

# New Synthesis: Animal Communication Mediated by Microbes: Fact or Fantasy?

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We are not alone. The metabolic potential of all animals is augmented by that of a vast diversity of resident microbes. All animals bear many, metabolically diverse microorganisms that are responsible for a significant fraction of the inventory of compounds in animal tissues and secretions (Nicholson et al. 2012). In principle, the metabolic capabilities of microorganisms enable animal hosts to sample chemical diversity unavailable from the animal genome, and the resultant chemical repertoire can permit innovation and rapid trait evolution. The microbial origin of much of animal chemistry raises the question whether microbial compounds mediate interactions among animals, especially in animal communication. Are microbial products utilized as cues or signals that indicate vigor or social status as kin, group member, mate, *etc.*? Additionally, what are the evolutionary processes that mediate the origin and persistence of microbial-mediated communication, as opposed to communication *via* chemical signals synthesized by the animal host?

The first step in the study of microbial-mediated communication among animals should be a sober assessment of the evidence, for large claims demand strong evidence. The task is somewhat equivalent to Koch's postulates to identify disease-causing microbes. Let us consider info-chemical *X*, which is produced in animal-A and alters the behavior of animal-B. Three lines of evidence are required to demonstrate that *X* is synthesized by the microbiota in animal-A: (1) Member(s) of the microbiota in animal-A can synthesize *X*. (2) Elimination of the microbiota from animal-A results in the co-incident loss of *X* and the behavioral trait of animal-B; and (3) the behavior of animal-B is reinstated by interaction with microbe-free animal-A supplemented with the info-chemical *X*. Most published studies on the role of microorganisms in animal communication do not meet all three criteria. Until these criteria are met in multiple studies, it will remain an open question whether microbial-mediated animal communication is a widespread phenomenon, and how its incidence varies across animal groups and with ecological circumstance *etc.*

In the best traditions of chemical ecology, resolution of the proximate questions should go hand-in-hand with analysis of the ultimate explanations: what are the selection pressures that favor animals to outsource the production of info-chemicals to members of their resident microbiota? In some situations, microbial products may be an honest signal of health, equivalent to brilliant coloration, a deft courtship dance, or a loud roar. The best evidence comes from the biomedical literature, including correlations between the composition of the gut microbiota or their metabolites and disease, including type 2 diabetes and cardiovascular disease (Nicholson et al. 2012). Microbial products also may be a reliable guide to kinship

or group identity of animals. Data for humans and laboratory mice are equivocal, but a role of microbiota in social communication has been suggested for hyenas, based on the limited evidence that the scent glands of hyenas bear bacterial communities that differ more between individuals of different social groups than members of the same social group (Theis et al. 2012).

Although the resident microbiota generally is beneficial for the animal host, the selective interests of animal and microbes may not be totally co-incident, resulting in conflict between the partners. For microorganisms, an animal host is a nutrient-rich habitat and a route for dispersal, and their selective interest in the survival and reproduction of the host depends critically on their residence time and incidence of vertical transmission to host offspring, respectively. We can envisage, for example, that many members of the gut microbiota would favor not only high rates of animal feeding, mobility, and defecation, but also social behaviors that promote their dispersal. Microbial manipulation of the host could result in signaling that is dishonest or otherwise poorly matched to host phenotype. Consider, for example, a microorganism with some capacity for vertical transmission from mother to offspring. Its inclusive fitness in male animals would be enhanced by preferential mating with female conspecifics bearing related microorganisms, even though this behavior may restrict the number of matings, and therefore the fitness, of the male host. A candidate example may be provided by *Drosophila melanogaster* (Sharon et al. 2010). Male flies have been reported to mate more readily with females bearing the same gut microbiota than with those bearing a different microbiota.

As we consider the evolutionary origins of microbial contributions to signal exchange in animals, we should not neglect that these interactions may be ancient. Unicellular eukaryotes (protists) are often colonized by non-pathogenic bacteria, suggesting that our ancestors were multi-organismal before they were multicellular. Just as many of the molecules mediating signaling within animal cells (*e.g.*, cAMP) evolved very early in cellular life, animal predisposition to utilize certain microbial products (*e.g.*, fermentation products) for among-individual communication may be an ancient inheritance. The discipline of chemical ecology has the exciting opportunity to dissect the role of microbial info-chemicals in communication among animals, and the evolutionary basis of these interactions.

## References

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