# Microbes and animal olfactory communication: Where do we go from here?

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**We know that microbes contribute to the production of odors that some animals use to communicate, but how common is this phenomenon? Recent studies capitalizing on new molecular technologies are uncovering fascinating associations between microbes and odors of wild animals, but causality is difficult to ascertain. Fundamental questions about the nature of these unique host-microbe interactions also remain unanswered. For instance, do microbes benefit from signaling associations with hosts? How does microbial community structure influence signal production? How do hosts regulate microbes in order to generate appropriate signals? Here, we review the current state of knowledge on microbially produced signals in animals and discuss key research foci that can advance our understanding of microbial-based signaling in the animal world.**

**Keywords:**
bacteria; chemical signals; microbes; olfactory communication; scent mark

## Introduction: Are microbes involved in animal communication?

The role that symbiotic microbes play in the lives of animals from development to physiology and health has gained increasing attention as new molecular techniques allow for the exploration of previously unknown relationships [1, 2]. The influence of microbes on animal behavior is particularly fascinating, and new discoveries are revealing that microbes can modulate a number of complex animal behaviors [3, 4]. This is especially true in the area of animal communication, where symbiotic microbes were first hypothesized to be important sources of olfactory signals over 30 years ago [5–7].

Olfactory communication via chemicals is one of the most common ways in which animals send and receive information [8, 9]. Animals acquire olfactory signaling molecules in several ways. These signals can be by-products of essential biochemical pathways [10], or gathered from the environment rather than synthesized [9, 11]. In addition to de novo synthesis and collection, many animals may use molecules produced by their microbial symbionts as olfactory signals [3, 11, 12]. How common microbial synthesis is, compared with other forms of signal production, is still poorly understood, but unraveling the extent to which microbes contribute to olfactory signaling could re-shape long-standing ideas about animal communication.

Causal inference has played a central role in studies of chemical communication since the identification of the first animal pheromone [13]. The same type of rigor is required to determine whether microbes are involved in the production of animal pheromones and other olfactory signals [14], but methodological challenges have impeded progress. Now, new technologies allow these methodological problems to be addressed, opening up a number of fascinating research directions. Here, we review the current state of knowledge on microbially produced signals in animals, and discuss three research foci that can advance our understanding of the phenomenon, including: (1) establishing causal relationships between microbes and olfactory signals; (2) investigating connections between the structure and function of microbial communities that produce olfactory signals; and (3) examining the evolutionary origins and maintenance of host-microbe signaling interactions. Throughout, we draw parallels between microbial-based signaling and other host-microbe associations to highlight theory and tools from other

DOI 10.1002/bies.201400016

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disciplines that can shed light on the role of microbes in animal communication.

## How common are microbially produced olfactory signals in animals?

A first step towards understanding the importance of microbial contributions to animal signaling is exploring the generality of the phenomenon. The idea that microbes play a role in producing chemicals that animals use for olfactory communication has roots in the fermentation hypothesis of chemical recognition (Box 1). However, decades after this hypothesis was first proposed, microbial production of olfactory signals has been described in mammals and insects, but few other taxa (Table 1). Studies on mammals range from those that identify or propose that microbes are present in host scent secretions that influence behavior (e.g. greater sac-winged bat [15], Asian and African elephants [16], European badger [17]), to those that report a correlation between microbial composition and host odor profiles (mouse [18], spotted and striped hyenas [19]), or provide experimental evidence that microbes produce signaling odors (Indian mongoose [7], mouse [20]).

Insect studies provide additional examples of microbial-based signaling, and highlight the fact that fermentation is not the only metabolic process by which microbes produce host odors. For instance, experiments on the desert locust (*Schistocerca gregaria)* tied gut bacteria to the production of a major component of a locust aggregation pheromone, the volatile guaiacol [21–23]. Bacteria convert vanillic acid, a locust digestive waste product, to guaiacol by decarboxylation [21]. Microbes other than bacteria also produce insect signals, as is the case in several bark beetle species, where fungi produce components of aggregation pheromones via fermentation or oxidation [24–27].

While the evidence points to a potentially broad distribution of microbial-based signaling in mammals, insect examples are more limited in taxonomic breadth (Table 1). Beyond mammals and insects there are no clear examples, so future work on other taxonomic groups is needed to establish whether this phenomenon is widespread or restricted to certain groups. Thus far, indirect evidence suggests that microbes may also be involved in the production of olfactory signals in other taxa (Table 1). In several bird species, for example, symbiotic microbes are found in the uropygial gland [28–30], and these glands also contain volatile compounds used for species recognition and other signaling purposes [31–33]. Bacteria in the uropygial gland are known producers of volatile antimicrobials that help birds counter feather-degrading bacteria [28, 30, 34], so it is conceivable that microbes produce chemicals used for communication as well.

### Box 1

### Decomposing the fermentation hypothesis of chemical recognition

Many mammals have specialized organs that secrete chemical compounds used as olfactory signals. These scent glands produce odorous secretions used for marking territories, attracting mates, and social aggregation [59]. The "fermentation hypothesis of chemical recognition" states that bacteria inhabiting mammal scent glands play a role in producing the odor of mammal scent secretions [59, 60]. Specifically, these odors are thought to be the products of bacterial metabolism [5, 6]. The fermentation hypothesis argues that bacterially derived odors are involved in individual recognition, and that differences among individuals in their symbiont communities drive individual variation in odor [7]. Common "group" odors may also arise because of cohabitation among group members and microbial cross-infection [5]. As such, signature odors originating from bacterial communities may help broadcast information about individual identity, group membership, and even kinship [7, 61].

Early work on the fermentation hypothesis showed that mammal scent glands often contain bacteria that are well-documented odor-producers [3]. However, a significant challenge to testing the hypothesis was the inherent difficulty in obtaining comprehensive information on the bacteria housed in these glands [59]. Now, new molecular techniques have helped re-invigorate work on this topic. For instance, use of next-generation sequencing revealed that anal scent gland secretions of spotted hyenas are densely populated with odor-producing bacteria [62], and over 300 bacterial OTUs have been characterized from hyena paste [19]. Other methods, including terminal restriction length polymorphism analysis (T-RFLP) and automated ribosomal intergenic spacer analysis (ARISA) were used to describe 56 distinct bacterial OTUs in the sub-caudal glands of European badgers [17], and 251 OTUs in the anal pouch of meerkats [63], respectively. Future studies spanning multiple taxonomic groups and integrating molecular, experimental, and culture-based approaches will help clarify the extent to which these diverse microbes are involved in mammal recognition in particular and animal olfactory communication more generally.

A recently deposited spotted hyena (*Crocuta crocuta*) scent mark emitting odors produced by symbiotic bacteria. A conspecific can take up some of the scent by depositing its own paste directly over the previous mark (Hyena photo credit: Sesh Sundararaman).

**Table 1. An overview of major animal taxa with evidence of microbial olfactory signal production, including taxonomic representation of species by order, number of species with experimental evidence of causation, and representative examples**

| Group | # Species | Taxonomic representation (# Species by Order) | Species with experimental evidence | Example | Description |
|---|---|---|---|---|---|
| Mammal | 21 | **Carnivora (7)** [6, 7, 16, 17, 19, 20, 63, 64] **Rodentia (5)** [18, 20, 65–72] **Chiroptera (1)** [15] **Artiodactyla (2)** [73–75] **Primate (3)** [76–78] **Proboscidea (2)** [38] **Lagomorpha (1)** [79] | **Carnivora (1)** [19] **Rodentia (1)** [20] |  | In the Indian mongoose (*Herpestes auropunctatus*), odorous volatiles produced by bacterial metabolism originate from the anal pocket and allow for individual recognition [6, 7]. |
| Insect | 9 | **Coleoptera (6)** [24–27, 80–82] **Diptera (2)** [53, 83] **Orthoptera (1)** [21–23] | **Diptera (1)** [53] **Orthoptera (1)** [21–23] |  | In desert locusts (*Schistocerca gregaria*), gut bacteria produce the volatile compound guaiacol, a key component of an aggregation pheromone [21–23]. |
| Bird | 0 | NA | NA |  | Bird species such as the European hoopoe (*Upupa epops*) have symbiotic bacteria in their uropygial glands that produce volatiles with antimicrobial properties [30]. These volatiles may also be involved in signaling [28, 29, 34]. |
| Reptile | 0 | NA | NA |  | Volatiles from femoral gland secretions in lacertid lizards (*Psammodromus algirus*) that may play a role in social communication may also be a product of bacterial metabolism [84]. |
| Amphibian | 0 | NA | NA | **?** | No known studies |
| Fish | 0 | NA | NA | **?** | No known studies |

Stars on the bird and reptile examples indicate that these are speculative cases. All images were downloaded from Wikimedia Commons. Publications for the table were derived from a systematic search of the literature using three databases: Web of Science, PubMed, and Google Scholar (for years spanning 1971–2014). Combinations of the following search terms were used: (a) behavioral terms: communication, scent mark, pheromone, odor, semiochemical, chemical signal; and (b) microbe-related terms: metabolite, microbe, symbiotic, microflora.

## Microbes and mammal odors: From correlation to causation

Mammals are the most-studied taxon in terms of microbial-based olfactory signaling, yet evidence from this group is still rather weak in two respects. First, only in a few cases have cause and effect relationships been established. Second, the specific microbes involved are typically unknown. Out of 21 mammal species with some evidence of microbial involvement in signal production, only two – Indian mongoose and mouse – have experimental support for causation (Table 1). However, a recent study by Theis et al. [19] on hyenas highlights how modern molecular tools are facilitating progress in new study systems. Theis and colleagues established a strong correlative link between the diverse communities of bacteria in hyena scent gland secretions (pastes) and volatile (odor) profiles using a combination of next generation sequencing and gas chromatography-mass spectrometry. Their results showed that bacteria communities and volatile profiles of paste co-varied significantly in two hyena species. They also found that paste bacteria profiles were related to individual characteristics in spotted hyenas (*Crocuta crocuta*); males, pregnant females, and lactating females from a single clan differed in the relative abundance of key members of their bacterial paste communities, and the odor profiles of the pastes varied in a consistent manner (Fig. 1). Taken together, these results provide some of the strongest support to date for microbial production of olfactory signals in non-laboratory mammals. The study suggests that differences in paste bacteria communities account for

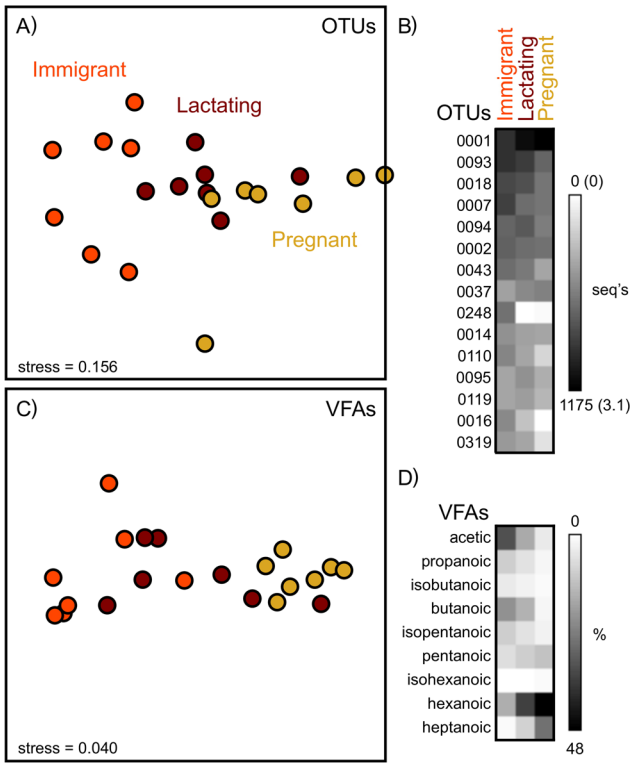


**Figure 1.** Bacteria (OTU) and odor (volatile fatty acid, VFA) profiles of immigrant male, lactating female, and pregnant female scent secretions from a single spotted hyena clan ($n = 7$ for each class). **A and B:** A plot of variation in bacterial community structure and a heat map of mean abundances of the most common bacteria. **C and D:** A plot of variation in odor profile, and a heat map of mean percent abundances of VFAs. A and B illustrate differences in composition and relative abundance of bacteria across sex and reproductive states; C and D show analogous variation in VFA profiles. Bacterial and VFA profiles of pregnant and lactating females showed significant covariation (A, C). Figure reproduced with permission from [19].

variation in hyena odor, and that the differences in odor profiles may be biologically meaningful in terms of signaling. However, causal links between specific microbes and odors have yet to be established.

Causal inference about microbially mediated signaling requires two critical steps: (1) establishing a direct link between microbes and signalers' odors; and (2) understanding the connection between microbes and the responses that the odors provoke in receivers. A recent study of the bacteria-derived olfactory signal trimethylamine (TMA) in laboratory mice (*Mus musculus*) fulfilled both criteria [20]. TMA is a highly volatile chemical attractant found in mouse urine. Li and colleagues found that mice treated with antibiotics, or fed a choline-free diet, produced urine with ~90% less TMA, and that mouse urine depleted of TMA was less attractive to other mice. Even though the specific microbes involved were unknown, causality was supported by demonstrating that removal of gut microbes nearly abolished both the specific chemical signal produced by senders and the attraction response in receivers.

Unlike mice, many mammals are not easily manipulated in the lab, so how can causal inference be extended from the laboratory to other situations? Molecular characterization of the relevant microbial communities is an important step because it can help identify target microbes that may be involved in odor production. Practically, sampling of many animal scent secretions (e.g. urine, feces, scent marks) can be done under non-laboratory conditions. Once microbial profiles are known, experiments are necessary. One experimental approach that can facilitate causal inference is testing whether the elimination of specific groups of microbes in vivo, possibly via the targeted application of antibiotics, can disrupt production of specific chemical compounds in signalers and corresponding behavioral responses in receivers. Many studies of free-ranging vertebrates use drug treatments to test effects of parasites on hosts [35–37], so related approaches for evaluating microbial contributions to olfactory signaling are feasible outside of the laboratory. Specific microbes involved in the production of important signals can also be narrowed down by re-introducing different subsets of cultivable microbes to animals that are microbe free, analyzing the odor profiles of these experimental signalers, and then testing for the restoration of effective communication between signalers and receivers.

Directly manipulating free-ranging animal hosts may not be practical or ethical in some instances, so manipulating scent secretions instead of animals themselves may provide an alternative. In elephants, for example, where preliminary studies suggest that microbes are involved in the temporal release of olfactory signals from male urine [38], adding cultured microbes to sterilized urine, and testing whether this restores the release of key volatiles would directly link microbes to signal production. For host species found in captivity, such as elephants, captive individuals could be used to test for effects of microbial addition on receiver behavior. Another approach would be to synthesize odors from candidate microbes cultured in the lab, and then test whether these artificial odors affect host behavior. For example, Theis et al. [19] suggested that a next step in their hyena studies could involve the production of synthetic mixtures of chemical compounds from cultivars of paste bacteria, followed by testing whether hyenas respond to these volatiles. Coupling in vitro chemical synthesis of odors with in vivo field bioassays that confirm signaling activity would directly tie specific groups of microbes to specific chemical mixtures that modify hyena behavior.

## Microbial signal production as an ecological problem

Microbial communities in animal scent secretions can be highly diverse (Box 1), and most microbes that produce animal chemical signals are likely members of multi-species communities or consortia. As such, interactions between species may be important drivers of variation in microbial communities themselves and the signals they produce. In the past few years, microbiologists have found that community ecology can provide a useful framework for understanding the structure and function of many host-associated microbial communities [39, 40]. Likewise, theory from community ecology can be used to

address questions related to how microbial communities involved in olfactory signal production assemble; the stability of these communities over time; and the relationship between microbial community structure and function in terms of the quality or quantity of signal production.

Environmental microbe communities are increasingly being used as models to explore relationships between diversity and ecosystem function, a hotly debated topic in ecology [41, 42]. One pattern that has emerged from these studies is of a positive, asymptotic relationship between species diversity and function, which suggests that multiple microbial species contribute to the same function. A recent review quantified the observed frequency of this redundancy pattern for soil microorganisms that contribute to carbon cycling. The study found that positive associations between diversity and function were observed 44% of the time for soil communities comprising 10 or more species; and where the shape of the positive relationship could be determined, a pattern consistent with redundancy was most common [43]. Intriguingly, functional redundancy may be an attribute of some microbial communities responsible for producing animal olfactory signals. In the desert locust, for example, production of guaiacol has been induced in vitro by inoculating fecal pellets of germ-free locusts with at least three distinct bacterial species: *Pantoea agglomerans*, *Enterobacter cloacae*, and *Klebsiella pneumoniae pneumoniae* [22]. Several other plant-associated microbes that constitute the locust gut microbiota may also perform this function, and it has been suggested that locusts associate with multiple "redundant" microbes to minimize the negative consequences of the loss of any one species on production of important compounds [22, 23].

Indeed, a prominent hypothesis about functional redundancy in ecological communities is that higher levels of redundancy increase the reliability with which ecosystems perform key functions [44], hence providing "insurance" against individual species fluctuations [45, 46]. Considered in the context of microbial signal production, if higher levels of functional redundancy are related to the reliability of signal production, one prediction is that high functional redundancy in the microbial community might be characteristic of signals for which reliable production is essential (e.g. species recognition signals). By contrast, signals that are more transient (e.g. signals related to the current status of an animal, such as reproductive state) might be associated with less redundant microbial communities (Fig. 2). Patterns observed for other host-microbe associations are consistent with this idea. For example, a study of the gut microbe community in lean and obese humans found that very different sets of bacteria species were associated with synthesis of essential vitamins in the two groups [47]. This may reflect high microbial redundancy for critical functions of the human gut microbiota.

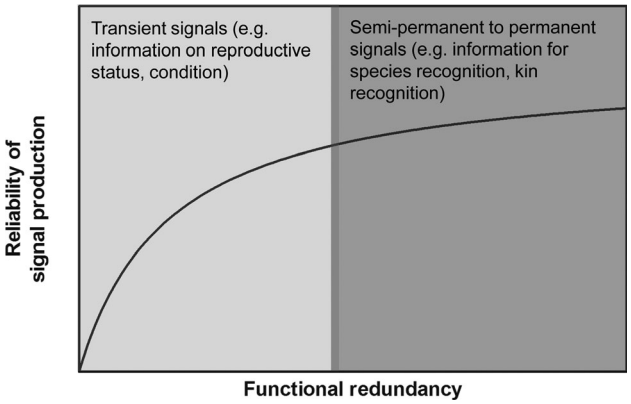


**Figure 2.** Hypothetical relationship between the level of functional redundancy in olfactory signal production in a microbial community and the reliability with which the signal is produced. At higher levels of functional redundancy, multiple species produce the same signaling compounds. The reliability with which a signal is produced (e.g. its quantity through time) is predicted to increase with increasing functional redundancy in a saturating manner. Transient signals that vary with host status – such as indicators of reproductive condition, body condition, or social status – might be more likely to be associated with less functionally redundant microbial communities. On the other hand, permanent signals – such as those that provide information for species and kin recognition – might be associated with highly redundant communities.

## Evolution of host-microbe interactions in the context of olfactory signaling

Many chemical signals may have evolved from pre-existing substances released by signalers (e.g. waste products) that convey inadvertent information to receivers [8, 11]. Where the reaction of receivers to these substances is beneficial to the sender, selection may act to improve the efficacy of information transfer by increasing the quantity or quality of the signal [8]. The action of microbes can be readily co-opted for this purpose, potentially explaining the evolutionary origin of certain classes of microbially produced signals. For example, hosts can exploit bacterial metabolism to amplify volatiles in dietary by-products, thereby increasing the quantity of signals produced. Indeed, both the production of guaiacol by desert locusts [22] and TMA by mice [20] rely on the action of bacteria on host dietary components. Vanillic acid, the precursor of guaiacol, is derived from locusts' food plants [21, 22], and biosynthesis of TMA in mice involves the metabolism of choline, an essential nutrient found in many plant products [20]. Interestingly, TMA production is both higher and more sex-specific in *Mus musculus* compared with related rodent species. The reason is that these mice have mechanisms to decrease gene expression of an enzyme that oxidizes TMA to a non-volatile, non-odorous form [20]. Thus, the evolutionary origins of abundant TMA production in *M. musculus* may involve both microbial metabolism of dietary components and sophisticated mechanisms of host gene control.

If microbes enhance the efficacy of host signaling by contributing new chemicals or amplifying existing ones, then animal hosts clearly benefit. But what's in it for the microbes? Are signaling associations between hosts and microbes mutualisms? If microbes receive resources (e.g. host dietary products such as vanillic acid and choline) or habitat (e.g. in specialized animal "scent" glands) that enhance growth, these are possible benefits. Another benefit for microbes could

be enhanced between-host transmission. In some host species, scent-sharing behaviors that facilitate exchange of odors are well-characterized. For instance, spotted hyenas from the same clan share scent via pasting and over-pasting behavior where one individual deposits a scent mark on vegetation and another takes up some of this scent while depositing its own secretion [48]. Similarly, badgers engage in allo-marking behavior where scent gland secretions are deposited directly onto conspecifics [49, 50]. These scent-sharing behaviors may facilitate the transmission of microbes along with odors [48–50], hence enhancing microbe fitness; however, whether this is truly the case or not is unknown. To test this idea, social network analyses and infectious disease modeling could be used to explore the contribution of scent-sharing behaviors to the population-level spread of odor-producing symbionts.

The possibility that specific host behaviors evolved to facilitate the exchange of odor-producing microbes – contributing to the maintenance of these host-microbe mutualisms – raises additional questions: How do hosts ensure that they obtain the "correct" microbes during exchanges rather than free-loaders? Also, if different olfactory signals are encoded by different microbial species, how does a host change its microbial community in a way that allows flexibility in signal production? Studies of the gut microbiota suggest a possible mechanism in which host physiology helps regulate the microbial community. In humans, the gut microbiome shifts drastically over the course of pregnancy, possibly as a result of changes in host immunity or hormone levels [51]. Likewise, physiological differences associated with attributes of the host (e.g. sex, age, genotype, diet) might help regulate microbial communities associated with odor production. In fact, if host physiology is tightly coupled to microbial composition or activity, this may help ensure the honesty of microbially produced signals, a key attribute of stable signaling systems [52]. As an example, when *Drosophila melanogaster* were fed a molasses vs. starch diet, different bacterial communities emerged, and these differences produced strong mating preferences [53]. The change in fly mating behavior was attributed to diet-based amplification of certain bacterial species and associated changes in sex pheromones. Since diet appears to regulate microbial community structure and signal production, the quantity of sex pheromones may be an honest indicator of individual diet quality or habitat.

## Conclusions: Moving forward

The idea that microbes contribute to animal olfactory communication is intriguing. Mammal and insect studies provide evidence that this phenomenon occurs in some animal groups, but where do we go from there? First, manipulative field studies can greatly enhance our understanding of the distribution of microbial-based signal production in nature. In birds, for example, where trait-based variation in gut and uropygial gland microbial communities has been described in some species [54, 55], manipulating free-ranging animals by eliminating microbes, swapping scent secretions among individuals with different traits of interest, and testing for changes in odor and conspecific behavior can causally link microbes to aspects of avian communication. In conjunction with molecular approaches, these studies could reveal exciting new examples of microbe-related signaling.

Second, creative laboratory studies can be used to test new ideas arising from ecological and evolutionary theory. A recent study combined germ-free mice, next generation sequencing, and mathematical modeling to explore ecological interactions among microbe species in the murine gut [56]. Similar methods can be used to examine relationships between structure and function in odor-producing microbes of mice, or investigate mechanisms underlying reliability in signal production. This approach can generate testable predictions about how specific microbial interactions influence odor production and how individual odor varies in response to physiological factors that affect abundance of certain species. Crucially, these predictions are amenable to testing in both lab and field settings. For example, animal manipulations employed by field biologists, such as hormone treatments and diet supplementation [57, 58], could be used to test whether specific perturbations alter microbial communities and odor production of wild mice in predicted ways. More generally, the potential to integrate experimental approaches with molecular and computational tools makes this an opportune time to explore fundamental questions about these unique host–microbe interactions.

**Acknowledgments**

We thank the editor for the invitation to write this review and Kevin Theis for providing Figure 1. Paul Snyder kindly assisted with the production of the figure in Box 1, and two anonymous reviewers provided constructive comments on earlier drafts. The writing of this review was supported by funding from a National Science Foundation CAREER Award to V.O.E (IOS-1101836).

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