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Social behavior and the microbiome

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Animals are home to diverse bacterial communities that can affect their hosts' physiology, metabolism, and susceptibility to disease. Here we highlight recent research that reveals surprising and important connections between an individual's microbiome and its social behavior. We focus on two recent discoveries: (i) that social interactions can affect the taxonomic and genic composition of animal microbiomes, with consequences for microbiome function and potentially host fitness, and (ii) that microbiomes can affect host social behavior by producing chemical signals used in social communication and by directly influencing host nervous systems. Investigating the reciprocal relationships between host behavior and the microbiome thus promises to shed new light on both the evolution of host social behavior and microbial transmission strategies.

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Introduction

In the last decade, biologists have gained a new appreciation for the roles that host-associated microbiomes play in the lives of animals, including effects on animal physiology, health, and evolution [1–4]. Thus far, some of the most surprising discoveries have involved links between microbial communities and host social behavior [5–11]. Here we focus on two emerging themes from this literature. The first is that social organization and behavior, either through direct physical contact or via shared environments, can influence the bacterial communities associated with individual animals (e.g. [12,13*,14,15*]). In turn, these social processes can alter the taxonomic and genic com-

position of the microbiome, with implications for the services microbiomes provide to their hosts (e.g. [13*,16**,17]). The second major discovery is that the microbiome can shape host social behavior. Because microbial metabolism can release volatile compounds detectable to animals, and because bacterial communities can vary with host traits, microbial communities have the potential to communicate considerable information about animals—a function that may be co-opted by their hosts for use in social signaling [5,7]. Furthermore, microbes may directly ‘hack’ the host nervous system to increase microbial transmission—essentially manipulating host behavior to benefit their own fitness [18]. Here we highlight the most compelling examples of both sets of findings for host-associated bacterial microbiota, focusing primarily on recent studies that use high-throughput profiling methods. Together, these studies provide some of the first insights into the unexpectedly intimate links between social behavior and the microbiome.

Social behavior affects the microbiome

Social effects on the composition of host-associated bacterial communities

Biologists have long appreciated the effects of host social behavior on transmission of parasites and pathogens [19–22]. However, recent high-throughput, culture-independent techniques have greatly expanded the scope of what we can measure, extending this perspective to whole bacterial communities. Significant correlations between microbiome composition and social co-residency or group membership have now been reported in humans, nonhuman primates, carnivores, rodents, insects, and birds [12,13*,14,15*,16**,23–27]. For example, breeding pairs of kittiwakes [14], chimpanzees or baboons that live in the same social group [13*,27], and humans that live in the same household [12,15*], all exhibit more similar microbial communities than individuals in their populations at large. In a few cases, these relationships have been extended to the genes encoded by host microbiota [13*,15*]. Thus far, studies of skin-associated and gut-associated communities dominate this literature, but research on other microbiota (e.g. the oral cavity, the vagina, the cloaca, and scent glands) suggests that the pattern may be widespread across body sites [12,24,25*,28].

While social structuring of the microbiome appears to be common, the mechanisms that underlie this phenomenon are not well understood. Because social partners are often exposed to shared environments or consume similar diets, disentangling bacterial transmission due to direct social contact from other explanations is challenging, especially in non-invasive or minimally invasive studies (but see [Box 1](#)).

For instance, social partners could be colonized by similar microbes due to contact with shared environmental sources, or behavioral similarities between partners could create similar ecological niches within microbial communities, particularly through consumption of similar diets [29,30]. In practice, the explanation for observed associations between social interactions and microbiome similarity often remains unclear. Excluding transmission via coprophagy, only a handful of studies have been able to make a strong case that direct transmission between hosts plays an important role in shaping microbiome composition [13^{*},14,15^{*},28]. However, these studies indicate potentially useful study designs for identifying such effects (Box 1) and have helped shape an emerging two-level paradigm for understanding social effects on the microbiome, with roles for both coarse social structure (e.g. group co-residency) and more fine-grained, individually differentiated social interactions (e.g. social networks within groups).

The functional and adaptive importance of social transmission

Microbial transfer between socially interacting hosts is often invoked as an important component in the cost-benefit calculus of group living [4–6,8,31]. However, our ability to accurately measure microbiome function remains limited, leaving the relationship between social transmission of microbes and host health or fitness opaque in most cases. Metagenomic and metatranscriptomic high-throughput sequencing methods may provide insight in this regard by opening a window into the genes encoded and expressed by microbial communities. Such studies have identified both disease-causing microbes and antimicrobial-resistance genes among the taxa and sequences shared through social contact [15^{*},32]. However, not all microbes are equally likely to transfer through social routes. Bacteria that are most dependent on specialized, host-associated environments might be the most likely to be transmitted via social contact [13^{*}], and the types of bacteria that transfer may also depend on the physiological state of their hosts [33,34]. Which taxa benefit most from social transmission remains an important open question, with the search for answers currently limited by our incomplete knowledge of bacterial life styles and their roles within hosts. Furthermore, while arguments linking social living to beneficial microbial transfer tend to assume long-term coevolution (e.g. [4,8]), environmental factors can lead to surprisingly rapid shifts in host microbial communities, at least in the gut [35^{*}]. This observation suggests either weaker coevolutionary coupling than previously believed, or a more complicated coevolutionary pattern (e.g. adaptation to dietary plasticity rather than a constant diet).

Consequently, relatively few studies have linked socially mediated microbial transfer to clear fitness-related outcomes, but those that have point to both positive and negative effects. In bumblebees, for example, transfer of gut microbiota from nest mates to emerging adults is

essential for defense against the trypanosomatid parasite *Crithidia bombi*, which severely restricts the fertility of infected queens [16^{**}]^{*}—a clear case of beneficial social transmission. However, bumblebee guts are relatively species poor, and for species with more complex gut microbiota, the influence of social transmission may differ. Indeed, a case of social transmission in mice reveals a more complicated pattern. In a colitis-susceptible mouse strain, high rates of intestinal colitis are associated with colonization by the gut microbes *Klebsiella pneumonia* and *Proteus mirabilis* [17]. Strikingly, cross-fostering wild-type pups to susceptible mothers leads to transfer of these microbes and associated susceptibility to colitis, whereas cross-fostering pups of the susceptible strain to wild-type mothers eliminates both effects. In this case, social transmission is protective in one context but deleterious in another: the ‘good’ versus ‘bad’ consequences of social transmission depend instead on what gets transferred.

The microbiome affects social behavior

Microbes create chemical cues that animals use in social communication

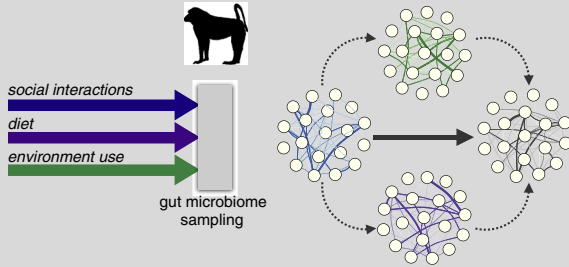
While social interactions can alter microbiome composition and function, microbes can also affect host social behavior. One of the main ways these effects arise is through chemical signals: considerable evidence indicates that some animals cultivate odor-producing bacteria in their scent glands, specifically for use in social communication [7,9,11]. Because animal-associated bacterial communities can be shaped by social contacts, family relationships, genotypes, and environments, bacterial communities have the potential to communicate substantial information about their hosts [24,25^{*},36,37]. In support, several studies have observed correlations between host traits (e.g. sex, dominance rank, social group membership), the bacterial communities living in scent glands, and the volatile compounds that emerge from these glands [25^{*},36].

Experimental approaches—including manipulations of diet or social interactions, clearing host microbiota using antibiotic interventions and reintroducing individual species, or using germ-free animals—are important for testing for causality and dissecting the mechanistic basis of these signals. For instance, experiments in fruit flies (*Drosophila melanogaster*) have shown that gut bacteria mediate olfactory cues involved in social attraction [38], mating preferences [39], and kin recognition [40]. Similarly, in lab mice, careful work has enabled researchers to elucidate the metabolic pathways involved in the production of trimethylamine (TMA), a volatile compound proposed to signal species identity [41^{**}]^{*}. TMA smells like rotting fish and is produced by gut bacteria during choline metabolism. In most mammals, including humans, TMA is converted into an odorless compound by enzymes in the liver. However, in male *Mus musculus*, but not other rodent species, these enzymes are down-regu-

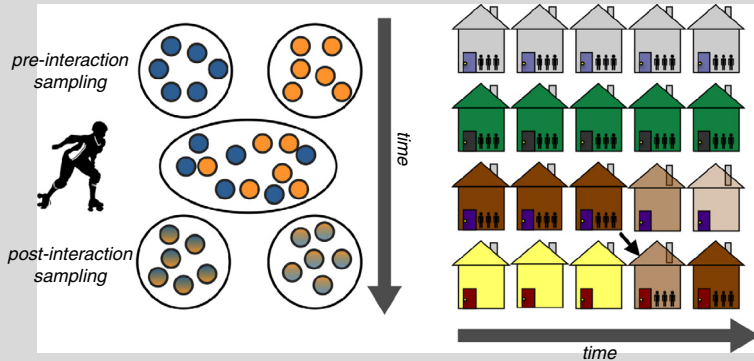
Box 1 Investigating social processes that affect microbiome composition in minimally invasive studies.

Invasive experimental manipulation (e.g. clearance of the microbiota and controlled reseeded) is one powerful strategy for testing social effects on the microbiome, but this strategy is not possible in all systems, including many human and wild animal populations. However, such systems are important for understanding how social contact maps onto microbiome variation in a natural context, and whether associations between social structure and the microbiome arise as a consequence of direct social contact or shared environmental exposures. Three types of study designs have emerged as informative in this regard. Population genetic tracking of strain migration could, in theory, be a fourth, although no microbiome-wide studies of this type are yet available.

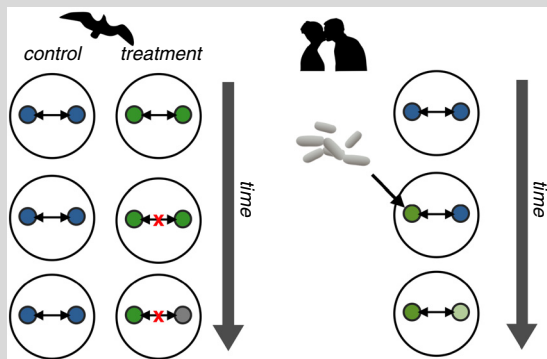
Fine-grained observation: Tung *et al.* [13*] combined network data on rates of grooming between baboons with parallel data on dietary similarity and environment use, collected for the same individuals during the same time span. Direct contact-based networks (blue) predicted gut microbiome similarity (gray) even after controlling for diet similarity networks (purple) or spatial proximity-based networks (green).



Longitudinal studies: Using repeated sampling, Meadow *et al.* [54] showed that members of competing roller derby teams exhibit more similar microbial communities following a 'bout' than beforehand, supporting transfer between players during the game (left). Lax *et al.* [15*] sampled host skin surfaces and household surfaces for seven families over 6 weeks, including 3 families that moved within the sampling window. Skin microbiota dominated household surfaces, which rapidly converged to mirror the skin microbiota of their owners. Hence, transfers between socially interacting individuals drive patterns of skin microbiota similarity, sometimes via intermediate surfaces.



Experimental studies: In kittiwakes, breeding pairs exhibit more similar cloacal microbiota than non-pairs (left). Blocking direct cloacal contact caused the microbial communities within breeding pairs to diverge, demonstrating that sexual contact was the mechanism driving similarities between mates [14]. Kort and colleagues [28] used 'marker' bacteria from a probiotic drink to track the effects of kissing on the salivary microbiome (right). Approximately 80 million bacteria were transferred in an intimate kiss.



lated at sexual maturity, allowing TMA to build up in *M. musculus* urine and tissues. Mice given antibiotics or low-choline diets produce much lower quantities of TMA, demonstrating a causal role for bacteria in driving this signal. Intriguingly, data from both fruit flies and mice show that microbes mediate odors involved in mate choice and pre-mating isolation, raising the possibility that bacterially produced odors also contribute to host speciation [39,41,42]. Microbes living in scent glands presumably benefit by gaining safe, nutrient-rich places to live, and opportunities to colonize new hosts during scent marking. However, how common these relationships are across host taxa and whether they constitute true host–microbe mutualisms remain important areas for future research.

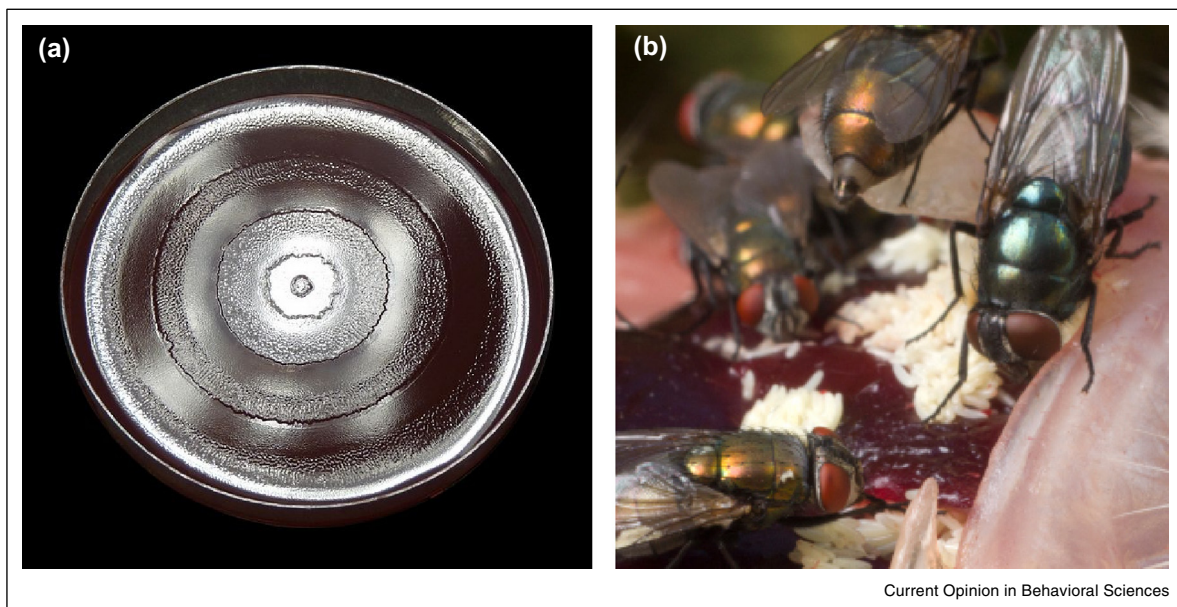
Bacteria may manipulate host social behavior to maximize microbial fitness

Microbes can also influence host social behavior by directly manipulating the host nervous system [18,43,44]. While it has long been known that parasites can manipulate host behavior to improve transmission [45], symbiotic bacteria should also benefit from behavioral manipulation if it increases their ability to access new hosts and new

environments. The bacteria *Proteus mirabilis* has just such a relationship with the blow fly, *Lucilia sericata*: *P. mirabilis* produces volatiles that attract flies to new food sources, while the flies serve to transport bacteria to new habitats [46] (Figure 1). However, behavioral manipulation may be more complex when hosts harbor more diverse microbiota. The fitness interests of bacteria occupying different body sites or utilizing different resources within the same body site could theoretically involve conflicting transmission strategies or resource requirements, making host manipulation more difficult to evolve.

Despite these limitations, there is some evidence that gut bacteria manipulate food cravings in hosts to obtain optimal resources for bacterial growth [18] and speculation that bacteria manipulate host social interactions to promote transmission [10]. The strongest evidence for direct effects of bacteria on host behavior comes from research on the gut-brain axis (interested readers should see several recent and excellent reviews of this topic: [44,47–50]). As in other areas of microbiome research, building the case that bacteria play a direct causal role remains challenging. However, a handful of exceptionally strong and careful studies have shown that experimental

Figure 1



Current Opinion in Behavioral Sciences

Symbiotic bacteria may benefit from manipulating hosts to increase their ability to access new resources and environments. The bacteria *Proteus mirabilis* is found in a large range of habitats, including rotting meat. *P. mirabilis* is also one of a handful of bacterial species capable of bacterial swarming. The image in (a) depicts *P. mirabilis* swarming in a classic bulls eye formation on a Petri dish (image from Wikimedia Commons). Swarming allows the colony to locate new resources over short distances, but *P. mirabilis* is limited in its ability to travel long distances to new carcasses. To solve this problem, *P. mirabilis* uses the blow fly, *Lucilia sericata* (b) as an insect taxi service. In fact, the same chemical signals *P. mirabilis* uses to initiate its own swarming behavior—lactic acid, phenol, sodium hydroxide, potassium hydroxide, and ammonia—also produce strong, volatile odors that attract blow flies [46]. Without these chemical cues, blow flies have difficulty locating carcasses. When blow flies locate a carcass undergoing bacterial decomposition, they lay their eggs. Once the larvae hatch, they consume the carcass and bacteria, including *P. mirabilis*. *P. mirabilis* survives consumption, residing in the fly's salivary glands until the larva pupates into adulthood, at which time the bacteria are transported by the newly emerged adult fly to a new carcass.

manipulations of the gut microbiome, through antibiotics or changes in diet, can lead to changes in host exploratory and cognitive behavior, as well as gene expression levels in the brain (e.g. [51,52]). These changes are independent of other changes in health or immune function and, most convincingly, fecal transplants are able to re-create similar effects in animal models [51,52]. However, we still do not know why bacteria might benefit from influencing these particular host behaviors, highlighting exciting opportunities for collaboration between evolutionary, ecological, and biomedical scientists.

Conclusions and future challenges

Who an animal interacts with and what they do together can have profound consequences for the composition of their microbiota. Microbes themselves can also play causal roles in host social interactions through chemical signaling and effects on host nervous systems. However, several major puzzles continue to confront research on social behavior and the microbiome. Foremost among them is the problem of measuring the stability and functional consequences of compositional variation in bacterial communities. As yet, most culture free techniques cannot reveal which microbes in a community are alive and functioning, and which are dead or dormant (although metatranscriptomics may lend insight here). Thus, the results of most profiling approaches primarily capture microbe presence, as opposed to their role in the host–microbe ecosystem, or their stability over time. This limitation makes it difficult to understand the effects of the microbial communities that we profile, and compounds the problem of evaluating whether social effects on microbial transmission are, on balance, positive or negative for hosts (an answer that itself may be context-dependent). While social contact can provide access to beneficial microbes [16], harmful bacteria could use the same transmission routes, and both processes are likely to have been at work throughout the evolution of host social behavior. Simple host–microbe systems seem to offer many advantages in addressing these problems because of the relative feasibility of measuring functional consequences for both hosts and microbes (e.g. [53]). However, it remains unclear whether one host–one microbe systems provide accurate analogs for complex microbial communities involving hundreds or thousands of microbial species.

Despite these challenges, now is an exciting time to be working at the interface between animal behavior and the microbiome. Untangling the relative costs and benefits of both social transmission and microbial effects on behavior will undoubtedly be a priority in the next generation of research on social behavior and the microbiome. Social relationships can be a double-edged sword, with beneficial consequences when they are positive but with deleterious effects on health and survival when they are negative or absent. Because host-associated microbes

appear to both shape and depend on these relationships, it is becoming increasingly clear that they, too, may play a key role in the health and fitness consequences of social organization and behavior.

Conflict of interest statement

Nothing declared.

Acknowledgments

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David and colleagues randomized human volunteers into either a group that consumed only animal products or a group that consumed only plant products. After only five days, the microbial activity in individuals assigned to animal products grew to resemble that associated with obligate carnivores, while microbial activity in the plant product group resembled that associated with herbivores. These results challenge the idea that host-microbe associations are the products of long-term coevolution, an assumption of arguments that microbial transfer may have helped drive the evolution of sociality.

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