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Transmission of mutualistic bacteria in social and gregarious insects

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Symbiotic microbes can confer a range of benefits to social, sub-social, and gregarious insects that include contributions to nutrition, digestion, and defense. Transmission of beneficial symbionts to the next generation in these insects sometimes occurs transovarially as in many solitary insects, but primarily through social contact such as coprophagy in gregarious taxa, and trophallaxis in eusocial insects. While these behaviors benefit reliable transmission of multi-microbial assemblages, they may also come at the cost of inviting the spread of parasites and pathogens. Nonetheless, the overall benefit of social symbiont transmission may be one of several important factors that reinforce the evolution of social behaviors and insect eusociality.

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Symbiont-conferred functional benefits in social and gregarious insects

Insects engage in mutualistic interactions with bacteria that confer novel traits to their hosts, enabling them to utilize a wide range of previously inaccessible resources or colonize new habitats [1]. In many instances, these partnerships have become so intimate that the partners cannot survive without each other [2]. The functional importance of mutualistic bacteria in social and gregarious insects has gained much attention over the past few decades, as they frequently play an important role in host nutritional ecology. In this review, we briefly summarize known functions of mutualistic bacteria in social insects and then focus on their transmission routes from one generation to the next, discussing the possible costs

and benefits of social symbiont transfer and its implications for the evolution of social behaviors. As the social transmission of microorganisms between conspecifics occurs from gregarious all the way to eusocial taxa, we will broadly cover bacterial mutualisms with insects across all levels of sociality.

In social and gregarious insects, symbionts have been described or implied to be involved in the biosynthesis of nutrients in bees and bugs [3–5,6*], pectin and lignocellulose degradation in bees, termites and wood roaches [1,6*,7], and carbohydrate metabolism in ants and bees [7,8]. In addition, several bacterial symbionts have putative roles in host nitrogen metabolism [1,8–10]. In termites, the hindgut community is essential to nitrogen fixation, recycling and upgrading, mitigating the low nitrogen content of their cellulose-based diet [10,11]. In ants, putative roles include recycling nitrogenous waste to essential amino acids in *Camponotus* and *Cephalotes* [1,12**], nitrogen fixation in certain *Tetraponera* species [8] and providing a tyrosine precursor for cuticle formation in *Cardiocondyla obscurior* [13]. In fact, symbiotic microbes may be one factor explaining why herbivorous ants can successfully exploit nitrogen-poor arboreal habitats [8,14].

Apart from influencing host nutrition, symbionts present an important component of the defensive arsenal in social and gregarious insects, providing protection to host individuals, their food sources and/or nesting environment against pathogens, parasites, and parasitoids [15]. In the cockroach *Cryptocercus punctulatus*, the application of feces to the nest plays a putative role in fungal defense. Antifungal compounds in the feces — potentially of microbial origin — may sanitize the nest, preventing growth of antagonistic fungi [16]. Similarly, in the termite *Zootermopsis angusticollis*, there is evidence that the hindgut microbiota synthesizes multiple functionally active β -1,3-glucanases with a putative role in fungal pathogen defense [17]. Recent studies in bees (*Apis mellifera* and *Bombus terrestris*) revealed that individuals with a native, undisturbed gut microbial community were less susceptible to *Lotmaria passim* and *Crithidia bombi* trypanosomatid parasites, respectively, likely due to competitive exclusion of the parasites by bacterial gut symbionts [18**,19*]. Other studies observed an effect of the whole gut microbiota and individual bacterial symbionts on the host immune system [20,21]. Kwong *et al.* [21] found that the native, non-pathogenic microbiota of the honey bee

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A. mellifera induces host immune responses, particularly an upregulation of genes coding for the antimicrobial peptides (AMPs) apidaecin and hymenoptaecin in gut tissue and, subsequently, an elevated apidaecin concentration in the gut lumen and hemolymph. Thus, immune priming by the native symbionts may play a role in regulating the microbiota and protecting against pathogens. In fungus-farming ants, antimicrobial compounds produced by actinobacterial symbionts protect the fungal cultivars from specialized *Escovopsis* fungal pathogens [22]. Interestingly, recent studies on the burying beetle *Nicrophorus vespilloides* (Coleoptera: Silphidae), which provide parental care for their offspring, suggested a potential food-preserving role of the symbionts in this taxon as well [23[•],24].

Lastly, growing evidence suggests that symbiotic bacteria can influence host social interactions [25]. In the German cockroach, volatiles emanating from feces-associated bacterial symbionts promote gregarious host behavior [26[•]]. Similarly, in the desert locust *Schistocerca gregaria*, some of the bacterial gut symbionts play a role in host aggregation by producing components of the locust's cohesion pheromone [27[•]]. In addition, bacterial symbionts have putative roles in nestmate recognition in eusocial insects [25]. For example, in the termite *Reticulitermes speratus* and the harvester ant *Pogonomyrmex barbatus*, bacterial associates have an effect on the hosts' chemical profiles and therefore on recognition [28,29].

Symbiont transmission routes

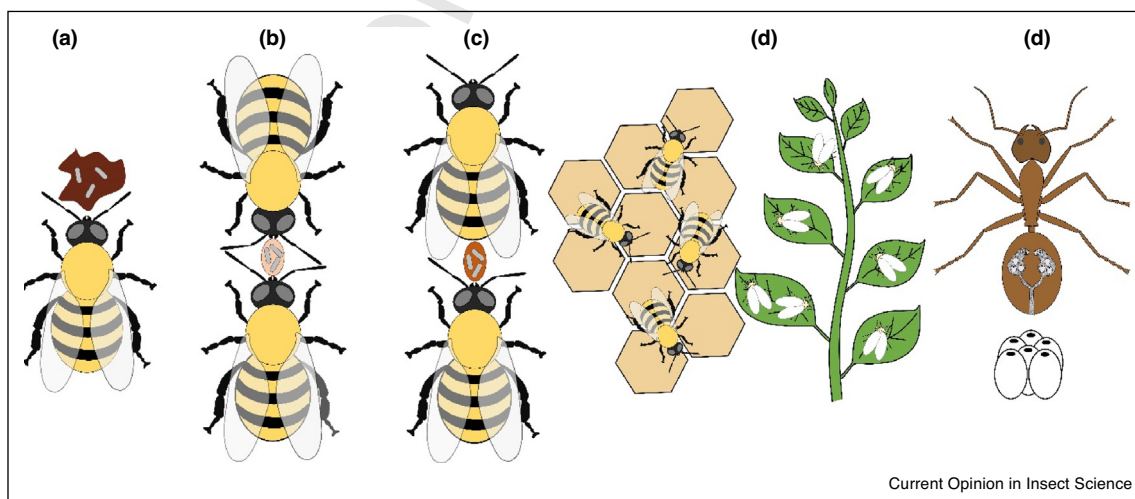
Insects that depend on symbionts to perform key functions are faced with the challenge of ensuring acquisition or successful transmission of specific symbionts in every

generation. Many solitary insects have evolved complex mechanisms that ensure high fidelity of symbiont passage to the next generation, including symbiont invasion of the oocytes prior to embryogenesis, specialized secretions or structures that harbor extracellular symbionts until egg hatching, or organs that allow for the selective colonization of specific environmental bacteria [30,31]. While social and gregarious insects can exploit similar mechanisms for symbiont transmission, their frequent contact with conspecifics opens up the possibility for direct symbiont transfer and thereby adds another dimension to the transmission of beneficial microbes. Behaviors such as coprophagy, trophallaxis and shared resources that are predominant in social and gregarious insects facilitate transmission or acquisition of appropriate microbes in addition to the transfer of nutrients or digestive enzymes.

a) Coprophagy

Coprophagy refers to the consumption of conspecifics' feces after excretion (Figure 1a) and is considered a major force shaping gut microbial communities of gregarious insects such as bugs, beetles, cockroaches and, to some extent, in eusocial bees and termites. In bumble bees and honey bees, for instance, naïve individuals reared in the presence of fresh feces collected from nurse bees acquire bacterial communities similar to those of nurses or wild bees [18[•],32[•]]. Gregarious Pyrrhocoridae and Reduviidae bugs (Hemiptera) exhibit a high degree of coprophagy, likely as a behavioral adaptation for symbiont acquisition [33,34]. For instance, when kissing bugs, *Rhodnius prolixus* (Reduviidae), the vectors of Chagas disease, hatch under sterile laboratory conditions and are raised separately from conspecifics, the nymphs lack the

Figure 1



Symbiont transmission routes in social and gregarious insects. (a) Coprophagy, (b) mouth-to-mouth feeding (stomodaeal trophallaxis), (c) anus-to-mouth feeding (proctodeal trophallaxis), (d) transmission through shared environment, and (e) transovarial transmission.

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