired with a reproductively active bee from a second nest at the same aggregation; (2) a reproductively inactive bee was paired with another reproductively inactive bee from the same nest; and (3) a reproductively inactive bee was paired with another reproductively inactive bee from a different nest. Comparisons between (1) and (3) address the relationship between reproductive activity and agonistic behavior, while comparisons between (2) and (3) address the relationships between familiarity and agonistic behavior.

I scored behaviors previously described for several social or communal sweat bees: (1) *frontal encounter* – two bees meet face to face, within one body length; (2) *withdraw*; (3) *aggression*; (4) *passing*; and (5) *backing and following* (for definitions, see Introduction).

There were different levels of activity among trials, so counts of each behavioral component were standardized by dividing the number of observed behaviors by the number of frontal encounters during each trial. More than one behavioral component sometimes occurred during a single encounter (e.g., one or both bees could initially adopt an aggressive posture, but then withdraw or pass), so the frequencies do not sum to one. Statistical tests are indicated in the text, and were done using SYSTAT on a personal computer (Wilkinson, 1989).

Voucher specimens from the 1988 collections are in the Snow Entomological Museum, University of Kansas (Lawrence, Kansas), while those from the 1995 and 1996 collections are in the Dry Reference Collection of the Smithsonian Tropical Research Institute (Balboa, Republic of Panamá).

Results

Social interactions among solitary bees

Bees from each category interacted, although there was considerable variability in expression. Bees did not interact at all during 7 of 27 trials (26%) for reproductively active bees; 5 of 20 trials (25%) for reproductively inactive bees from different nests; or 4 of 18 trials (22%) for reproductively inactive bees from the same nests. These trials were excluded when calculating relative frequencies of behaviors or the proportion of trials in which a particular behavior occurred.

Reproductively active bees from different nests. Withdrawal and overt aggression occurred in each of 18 trials involving reproductively active bees from different nests. Both females were aggressive in 14 of the 18 trials in which aggression occurred. In 4 trials only one female was aggressive, and in one of these trials the aggressive individual backed and the other followed. Passing occurred in 60% of 20 trials.

Almost half (49%) of 127 frontal encounters ended in withdrawal, or in an aggressive posture by one or both bees (41%). Bees passed one another during 14% of the encounters, and backing with following occurred in 0.8% of frontal encounters.

Reproductively inactive from different nests. Withdrawal occurred during 93.8% of 15 trials, while overt aggression occurred in 43.8% of the trials. Both females were aggressive in 6 of the 7 trials in which aggression occurred, while only one female was aggressive in the other. Backing with following occurred during 3 trials (18.8%). One of the bees that followed was the passive bee during a trial in which aggression occurred. Passing occurred during 50% of the trials.

More than half (64%) of 75 frontal encounters ended in withdrawal for reproductively inactive bees from different nests, which was significantly different from reproductively active bees (Mann-Whitney $U = 192$; CHI-SQUARE approxima-

tion = 4.29, $df = 1$, $P = 0.038$). Slightly less than half (42%) of the encounters resulted in an aggressive posture by one or both bees, similar to reproductively active bees (Mann-Whitney $U = 155.5$; CHI-SQUARE approximation = 0.554, $df = 1$, $p = 0.457$). Bees passed one another during 13.4% of the encounters, but again this was not significantly different from the passing frequency observed for reproductively active bees (Mann-Whitney $U = 141.5$; CHI-SQUARE approximation = 0.058, $df = 1$, $P = 0.808$). Backing and following occurred more frequently among these inactive bees (3% of 75 encounters) than reproductively active bees, but the difference was not significant (Mann-Whitney $U = 155$; CHI-SQUARE approximation = 1.626, $df = 1$, $P = 0.202$).

Reproductively inactive bees from the same nests. Withdrawal occurred during 85.7% of 14 trials involving reproductively inactive bees from the same nest, while overt aggression occurred in 64.3% of the trials but was infrequent during any given trial. Both females were aggressive in 7 of the 9 trials in which aggression occurred. Backing with following occurred during 2 trials (14.2%). One of the bees which followed was the passive bee during a trial in which aggression occurred, but in the other case both bees displayed aggression. Passing occurred during 85.7% of the trials.

More than half (56%) of 66 frontal encounters ended in withdrawal, which was not different from the other classes of bees (inactive bees from different nests: Mann-Whitney $U = 83.5$, $P = 0.339$; active bees from different nest: Mann-Whitney $U = 159$, $P = 0.202$). Only 16% of these encounters resulted in an aggressive posture by one or both bees, which was significantly different from frequencies observed for reproductively active bees (Mann-Whitney $U = 26.5$; CHI-SQUARE approximation = 14.4, $df = 1$, $P < 0.0001$) or reproductively inactive bees from different nests (Mann-Whitney $U = 38.5$; CHI-SQUARE approximation = 8.61, $df = 1$, $P = 0.003$). Reproductively inactive bees from the same nests passed one another more frequently (21% of 66 frontal encounters) than reproductively active bees (Mann-Whitney $U = 184.5$, CHI-SQUARE approximation = 5.042, $df = 1$, $P = 0.025$), but differences were not significant for the comparison with reproductively inactive bees from different nests (Mann-Whitney $U = 135$, $P = 0.181$). Backing and following occurred in 2% of the encounters, similar to the frequencies observed for the other classes.

Social environment and behavior

Each member of a dyad experienced a different effective environment because one bee entered an empty tube, while the other entered an already occupied tube. These occupancy effects influenced the expression of social behavior.

Aggressive postures. For reproductively active bees, the occupant was significantly more likely to first behave aggressively (14 of 18 trials, $X^2 = 4.556$, $df = 1$, $P < 0.05$), but there were no such effects for reproductively inactive bees, regardless of whether they were from the same nests or different ones (same nests: 4 of 7 trials, $X^2 = 0.1429$, $df = 1$, $P > 0.5$; different nests: 4 of 9 trials, $X^2 = 0.111$, $df = 1$, $P > 0.5$).

Withdraw. The second introduced bee was significantly more likely to withdraw from the occupant for reproductively active bees (15 of 18 trials, $X^2 = 8$, $df = 1$, $P < 0.005$), but there was no significant difference for reproductively inactive bees from the same nest (9 of 12 trials, $X^2 = 3$, $df = 1$, $P > 0.05$) nor for reproductively inactive bees from different nests (10 of 15 trials, $X^2 = 1.67$, $df = 1$, $P > 0.1$).

Backing with following. Small sample sizes precluded any statistical tests because backing-following was observed only 6 times. For reproductively active bees the single individual that backed was the occupant. The backer was the occupant in 1 of 3 occurrences for reproductively inactive bees from different nests, and in 1 of 2 occurrences the backer was occupant for reproductively inactive bees from the same nests.

Body size, ovarian development and behavior

The lengths of female *L. (D.) figueresi* forewings' range from 6.4–6.8 mm; the size distribution is unimodal, and there are no significant seasonal size differences (see Wcislo et al., 1993). In this study the first bee to adopt an aggressive posture was not more frequently the larger bee in each pair (one-tailed sign test, $T = 20$, $P > 0.05$, $N = 45$ pairs), nor was the first bee to withdraw more frequently the smaller bee in each pair (one-tailed sign test, $T = 27$, $P > 0.05$, $N = 45$ pairs). There was no significant correlation between body size (forewing length) and ovarian width ($r = 0.31$, $N = 39$ bees, using only reproductively active bees).

Among pairs of reproductively active bees the first bee to adopt an aggressive posture more frequently had larger ovaries (sign test, $T = 29$, $P < 0.05$, $N = 18$ pairs), while the first bee to withdraw more frequently had smaller ovaries (sign test, $T = 31$, $P < 0.05$, $N = 18$ pairs).

Discussion

This study shows that solitary bees have the perceptual and motor systems needed to engage in context-dependent social interactions. An ability by solitary animals to behave appropriately in different contexts may be evolutionarily co-opted and elaborated to form the perceptual systems used to assess social status and kinship in social animals (Box and Fragarzy, 1986; Wcislo, 1992 a, b). This conclusion may be premature for this study, however, because several morphological traits suggest that solitary behavior of *L. (D.) figueresi* may be secondarily derived (W.T. Wcislo, unpubl.), as known for some other halictines (e.g., Richards, 1994; reviewed in Wcislo, 1997). Moreover, a low percentage of females live in two- or three-female groups, so the social behaviors observed here may be used when females live in groups.

One might challenge the experimental design I used, by noting that if two solitary bees walk around a circular arena, then they must do something when they meet (e.g., pass, turn around and retreat, or fight); observations of bees actually doing something does not necessarily mean that they express social behaviors or

precursors of social behavior. This criticism is unwarranted, however, for several reasons. First, bees are not compelled to walk around the arena, so it is not necessarily true that they must encounter one another and do something; they can do nothing, or be consistently aggressive. If interacting females are behaving at random, then the different behaviors should, on average, occur with equal frequency, but they do not. As noted in the Introduction, social roles in halictines are based on relative frequencies of behaviors, and this study showed some consistent differences among classes of females.

Social animals create parts of their own environment, and thus context is always important in understanding their behavior (see Wcislo, 1989; Pereira, 1995; Odling-Smee, 1996). Social relationships in halictines can be modulated by relative size, age, and genealogical relatedness (e.g., Michener and Smith, 1987; Smith, 1987, 1988; Kukuk and May, 1988). For example, the oldest bee in experimental colonies of *L. (Evyllaetus) albipes* tends to be the dominant reproductive (Plateaux-Quénu, 1991). Such observations are conventionally interpreted as an age-effect for caste determination (e.g., Michener, 1990). The oldest bee is, however, the first adult occupant, so nest ownership may be more important than age *per se*. For reproductively active *L. (D.) figueresi*, the first bee placed in a tube was significantly more likely to adopt an aggressive posture, while the second bee placed in the nest was more likely to withdraw from a social encounter, showing the importance of prior residency in determining the outcome of social competition (e.g., Beaugrand et al., 1996; Eshel and Sansone, 1995).

Among reproductively active *L. (D.) figueresi* bees, the bee with the larger ovaries more frequently was first to adopt an aggressive posture, while the bee with smaller ovaries more frequently was the first to withdraw. The reproductively active bees in this study all had relatively developed ovaries, while reproductively inactive bees had undeveloped ovaries (see Wcislo et al., 1993). Overall, reproductively active bees did not have a significantly greater frequency of aggressive postures than did reproductively inactive bees, suggesting that there is not a simple and direct relationship between ovarian development and aggressive behavior.

McConnel-Garner and Kukuk (1997) showed that aggressive behavior in solitary *L. (Ctenonomia)* and *L. (Chilalictus)* (Halictidae) was not associated with ovarian width nor body size. In contrast, laboratory studies showed that the outcomes of agonistic encounters between paired gynes of both *L. (E.) malachurum* and *L. (E.) pauxillum* sweat bees are influenced by size differences between the two bees, with larger bees, on average, being more aggressive (Smith and Weller, 1989). No data were obtained on ovarian development for these two *L. (Evyllaetus)* species.

A *L. (D.) figueresi* bee paired with a conspecific from a different nest was significantly more likely to adopt an aggressive posture than a bee paired with an individual from its nest. This finding suggests that solitary *L. (D.) figueresi* females recognize related or familiar individuals and appropriately modify their behavior. Similar capabilities occur in social congeners (e.g., Michener and Smith, 1987), a communal *L. (Chilalictus)* (Halictidae) (Kukuk, 1992), or a solitary wasp, *Sphecius* (Sphecidae) (Pfennig and Reeve, 1989).

Approximately 50% of all encounters between *L. (D.) figueresi* bees ended when one or both bees withdrew without further interactions. Reproductively active bees were less likely to withdraw than were reproductively inactive bees from

different nests, providing evidence for a positive association between reproductive behavior and tolerance of social interactions. Other solitary halictines, in contrast, are tolerant of same-sex conspecifics only when they are reproductively inactive; after reproductive activity begins, one bee dominates and evicts the others (e.g., Batra, 1968; reviewed in Wcislo, 1997).

L. (D.) figueresi females can express behaviors apparently similar to those used for cooperative and competitive social interactions within social groups, although some behaviors occurred at low frequencies (e.g., backing with following). Solitary *L. (Ctenonomia)* sp. (Halictidae) and *L. (Chilalictus) platycephalum* (Halictidae) females also show components of social behavior during experimental encounters (McConnell-Garner and Kukuk, 1997). Certain behaviors (e.g., an aggressive posture) have direct precursors in solitary bees since they occur in contexts such as defending the nest against conspecific intruders (pers. obs.). For other behaviors, it is more difficult to identify potential precursors because we do not know exactly what evolves during social evolution (see discussion in Wenzel, 1992). With “back-follow,” for example the motor patterns for the behavior (i.e., walking backward, or walking forward) occur in solitary bees (pers. obs.). The social *response* of a dominant individual to withdraw backwards coupled with the advance of a subordinate, however, is presumably novel, since it is contrary to usual dominant-subordinate interactions: dominants usually advance while subordinates usually retreat (e.g., West-Eberhard, 1979).

The latent presence of social capabilities in solitary bees may help explain the frequent and apparently rapid evolution of eusocial behavior (*sensu* Michener, 1974), or its loss, within Halictinae, without intervening steps of intermediate kinds of societies (Michener, 1990). They invite further study of the variation for selection for the increasingly complex behaviors that characterize eusocial animals.

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