

## OPINION

**Trophallaxis in weakly social bees (Apoidea)**

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The hypothesis that trophallaxis, the transfer of symbionts, nutrients, and semiochemical signals within groups, functions as a social glue to bind group members together can be traced to ideas of the ‘social stomach’ developed by Rouboud, Janet and Forel, and popularised by Wheeler (1928) (see Sleight, 2002 for references and a history of ideas relating trophallaxis to sociality). Recently, Nalepa (2015a) argued that a critical factor in the evolution of termite eusociality was the occurrence of trophallaxis, as it would help integrate ‘social, nutritional and microbial environments’. This publication stimulated an exchange of ideas about the merits of this argument, which centred in part on the potential benefits and costs of trophallaxis, its occurrence in extant relatives of termites, and the relative importance of other traits (Korb, 2015; Roisin, 2015; Nalepa, 2015b). Does a consideration of the benefits and costs of trophallaxis for the evolutionary *origins* of sociality in bees shed light on this exchange?

Ample evidence indicates that trophallaxis represents an important societal-level benefit in the evolutionary elaborations of bee sociality, at least in some lineages. In the obligately eusocial corbiculate bees (stingless bees [Meliponini], bumble bees [Bombini] and honey bees [Apini]; Apidae), for example, numerous studies have shown that the exchange of food, symbionts, glandular secretions, and contact stimuli, between adults and immatures, or among adults, plays a key role in integrating these complex societies (e.g. Seeley, 1995; Page, 2013), and facilitates olfactory learning (Gil & De Marco, 2005).

**Trophallaxis and the origins of bee social behaviour**

The general significance of trophallaxis is less obvious on facultatively eusocial bees, or weakly social ones. To better understand the costs and benefits of trophallaxis relative to the *origins* of social behaviour, I compared weakly social bees that do and do not express this behaviour. Unless stated otherwise, ‘trophallaxis’ is used narrowly to describe an exchange of liquid. This restriction is merely pragmatic, because for weakly social bees little is known of chemical signaling, how their symbiotic microbiota are acquired and transferred, and the role of behavioural contact in mediating social interactions. Reviewing nutrient transfer in such bees nearly 25 years ago Kukuk (1994) wrote that a major impediment was a lack of data. The intervening years have not witnessed much progress. At the outset, it is important to highlight two well-known facts. Social

bees, and their solitary ancestors are holometabous insects, and hence their young are completely dependent on adults for food. Second, food provisioning is but one aspect of brood care.

Bees are derived from a paraphyletic group (Sphecidae *sensu* Michener, 2007) of prey-hunting wasps, many of which are ground-nesters. Nearly all sphecids wasps are solitary or communal (Wcislo & Tierney 2009), with confirmed examples of eusociality in *Microstigmus* (Ross & Matthews, 1991). Trophallaxis has been demonstrated in *M. nigrophthalmus* Melo: the donor usually was older than the recipient, and gave liquid both to other females and males, suggesting the behaviour represents a prolongation of maternal care provided to young adults; larvae are not involved in food exchange as they feed on provisioned nymphs of true bugs (Cicadellidae) (de Melo & Campos, 1993).

Eusociality arose multiple times within bees (see Michener, 2007, p. 15), especially in the families Halictidae and Apidae (Cardinal & Danforth, 2011). Two observations led to a long period in which the importance of trophallaxis for bee social origins was downplayed, as for nutritional considerations more generally (cf. Michener, 1990a; Hunt & Nalepa, 1994 and references therein). First, although sociality repeatedly evolved in halictid bees, trophallaxis is rare, and was documented in eusocial forms only recently (see Kukuk, 1994; Wcislo & Gonzalez, 2006; Kapheim *et al.*, 2015). The then-absence of trophallaxis in eusocial Halictidae led Michener to conclude that it was not necessary for the evolution of caste-based societies (references in Michener, 1990a). Second, many bees, including halictids and ceratinines, are mass-provisioners, whereby a female places nectar and pollen in a cell before oviposition, and the cell is sealed. This provisioning behaviour was assumed to preclude contact between adults and immatures, but this assumption is no longer tenable. Recent studies show that there is more contact between adults and young than previously believed, at least in some species, because sealed cells are sometimes opened by an adult, inspected, and re-sealed; or, if need be, refurbished (Quiñones & Wcislo, 2015; and references therein). Adults manipulate some aspects of the nutritional quality of their provisions before oviposition and cell closure (Kapheim *et al.*, 2011), but it is unknown whether adults add liquid food to the provision masses of healthy larvae when they re-open cells.

Within the family, Apidae trophallaxis may play a role in the origins of social behaviour. In large and small carpenter bees (Xylocopini and Ceratinini), mothers tend to transfer liquid solutions to young adults via trophallaxis, and in some cases also pollen (reviewed in Michener, 1990b; Kukuk, 1994). Such mother–young adult offspring interactions are not limited to social species. Many species of *Xylocopa* carpenter bees,

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for example, are essentially solitary, but one or more female offspring might eclose as adults before the death of the mother (*op. cit.*). In such cases the mother, returning from foraging, feeds these young adults, which crowd near the entrance. Similarly, in *X. pubescens* a foundress mother rears some brood and when the young emerge they block the entry way and tunnel until they are fed by the mother (reviewed in Michener, 1990b). Such behaviour is reported for small carpenter and allodapine bees, and in some cases liquid is transferred among adults of the same cohort (*op. cit.*). As with *Microstigmus* wasps, trophallaxis in carpenter bees is probably best construed as an extension of maternal care, although young may compete among themselves to be in the best position to receive food.

Food transfer among adults of facultatively eusocial halictid bees, where it occurs, is sometimes the reverse of this pattern (Wcislo & Gonzalez, 2006; Kapheim *et al.*, 2015). In established two-bee social nests, liquid food typically flows from the foraging bee to the nest resident (i.e. from the subordinate to the social dominant) (Wcislo & Gonzalez, 2006). In multi-female nests, the dominant bee might then redistribute the food to other younger bees (*op. cit.*). Established workers (older > 10 days post-eclosion) forage and perform trophallaxis as donors, more than queens, but this difference is not apparent when workers are young (< 10 days post-eclosion) (Kapheim *et al.*, 2015). Thus, the initial recipient is fed in the context of dominance interactions suggesting ritualised competition may be important. Foraging costs are unknown, but such observations suggest that food-sharing behaviour might be altruistic rather than cooperative (analyses of data indicating fitness benefits in these bees are best explained by maternal manipulation rather than worker altruism, see Kapheim *et al.*, 2015). When the dominant female redistributes the food as a donor, however, it may represent extended maternal care. Experimental studies have shown that indirect access to food via trophallaxis increased survivorship in caged *Megalopta* bees relative to bees that could not physically contact a fed bee (Wcislo & Gonzalez, 2006). The ecological significance of trophallaxis in *Megalopta* is not clear but may relate to increased dampening of environmental unpredictability, when there are frequent runs of missed foraging opportunities as a result of inclement weather at some times of the year. The other halictid with trophallaxis, the communal *Lasiglossum hemichalceum*, 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. Other halictids that lack trophallaxis co-occur in these habitats (W. T. Wcislo, pers. obs.), however, raising doubts about the generality of this hypothesis.

### Trophallaxis and the bee microbiome

Microbial studies of the highly eusocial honey bees and bumble bees demonstrate that they have an intestinal bacterial fauna, including acidophilic bacteria, characterised by relatively low diversity and that these corbiculate apids have probiotic *Lactobacillus* that are relatively specific, consistent with vertical transmission (references in McFrederick *et al.*, 2012). In contrast, little is known about the microbiota of weakly social bees. In facultatively eusocial *Megalopta*, for example, the associated

*Lactobacillus* group phylogenetically with lactobacilli that can be found in the environment on flowers, consistent with horizontal transmission (McFrederick *et al.*, 2012). Sweat-bee associated lactobacilli were abundant in pollen and faeces within cells, suggesting they may play a role in hygiene (*op. cit.*), but functional studies of the microbiota in primitively social bees are lacking.

Social transmission of symbionts, and the specific life stages to which they are transferred shape the structure and diversity of bacterial communities in highly eusocial insects, but these questions have received less attention in the weakly social bees. McFrederick *et al.* (2014) tested whether bacterial communities differed by the bees' social structure (solitary *versus* eusocial), developmental stage or source (nest substrate, pollen, egg, young larva, old larva, pupa, adult, and faeces), and bee species (*Megalopta genalis* and *M. centralis* [= *ecuadoria*]). There were no differences as a result of social structure, but there were differences with bee species and developmental stadia. These differences were driven by environmentally-acquired bacteria, especially from the *Lactotobacillus kunkeei* clade, probably acquired by adults foraging at flowers. Thus, in these bees environmental transmission appears to be more important than social transmission for bacterial symbiont acquisition.

### Benefits and costs of trophallaxis in weakly social bees

Trophallaxis in weakly social bees is usually not reciprocal, and the functional significance may differ in different lineages. In large and small carpenter bees, trophallaxis is probably best described as a form of extended maternal care, with a foraging mother feeding her newly-eclosed offspring. In halictid bees, in contrast, in a communal species food exchange appears to be unrelated to social competition, whereas in two neotropical sweat bees trophallaxis is associated with a dominance behaviour as the primary recipient is the dominant female. Although few data are available, there is no evidence trophallaxis shapes microbial symbiont diversity. Thus, at the origins of bee sociality trophallaxis does not appear to generally function more broadly as a social medium, as suggested by Wheeler (1928), and as noted long ago by Michener (references in Hunt & Nalepa, 1994). Such conclusions are provisional owing to a dearth of data, especially concerning the benefits and costs, yet they do not discount the potentially important role of nutritional bias in social evolution (Hunt & Nalepa, 1994; Kapheim *et al.*, 2011).

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