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Research article

Social and ecological contexts of trophallaxis in facultatively social sweat bees, *Megalopta genalis* and *M. ecuadoria* (Hymenoptera, Halictidae)

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Abstract. Exchange of liquid food among adults (trophallaxis) is documented for the first time in New World sweat bees (Halictinae). *Megalopta genalis* and *M. ecuadoria* are facultatively social, and in social groups foragers regularly give food to the oldest resident female bee, which dominates social interactions. In turn, the oldest resident sometimes re-distributes this food, and shares it with younger foragers. Food is sometimes offered freely, but often the dominant bee exhibits escalating aggressive behavior until she is fed, whereupon she immediately ceases to be aggressive. The occurrence of trophallaxis in a species with mass-provisioned larvae provides an opportunity to examine the ritualization of social behavior. Trophallaxis also increases survivorship of males and females by almost 50 % under experimental conditions, suggesting the behavior is also important in ecological contexts.

Keywords: Trophallaxis, ritualization, sociality, *Megalopta,* Halictidae.

Introduction

Food exchange acts as a social bond and plays a role in developmental regulation in many social insects [e.g., termites (Isoptera), ants (Formicidae)] (e.g., Wheeler, 1911, 1928; Raboud, 1916; Hölldobler, 1985; Hölldobler and Wilson, 1990; Melo and Campos, 1993; Hunt and Nalepa, 1994; Anderson and McShea, 2001; see Sleigh, 2002; for a history of ideas relating trophallaxis to the origins of sociality). Among bees food transfer among adults is largely restricted to the family Apidae (*sensu* Michener, 2000), and its social functions are especially conspicuous in corbiculate species with relatively large colonies [e.g., honeybees (Apini) and stingless bees (Meliponini)] (Moritz, 1994; Sommeijer and Bruijn, 1994; Seeley, 1995; Crailsheim, 1998). In apid bees with less differentiated societies (Allodapini, Xylocopini, Ceratinini), trophallaxis is often associated with extended maternal care: the mother continues to feed her adult young before they disperse, or until one of them inherits the nest (see Velthuis, 1987; Michener, 1990b; Kukuk, 1994; Hogendoorn and Velthuis, 1995; Schwarz et al., 1998).

Social sweat bees (Halictinae) are an important contrast to these other taxa because there is no evidence for trophallaxis between adults and immatures (Michener, 1990a). Furthermore, trophallaxis between adults is extremely rare in this taxon, and to date is known only for the communal *Lasioglossum hemichalceum* (Cockerell) (Halictini), which lack division of labor, and females share food without evident discrimination and without aggression (Kukuk and Crozier, 1990; McConnell-Garner and Kukuk, 1997). Here we present data on an independent evolution of trophallaxis in facultatively social sweat bees, *Megalopta* (Augochlorini). We also examine how trophallaxis influences longevity under experimental conditions for both males and females. The Discussion addresses the evolutionary origins of adult-adult trophallaxis as a mechanism for regulating aggression, and also considers how food-exchange behavior may enhance survivorship where inclement weather may prevent foraging for extended periods.

Synopsis of Megalopta *biology*

Megalopta genalis Meade-Waldo and *Megalopta ecuadoria* Friese share general features of their natural history. Bees construct tunnels with lateral brood cells in dead, broken tree branches, vines and lianas. Nests are initiated at the start of the dry season (~mid-December), usually by a solitary, mated female; ~25–30% of nests were co-founded (Wcislo et al., 2004). We do not know where or when mating occurs. In central Panama foraging occurs throughout the dry season (December–May) and most of the wet season until September; most bees are inactive during October and November.

Females are facultatively social, such that some live as solitary nesters while others live within small social groups. Some nests remain solitary while ~25–50% of nests contain from 2–11 females, varying both among years and within seasons (Smith et al., 2003; Wcislo et al., 2004). Social dominance relations are resolved via behavioral interactions among adults (Arneson and Wcislo, 2003), and dominant bees tend to be larger with well-developed ovaries (Smith et al., submitted). Bees forage at night for approximately 70 min after sunset and again for the same duration before dawn, visiting both night- and day-blooming flowers for nectar and pollen (Wcislo et al., 2004; Kelber et al., in press). Pollen and nectar are mixed to form a dough-like mass in a cell; a female deposits an egg on the mass, and the cell is then closed. This cycle repeated itself. Individual nests in nature persist for up to 10 months, but 50–60% of all nests fail within 5 weeks of being founded (Smith et al., 2003; Wcislo et al., 2004).

Materials and methods

Social behavior

Social interactions were studied in the Barro Colorado Nature Monument (BCNM), Panamá Province, Republic of Panamá, between January–September, 2001, using artificial observation nests. Behavioral observations were made using 8 observation nests of *M. genalis* located within the forest on Barro Colorado Island (BCI); qualitative details were obtained for 3 observation nests of *M. ecuadoria.* Observation nests consisted of a piece of balsa wood (~15 × 20 cm) with an artificial tunnel, sandwiched between two panes of glass or transparent acrylic that were covered with a ~7 mm thick piece of styrofoam, and held together with clips; a section of styrofoam could be removed for observations. To obtain bees for the observation nests we collected natural nests in the early to mid-dry season (January–February) when nests were likely to have some mature brood. Nests were transported to the laboratory where they were opened, and we removed sealed, intact brood cells. We transferred one or two cells to each observation nest by placing each cell into a separate cavity that we excavated adjacent to the nest tunnel such that the cell entrance faced the tunnel. These observation nests were then placed in stands in the forest ~1 m off the ground, and females were allowed to emerge naturally. The base of the stands were covered with sticky Tanglefoot® to prevent ants from attacking the nests. One or two days after a bee emerged, the nest was opened in a nearby screen-house to uniquely mark each bee on the thorax with quick-drying Decocolor® paint markers. We returned marked bees to their nests, which were returned to the stands. Females were allowed to forage freely. Weekly counts of open or closed cells allowed us to determine when new bees emerged. These bees were also marked, so that in multi-female colonies we knew the ages of nest-mates. In the following analyses the oldest female within an observation nest is ranked "*bee A*" and progressively younger bees are labeled *bee B, C* and *D*.

Social behavior was observed using ITT® 3000 night-vision goggles, or using a Bausch & Lomb® Stereozoom 5 microscope with a boom stand, and a Techniquip® fiber optic dimmer light with a red filter (Schott glass, 610 nm). Behavioral interactions also were recorded using a Sony® TRV10 or TRV510 digital video camera with infrared illumination. Observations of trophallaxis were made between 05:00–06:30 h, and between 18:00–19:30 h, when most foraging occurs (Warrant et al., 2004; Wcislo et al., 2004), from February to September 2000 and 2001. Fifty miniDV video cassettes, each with approximately one hour of video recordings, were randomly selected from the video recordings, and behavior was scored from a video monitor, based on 8 observation nests.

A behavioral interaction occurred when the focal bee moved to within a body length of a nest-mate. Aggressive interactions involved i) head butts (a bee nudged the other with its head); ii) biting with the mandibles (a bee snapped at the other with mandibles); and iii) a C-posture (a bee curled the abdomen [metasoma] forward to expose the sting) [definitions follow Michener (1990a); Arneson and Wcislo (2003)]. Attempted trophallaxis occurred when one bee exuded a droplet of liquid and presented it to the other bee. To ascertain where social interactions occurred, the linear nest tunnel was divided into four equal sections and the positions of residents were recorded using scan sampling.

Nourishment transfer and longevity

To test whether a recipient gains nourishment from the transfer of liquids, females from the same nest were paired in small tube-like cages (~4 cm long; ~2 cm diameter), separated by fine screening (mesh ~1.3 mm^2). Adult female *M. ecuadoria* were collected from nests in the BCNM between April–September 2001. Females are nocturnal foragers, so we collected nests during the day to ensure that all residents were collected. In the laboratory we opened nests and removed intact cells, which were maintained at ambient temperatures until bees emerged. We used experimental cages that were divided into two chambers, and we placed one bee in each chamber. In half the cages a single screen wall divided the two chambers, and neighbors could touch mouthparts through the screen. In the other half a second screen wall ~3 mm from the first screen prevented direct physical contact between bees in adjacent cages. For each pair, one bee to be fed was randomly selected. Fed bees had access to an *ad lib* mixture of honey and water (50:50) with a drop of nontoxic food coloring, which was placed in a small vial stopped with cotton and the vial was attached to one cage. The bees readily fed on the honey-water, as confirmed by direct observations, and autopsies of these bees showed that their stomachs were colored. Cages were maintained in a styrofoam container placed in a shaded screen-house on BCI at ambient temperature; the container was surrounded by a water moat to defend against ants. The number of days each bee survived was recorded. After bees died they were dissected under a microscope to confirm the transfer of food (colored dye in the stomach).

The above experiments were repeated with males as recipients and females as donors, with the exceptions that individuals were reared from nests collected between February and May 2005, and maintained at ambient temperatures at STRI's Tupper Center in Panama City.

Statistical treatment and voucher material

Statistical tests are indicated in the text, and were done using SYSTAT® v10.0 on a personal computer or taken from Sokal and Rohlf (1995). Mean values are reported with their standard deviations. Voucher specimens of *M. genalis* and *M. ecuadoria* are deposited in the Dry Reference Collection of the Smithsonian Tropical Research Institute (STRI), Balboa, Panamá; duplicates are deposited in the Museo de Invertebrados "Graham Fairchild," Universidad de Panamá, República de Panamá, and the Natural History Museum, University of Kansas, Lawrence Kansas, USA. QuickTime® video of trophallaxis behavior is available from the first author or *http://striweb.si.edu/wcislo/videos/forager_donate_food.mov.*

Results

Social behavior of donors and recipients

In multi-female nests, the oldest bees rarely foraged, while younger females were the major foragers (Fig. 1). On average *bee A* was 44 ± 22 days older than *bee B* (N = 7 nests); *bee B* was 40 ± 33 days older than *bee C* (N = 4 nests); and

bee C was 19 ± 11 days older than *bee D* (N = 3 nests). Bees from the *A* cohort used in this study survived from 48–188 days (× = 97.1 ± 41.5 days, N = 8), which was considerably longer than the mean egg to adult development time (*M. genalis*: 36.6 × 3.2 days, N = 87). Longevities of females in the other cohorts were not tracked.

Food exchange behavior

Body positions during food transfer depended on the recipient: if she faced the entrance when a forager arrived, then the recipient was fed with both bees facing head-to-head, and then later the donor rotated her body to pass by the recipient, ventral surface to venter, as shown in supplementary video (see Methods). If, however, a bee approached the recipient from behind, then the latter somersaulted to receive a droplet in an upside-up position. A donor opened its mandibles and regurgitated a drop of liquid between them and under the raised labrum with her proboscis retracted. The recipient extended her proboscis slightly, and during food transfer both bees often antennated the other's head. At times the recipient also touched the donor's head with her forelegs. Trophallaxis usually involved two bees, but occasionally involved one donor and two recipients (n = 4); these three-way interactions were apparently opportunistic since the second recipient joined after trophallaxis already started; the second recipient was the youngest bee in 3 of 4 cases. Trophallaxis lasted from 1–34 s (× = 13.5 ± 8.3; n = 60), excluding brief contacts when it was not possible to distinguish donor from recipient. Mean duration is probably an overestimate, given that detailed studies of honey bees *(Apis*) show that extremely brief contacts (< 1 s) result in food transfer (Farina and Wainselboim, 2001). We do not know what sensory modalities are involved in initiating or coordinating exchanges between donors and recipients, but presumably tactile and olfactory information is important. Bees are able to see at very low light levels (Warrant et al., 2004), but presumably not at the low light levels within natural nests; females produce substrate vibrations but their occurrence is not consistently associated with trophallaxis (WTW, unpubl. data).

Social contexts of trophallaxis and its frequency of occurrence

Trophallaxis events occurred during the periods when bees foraged. No food exchanges were observed during >50 h of observation at other times of the night, nor during >30 h observation between sunrise and sunset (WTW, unpubl. data). Dividing the linear nest into four equal-sized sections, most social encounters occurred in section 1 near the nest entrance (44 % of 342 encounters from 5 nests) or in section 4 near cells that were being provisioned (30 %), while 16 % and 10 % of encounters occurred in the intervening sections 2 and 3, respectively. Encounter rates were homogeneous for different nests (G test for heterogeneity, $G_H = 4.9$, $X^2_{.05\,[12]} = 21.06$, NS; Sokal and Rohlf, 1995), so we pooled the data.

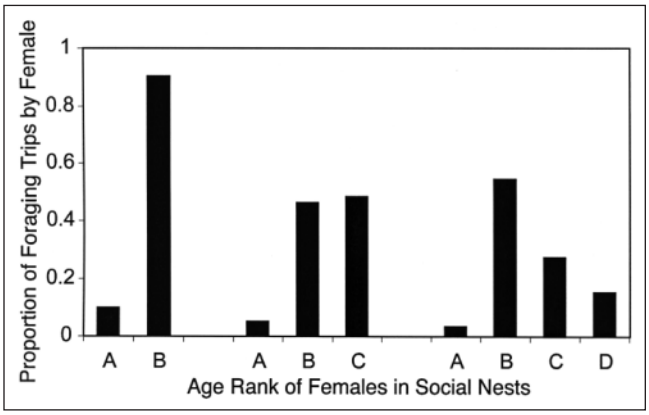

Figure 1. The proportion of total foraging trips made by different females within multi-female nests of *Megalopta genalis. A* is the oldest bee in each nest, *B* the next oldest, etc.

We used encounter rates in different nest sections as the expected distribution for the within-nest distribution of trophallaxis. Trophallaxis also occurred most frequently near the nest entrance (67 %), but was more frequent than expected based on relative encounter rates ($G = 44.9$, $X^2_{.001\,[3]} = 16.27$, $P < 0.001$, G test; Sokal and Rohlf, 1995).

The recipient was mildly to highly aggressive prior to trophallaxis in 83 % of 115 food exchanges. *Bee A* was aggressive by opening and closing her mandibles in front of the forager/donor, or she stood up on her second and third legs and repeatedly snapped at the forager with her mandibles. Escalated aggressive behavior included nudging, whereby the recipient crashed head-first into the donor, from the front or rear, or she adopted a stationary posture and blocked the passageway when she curled her abdomen (metasoma) beneath her and exposed her sting. Usually these aggressive interactions were very brief (x = 1.9 ± 1.1 s, n = 35), though some lasted nearly 5 s. In all cases aggression ceased immediately when the recipient was offered food. Apart from interactions with newly eclosed bees, sometimes (~17 % of 115 food exchanges) a donor offered food prior to any physical contact, and most of these cases occurred immediately after a returning forager entered the nest. In 5 cases there were aggressive interactions between the donor and recipient during a 5 min period before the forager departed, while in the remaining 15 cases there were no aggressive interactions during this time.

Non-aggressive solicitations among mature nest-mates occasionally led to trophallaxis, but were uncommon (~7 % of 115 interactions), and usually involved a younger bee soliciting from the oldest bee in three-bee nests. The solicitor approached the donor and rapidly antennated her head, including the labrum, while the solicitor had her glossa extended. Most examples of non-aggressive food exchange involved adult females and newly eclosed male and female brood. When a new bee emerged, the dominant female repeatedly inspected the cell and fed the callow adult, even when the latter was still inside the cell, and the callow bee solicited food as described above. Likewise, in multi-female

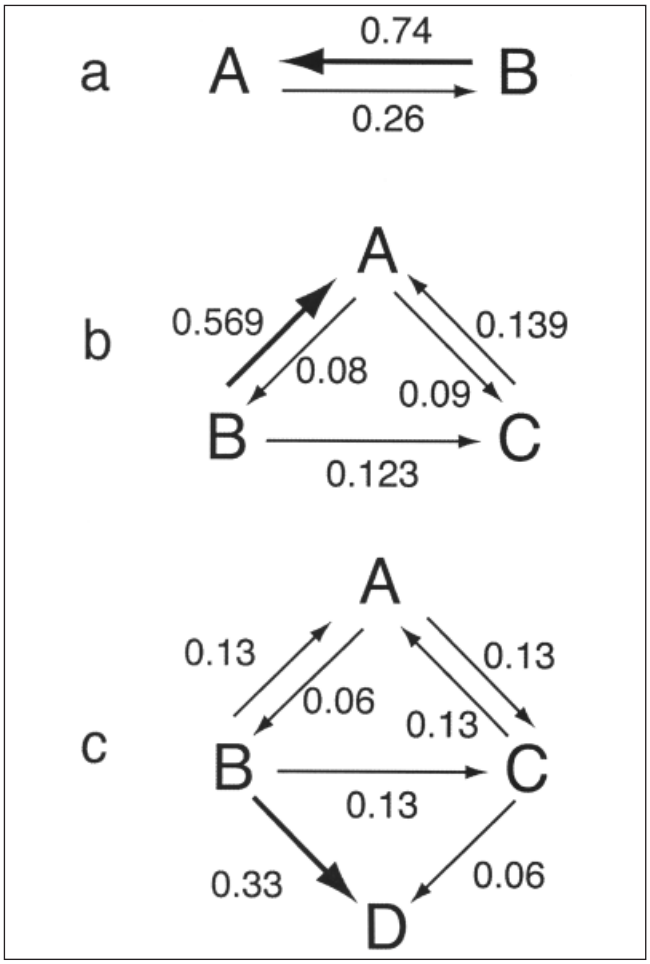

Figure 2. Frequency of food exchange between donor –> recipient in nests of *Megalopta genalis* with differing numbers of bees: (a) two-bee nests, N = 7 observation nests, 27 h of observations, and 35 trophallactic events; (b) three-bee nests, N = 4 observation nests, 48.5 h of observations, and 65 trophallactic events; and (c) four-bee nests, N = 3 observation nests, 7 h of observations, and 15 trophallactic events.

nests, foraging females immediately went to the cell with the newly emerged bee and fed it without aggressive interactions.

Initially males were regularly fed by adult females for 1–15 days, and males left the nest approximately 7.3 ± 3.2 days (N = 34) after emergence. If a returning forager passed close to a male, then the male attempted to block the tunnel, while head-butting and biting the female's head (N = 5 interactions). Usually the female ignored him, and the male then followed the female for up to 30 min, harassing her by attempting to block the tunnel, or biting and head-butting her.

In nests with 2 or 3 females, the intended recipient sometimes (9.9 % of 115 interactions) regurgitated her own droplet when offered a droplet by a donor, and effectively declined the proffered food. The two bees faced each other with their droplets exposed for several seconds; usually the forager was first to swallow her droplet, and the other bee then did the same and they passed one another.

Food is transferred among all colony members, but the oldest female (*bee A*) was the main recipient of food in two-bee and three-bee nests (Figs 2a,b), and overall was involved in most transfers as donor or recipient (78.8 % of 80 events). In two-bee nests (Fig. 2a) the oldest bee (*bee A*) received food in almost 75 % of food exchanges. The oldest bee also dominated transfers in three-bee nests (Fig. 2b, *Bee A* offers droplet, G = 15.9, $X^2_{.001\,[2]}$ = 13.8, P < 0.001; receives droplet, G = 8.9, $X^2_{.025\,[2]}$ = 7.38, P < 0.025; G test, Sokal and Rohlf, 1995). In four-bee nests, however, the flow of food toward *bee A* dropped markedly, and she was the recipient in <30 % of exchanges (Fig. 2c). Older, dominant bees appear to receive lower proportions of the exchanged food, and the youngest bees receive more, as the number of females per nest increases, but these data are not independent because some of the two-bee colonies became three-bee colonies, etc. In general the older forager(s) gave food to the dominant non-forager more frequently than to a younger forager(s), while the oldest non-forager shared food with the youngest bee more frequently than she returned food to the main forager. Younger bees also exchanged food among themselves in nests with ≥2 bees (21.2 % of 80 events).

Trophallaxis and individual longevity

Females with *ad lib* access to sugar-water lived for 17.1 ± 7.9 d (n = 37). Unfed females separated by one screen from a nest-mate with access to food lived for 5.2 ± 2.8 d (n = 18), while females separated by two screens, which precluded trophallaxis, lived 2.4 ± 0.8 d (n = 25) (Mann-Whitney U = 379, $X^2_{[1]}$ approximation = 15.3, P < 0.0001) . Autopsies showed that none of the females separated by two screens had food coloring in their stomachs, indicating that no food exchange occurred, while all unfed bees separated by one screen had food coloring in their stomachs, indicative of trophallaxis. Similar patterns were obtained for males that were paired with females, such that access to food had a significant affect on survivorship (Kruskal-Wallis test = 43.07, P < 0.0001). Males with *ad lib* access to sugar-water lived for 11.5 ± 4.1 d (n = 19). Unfed males separated by one screen from a nest-mate female with access to food lived for 3.8 ± 1.4 d (n = 19), which was significantly longer than males separated by two screens from a nest-mate female with access to food, which lived 2.0 ± 0.9 d (n = 25) (Mann-Whitney U = 310.5, $X^2_{[1]}$ approximation = 15.15, P < 0.0001). Postmortem analyses of males also showed that no males separated by two screens had food coloring in their stomachs, while unfed males separated from a female by one screen had coloring in the stomach. For both males and females, bees that received food via trophallaxis did not live as long as those bees with *ad lib* access to food, which implies that trophallaxis does not provide all the required nourishment.

Discussion

Several observations suggest that trophallaxis plays a role in social differentiation in *Megalopta.* First, aggressive behav-

ior usually stimulated trophallaxis, which ceased following a food offering, as typical for dominant-submissive behavior (e.g., Darwin, 1872). Second, the recipient was usually older than the donor, and previous studies have shown that, within a cohort, older bees tend to be larger and more often have developed ovaries than younger bees (Arneson and Wcislo, 2003; Smith et al., submitted). Overall there was an asymmetrical flow of nutrients toward the dominant bee in multi-female nests, as known for other social insects (e.g., Kukuk and Crozier, 1990; Liebig et al., 1997; Hölldobler and Wilson, 1990; Crailsheim, 1998). In contrast, there is indiscriminate sharing of food in a halictid bee without strong reproductive differentiation (Kukuk and Crozier, 1990).

The fact that food offerings are part of a social exchange system, even in two-bee colonies of a facultatively social species, supports Michener's (1985) contention that the components of social behavior are assembled rapidly in halictid social evolution (also Wcislo, 1997). Antennation accompanies trophallaxis, as occurs in obligate social insects (e.g., Michener, 1972; Kukuk and Crozier, 1990; Liebig et al., 1997; Hölldobler and Wilson, 1990; Crailsheim, 1998), but we do not know whether such contact solicits food exchange, or whether it represents ritualized aggression (e.g., Powell and Tschinkel, 1999). Food transfer occurred in the experimental cages where physical aggression was impossible, suggestive of ritualization (e.g., Liebig et al., 1997; de Waal, 2000). Alternatively, Michener (1974) has suggested that antennation also functions simply to help keep the two bees properly oriented for food transfer.

Trophallaxis occurred more frequently near the nest entrance, where the primary resident spent most time while nest-mate(s) foraged, and where she immediately encountered a returning forager (also e.g., Maeta et al., 1992). In carpenter bees (*Xylocopa*) trophallaxis also occurs more frequently at the nest entrance, although usually the oldest bee forages, and there is competition among younger bees to be closest to the entrance (e.g., Hogendoorn and Velthuis, 1993). No apparent competitive interactions were observed in *Megalopta* females vying for the first position near the nest entrance, although non-foraging females sometimes switched positions near the entrance when a forager was out.

Although the sample size of four-bee nests was small, the oldest female monopolized a smaller percentage of exchanged food (~26 %) relative to the smaller multi-female nests in which she monopolized >70 % of exchanges. Larger colonies are more common toward the end of the active season (Wcislo et al., 2004), so dominant ("*bee A*") females are considerably older than the other bees relative to two- and three-bee colonies, and they may be already senescing and thus receive less food (see Koedam et al., 1995).

Under experimental conditions trophallaxis increased the longevity of bees that lacked direct access to food by almost 50 %. Under natural conditions food exchange may be especially important where it is difficult for bees to regularly forage at certain times of the year when inclement weather is unpredictable. In central Panama most foraging takes place in the dry season when little rain falls (Wcislo et al., 2004); the duration and frequency of rainfall increases throughout the wet season. Temporal (hourly, daily, weekly) patterns of rainfall on BCI are serially correlated, so that the best predictor of rainfall on a given day is knowledge of rainfall on previous days (Windsor, 1990; Windsor et al., 1992). This autocorrelation implies that there will be runs of days (nights) when bees cannot forage, and food-sharing might dampen environmental unpredictability. The other halictid with trophallaxis, *Lasioglossum hemichalceum* (Cockerell), has been studied in heath forests of southern Australia (Victoria), where there are also runs of days with inclement weather from storms off the southern ocean, when it is impossible for bees to forage.

Within-nest observations of social behavior are available for only a minute fraction of Halictidae, and conventional methods of inferring social behavior from nest excavations and dissections (e.g., Wcislo et al., 1993) cannot detect trophallaxis. Nevertheless the conventional view is that this behavior is rare in the family, and thus trophallaxis is neither necessary nor sufficient for expression of social behavior (Kukuk and Crozier, 1990; Kukuk, 1994; Michener, 1990a; Wcislo, 1997, 2000). The independent evolution of trophallaxis in *Megalopta* provides an opportunity to test ideas concerning its social and ecological contexts.

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