

Trophallaxis in a communal halictine bee *Lasioglossum (Chilalictus) erythrurum*

(sociality/recognition/cooperation)

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ABSTRACT Food exchange by means of oral trophallaxis was confirmed for a communal halictine bee *Lasioglossum (Chilalictus) erythrurum*. These results demonstrate an independent evolution of trophallaxis in bees. The occurrence of trophallaxis in a communal species questions the role of trophallaxis in the evolution of sociality. Neutral arena encounters between one fed and one unfed female indicate that food exchange is not associated with familiarity. Donor females fed nestmates and nonnestmates in the same proportion, even when nonnestmates were from a separate nest aggregation located 7 km away. Such universal acceptance is expected if positive fitness benefits accrue from nearly all interactions with conspecifics in nature.

Trophallaxis among adults is a hallmark of highly social Apidae (1) and is known to occur commonly in the social anthophorids (2–8). Despite thousands of hours spent observing primitively eusocial halictine bees, principally *Lasioglossum (Dialictus) zephyrum*, trophallaxis has not been reported (9).

In contrast to *L. zephyrum*, a primitively eusocial species with an overlap of generations and reproductive castes, *Lasioglossum (Chilalictus) erythrurum* is apparently communal, as are all group-living Australian halictids (10). All adult females jointly occupying a nest (up to 40) have well developed ovaries and are mated (10–13). This suggests that all colony members mutually benefit from group living and that there is no reproductive division of labor in the colony.

Apparent trophallaxis was recently observed in the communal species *L. erythrurum* between females (13) and between females and macrocephalic males (14). The experiments reported here confirm that food transfer does occur between females. Moreover, familiarity does not play a role in food exchange between pairs of females obtained from nests during the late brood rearing and preoverwintering phases of the colony cycle.

MATERIALS AND METHODS

Colonies of *L. erythrurum* were excavated from two nest aggregations about 7 km apart in the Cabboboonee State Forest of southwestern Victoria, Australia, by using the methods of Abrams and Eickwort (15), in February and March 1989. At this time, nests contained maturing brood and adults. In February, nests from one aggregation also contained young brood, eggs, and fresh provision masses. Adult females were placed along with their nestmates in glass vials, chilled, and transported to the laboratory in Sydney. They were then placed in small petri dishes with their nestmates, supplied with moist absorbent tissue, and fed a mixture of

50% honey and water. The females in petri dishes clustered near one another under or within the tissue.

In addition, four observation nests, as described by Michener and Brothers (16), were established. Each contained adult females from each of two or three separate field nests, resulting in colonies of 10–12 adult females, individually marked with colored enamel paint. Their interactions were observed for 5 days after placement in nests. All head-to-head encounters between pairs of females were noted as were instances of apparent trophallaxis between females. Trophallaxis was distinguished from other head-to-head encounters by extension of the recipient bee's mouth parts and the placement of her glossa behind and below the closed mandibles of the donor female for 10 sec or longer.

The occurrence of food exchange was confirmed by using neutral-arena encounters in which a pair of females, one fed and one unfed, were placed simultaneously in a "circle tube" (17) consisting of a 15-cm length of plastic tubing formed into a circle by joining the ends together. Pairs of females were from either (i) the same field nest, (ii) different field nests but the same nest aggregation, or (iii) different nest aggregations. Each field colony was divided into two groups and held in two separate petri dishes for 48 hr. One group was fed honey-water dyed with red food coloring, and the other group was not fed. All females were marked according to colony and group with quick-drying enamel paint in a code unknown to the observer, so that all experiments could be conducted blind.

Females were allowed to interact within the circle tubes for 20 min, removed, placed on a piece of clean, white filter paper, and subjected to gentle pressure on the abdomen causing regurgitation of crop contents. A small pink dot indicated the presence of dyed honey-water in a female's crop. Three separate experiments were done for a total of 150 encounters. No female was used more than once.

χ^2 tests for independence were used to evaluate the null hypothesis that trophallaxis was equally frequent between nestmates and nonnestmates. The power of the tests used was also calculated (18).

RESULTS

To solicit feeding, an unfed female drummed with both her antennae and front legs on the head of a fed female and extended her proboscis. The tip of the solicitor's proboscis was placed directly behind the folded mandibles of the upright donor female.

A total of 373 head-to-head encounters occurred in laboratory nests (see Table 1). Of 14 instances of apparent trophallaxis, only a single case occurred between females that were nestmates in the field. This is significantly fewer

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Table 1. Trophallaxis between pairs of female *L. (Chilalictus) erythrurum* in four laboratory observation nests

| | Source of female | |
|---------------------|------------------|----------------|
| | Same nest | Different nest |
| Encounters | 156 | 217 |
| Trophallaxis events | 1 | 13* |

Each laboratory colony was made up of females from either two or three separate field colonies. Observations occurred during the first 5 days after females were introduced into laboratory nests. All head-to-head encounters between two females were noted, as were all apparent trophallaxis events.

* $\chi^2 = 7.057$, $df = 1$, $P < 0.01$.

than the expected based on the numbers of encounters observed ($\chi^2 = 7.057$, $df = 1$, $P < 0.01$).

Of 150 total encounters in circle tubes, 33 resulted in food transfer. Results from the third (and largest) experiment are shown in Table 2. There are no significant differences between the frequency of food transfer based on nest of origin for the paired females. Moreover, the power of this test, 0.97, indicates that the probability of a type II error (accepting a false null hypothesis) is 0.03 (17). The first experiment consisted of 35 encounters (17 between nestmates and 18 between nonnestmates from the same aggregation) and resulted in twelve exchanges; three to nestmates and nine to nonnestmates leading to a nonsignificant χ^2 value of 1.12 ($df = 1$). The second experiment involved a total of 48 encounters (26 between individuals from the same nest and 22 between individuals from different nest aggregations) and resulted in a total of five food exchanges, two between nestmates and three between nonnestmates, also resulting in a nonsignificant χ^2 value.

DISCUSSION

These results elucidate an independent origin of trophallaxis in bees, in the Halictidae, whereas previously it was known only for the Apidae and Anthophoridae.

Trophallaxis has been observed in highly social species, particularly in the Apidae, where it plays an important role in communication and colony integration (1, 19). In the large carpenter bees it may also serve an important nutritional function, as teneral females are fed considerable amounts of pollen and nectar (6); this situation may be true for allodapine bees as well (5). In the large carpenter bees, trophallaxis also may be forced. A female entering a nest may be obliged to share nectar in order to move past another female in the tube-shaped nest, but food sharing also occurs voluntarily (6). In addition, trophallaxis occurs in several contexts as a means of appeasement when an attacked or threatened individual offers food to her attacker. This behavior occurs on rare occasions in the bumblebees (4) and has even been seen between species in ants (20). The role of trophallaxis in *L. erythrurum* is not yet known.

Table 2. Results of encounters between pairs of female *L. (Chilalictus) erythrurum*

| Source | Trophallaxis | No trophallaxis | Total |
|-----------------------|--------------|-----------------|-------|
| Same nest | 3 | 17 | 20 |
| Different nest | | | |
| same aggregation | 11 | 16 | 27 |
| Different aggregation | 5 | 15 | 20 |
| Total* | 19 | 48 | 67 |

Pairs were made up of females from the same field nest, from different field nests found in the same nest aggregation, or from different nest aggregations.

* $\chi^2 = 3.87$, $df = 2$, not significant. Power = 0.97, $b = 0.03$ (18).

Hunt (21) argues that the flow of nourishment, particularly proteins, should be considered an important extrinsic factor (sensu Evans [22]) requisite to hymenopteran social evolution. However, the occurrence of trophallaxis in a communal halictine and its absence in related eusocial species (9) clearly indicate that trophallaxis is neither necessary nor sufficient for evolution of eusociality in the Halictidae.

L. erythrurum females do not preferentially feed familiar conspecifics—i.e., nestmates. This fact does not necessarily imply that these females are unable to recognize familiar conspecifics. The lack of a preferential response could be from an inability to recognize familiar individuals or from an absence of preferential treatment for recognized, familiar individuals. Either mechanism would result in universal rejection or (as in this case) universal acceptance.

Reeve (23) suggests that stable, universal acceptance of all conspecifics will evolve if the rate of interactions with "desirable" conspecifics (those that confer fitness benefits) greatly exceeds the rate of interactions with "undesirable" conspecifics. Assume, for the moment, that *L. erythrurum* nestmates are related and that cooperation is selected for through kin selection. If females encountered nonnestmates only rarely, then positive fitness benefits would accrue in most interactions between conspecifics, and universal acceptance might occur. Because nests occur in aggregations, however, females are likely to encounter nonnestmates due to drifting of females from one nest to another. Such movement between nests has been demonstrated in another communal halictine bee, *Agapostemon virescens* (24).

Conversely, universal acceptance would evolve if fitness benefits were positively associated with colony size during the late brood rearing and overwintering phases of the annual colony cycle because all conspecifics would be "desirable" even when they were not relatives. This hypothesis suggests that universal acceptance of conspecifics in *L. erythrurum* is due to positive fitness benefits associated with group living. Additional information concerning nest fidelity and intracolony relatedness is needed to distinguish between these alternatives with more certainty. Moreover, additional behavioral data for *L. erythrurum* must be obtained throughout the year to elucidate any changes in acceptance thresholds that are correlated with colony cycle.

Nevertheless, the communal social structure of *L. erythrurum* clearly involves a high level of cooperative interaction among conspecifics. Given that in cooperative groups, a "cheater" may have an advantage over cooperative individuals (25, 26), food sharing may provide a useful tool for the study of mechanisms involved in "cheater" avoidance.

Note Added in Proof. Recent reassessment of the species identification indicates that while all individuals used in this study are of the same species, they could be either *Lasioglossum (Chilalictus) erythrurum* or *L. (C.) hemichalceum* (K. Walker, personal communication). Voucher specimens are housed in the Museum of Victoria, 71 Victoria Crescent, Abbotsford, Victoria 3067, Australia.

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