Animal Behavior and the Microbiome

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Science **338**, 198 (2012);
DOI: 10.1126/science.1227412

MICROBIOLOGY

Animal Behavior and the Microbiome

Feedbacks between microbiomes and their hosts affect a range of animal behaviors.

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Human bodies house trillions of symbiotic microorganisms. The genes in this human microbiome outnumber human genes by 100 to 1, and their study is providing profound insights into human health. But humans are not the only animals with microbiomes, and microbiomes do not just impact health. Recent research is revealing surprising roles for microbiomes in shaping behaviors across many animal taxa—shedding light on how behaviors from diet to social interactions affect the composition of host-associated microbial communities (*1*, *2*), and how microbes in turn influence host behavior in dramatic ways (*2*–*6*).

Our understanding of interactions between host behavior and microbes stems largely from studies of pathogens. Animal social and mating activities have profound effects on pathogen transmission, and many animals use behavioral strategies to avoid or remove pathogens (*7*). Pathogens can also manipulate host behavior in overt or covert ways. However, given the diversity of microbes in nature, it is important to expand the view of behavior-microbe interactions to include nonpathogens.

For diverse animals, including iguanas, squids, and many insects, behavior plays a central role in the establishment and regulation of microbial associations (see the first figure). For example, the Kudzu bug (*Megacopta cribraria*), an agricultural pest, is born without any symbionts. After birth it acquires a specific symbiont from bacterial capsules left by its mother. If these capsules are removed, the bugs show dramatic wandering behaviors, presumably to search for symbiont capsules left with nearby eggs (*8*).

Social contact is another mechanism that can mediate the acquisition and exchange of microbial symbionts. Indeed, a bene-

	Animal	Microbial species or consortium	Interaction with behavior	Implication
Behaviors impact microbiomes	Kudzu bug (*Megacopta cribraria*)	*Ishikawaella capsulata*	When born, bugs feed on capsules of symbionts; if no capsules are present, nymphs wander in search of microbes	Behaviors shape symbiont acquisition
	Green iguana (*Iguana iguana*)	Gut microbiota	Juvenile iguanas eat soil or feces to tailor the microbiota to their current diet	Animals may adjust the microbiota at different life-history stages
	Bobtail squid (*Euprymna scolopes*)	*Vibrio fischeri*	Squids eject bioluminescent bacteria daily	Suggests animals can actively control their symbiont populations

Behaviors alter microbiomes. In Kudzu bugs (*8*), green iguanas (*15*), and bobtail squid (*16*), host behaviors alter microbial acquisition and maintenance.

fit of social living in many species may be the transmission of beneficial microbes (*9*). Koch and Schmid-Hempel have shown that in the case of bumble bees (*Bombus terrestris*), either direct contact with nest mates or feeding on feces of nest mates was necessary for establishing the normal gut microbiota. Bees never exposed to feces had an altered gut microbiota and were more susceptible to the parasite *Crithidia bombi* (*1*).

Social context also shapes establishment of mammalian microbial associations. For example, chimpanzees from the same community have more similar microbial consortia than do chimpanzees from different communities (*10*).

Yet, despite these and other examples of behavior facilitating microbial colonization, questions remain. To what extent is juvenile behavior driven by the search for beneficial microbes? How frequently does host choice influence the acquisition of microbial partners? And, if there is strong selection for animals to acquire microbes from each other, what role do beneficial microbes play in the evolution of sociality?

Once host-microbe associations are established, microbes can influence host behavior in ways that have far-reaching implications for host ecology and evolution (see the second figure). Sharon *et al.* recently found that fruit flies (*Drosophila melanogaster*) strongly prefer to mate with individuals reared on the same diet on which they were reared. Antibiotic treatment abolished the mating preference, and inoculation of treated flies with microbes from the dietary media restored the preference, indicating that microbes, and not diet, altered mate choice. Changes in presence of one bacterium, *Lactobacillus plantarum*, were linked to the induction of mating preferences (*2*). Flies reared on different diets showed differences in major cuticular hydrocarbons, which are known to influence mating, suggesting that the bacteria alter these crucial chemical signals. Similarly, communities of scent gland–inhabiting odor-producing bacteria vary across hyena clans (*3*), suggesting that microbes could fundamentally alter social interactions in these animals via effects on their chemical communication.

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Published by AAAS

Microbial effects on animal chemistry also recently have been linked to changes in predator-prey interactions (*11*) and feeding behavior (*12*). Females of the African malaria mosquito, *Anopheles gambiae*, use chemical cues released from human skin to locate hosts. By analyzing skin emanations from 48 subjects, Verhulst *et al*. (*12*) found that humans with higher microbial diversity on their skin were less attractive to these mosquitoes. High abundances of *Pseudomonas* spp. and *Variovorax* spp. were also associated with poor attractiveness to *A. gambiae*. These bacteria may produce chemicals that repel mosquitoes or mask attractive volatiles emanating from human skin. Given the importance of chemical communication throughout the animal kingdom, symbiont alteration of host chemistry may be a potent force that shapes many fundamental animal behaviors.

Animal microbiomes often consist of thousands of species of bacteria, many of which cannot be cultivated outside the host. Rapid advances in metagenomics are allowing characterization of microbiomes beyond the few cultivable microbes (*10*, *13*, *14*). However, determining which animal behaviors influence and are influenced by microbial symbionts, and the mechanisms underlying these interactions, will require a combination of molecular and experimental approaches. For example, Huang *et al*. have studied the settlement behavior in the marine tubeworm *Hydroides elegans*. Bacterial biofilms play a key role in the settlement behavior of many marine invertebrates, from corals to sea urchins. To study the *H. elegans* system, the authors used transposon mutagenesis to knock out a number of genes from the bacterium *Pseudoalteromonas luteoviolacea*, which is required for larval settlement. Mutagenesis of four genes related to cell adhesion and secretion generated bacterial strains that altered worm settlement behavior and metamorphosis (*4*). It remains to be shown whether similar bacterial phenotypes drive this important life-history transition across metazoans.

Microbiomes impact behaviors

Animal	Microbial species or consortium	Interaction with behavior	Implication
 Fruit fly (*Drosophila melanogaster*)	Gut microbiota	Diet-specific microbiota influence mating preferences	Microbes could drive speciation
 Mosquito (*Anopheles gambiae*)	Human skin microbiota	Skin microbes of humans influence attraction to mosquitoes	Differential attraction could impact disease spread
 Mouse (*Mus musculus*)	*Lactobacillus rhamnosus*	The probiotic *L. rhamnosus* decreases anxiety in mice	Suggests bacteria can alter mood

Microbiomes alter behaviors. In fruit flies (*2*), mosquitoes (*12*), and mice (*5*, *6*), microbes alter mating, feeding, and anxiety levels.

PHOTO CREDITS SECOND FIGURE: (MOSQUITO) J. GATHANY/CENTER FOR DISEASE CONTROL; (MOUSE) G. SHUKLIN/WIKIMEDIA COMMONS; (FLIES) T. CHAPMAN/UNIVERSITY OF EAST ANGLIA

Some animal behaviors will be linked to single microbial species, but many will involve communities of multiple microbial species. It is unclear how fluctuations in the microbiome throughout the host life cycle drive behavioral traits and vice versa. Another challenge is to identify when behavior shapes the microbiome, when the microbiome shapes behavior, and when there is a complex feedback between the two. This requires manipulative experiments and will be facilitated by studying the underlying mechanisms by which signals are sent between hosts and microbes.

Recent experiments with mice, showing that the gut microbiome can influence stress, anxiety, and depression-related behavior via effects on the host's neuroendrocrine system, provide insight into how information can be passed between a host and microbe (*5*, *6*). Mice fed with the probiotic *Lactobaccillus rhamnosus* fared better in a forced swim test, an indication of lower anxiety, and showed higher expression of γ-aminobutyric acid receptors in the brain. Partial removal of the vagus, a central communication nerve between gut and brain, obliterated the probiotic effect, suggesting that this nerve transmits information on gut bacteria to the brain (*5*). If beneficial microbes are also found to modify neural and endocrine activity in the brain in other animals, then they have enormous potential to influence how animals behave toward one another.

Experimental approaches that evaluate the behavioral consequences of microbiome manipulation will be key to addressing outstanding questions. Similarly, studies that manipulate animal behavior—for example, by swapping social or mating partners or by enhancing or blocking neuroendocrine function—can be used to identify behaviors that alter microbiomes. Through either approach, the interface between the fields of microbiology and behavior is poised to expand our understanding of complex microbial communities already known to shape animal nutrition and health (*13*, *14*) and to unveil a hidden dimension of animal behavior.

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Acknowledgments: This perspective was made possible thanks to NSF meeting grant IOS 1229439 "Meeting: The Future of Research in Animal Behavior." We thank B. Parker, A. Laughton, B. Wehrle, C. Fontaine, and D. Ditmarsch for discussion and comments.

10.1126/science.1227412