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Leveraging non-human primates for exploring the social transmission of microbes

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Host social interactions can provide multiple complex pathways for microbial transmission. Here, we suggest non-human primates as models to study the social transmission of commensal or mutualistic microbes due to their high sociality, wide range of group compositions and dominance structures, and diverse group interactions. Microbial sharing from social interactions can positively impact host health by promoting microbial diversity and influencing immunity. Microbes may also drive their own transmission by shaping host behavior, which could lead to fitness benefits for both microbes and hosts. Variation in patterns of social interactions at both the individual and group scale make non-human primates an ideal system to explore the relationship between social behavior, microbial sharing, and their impact on host health and evolution.

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Introduction

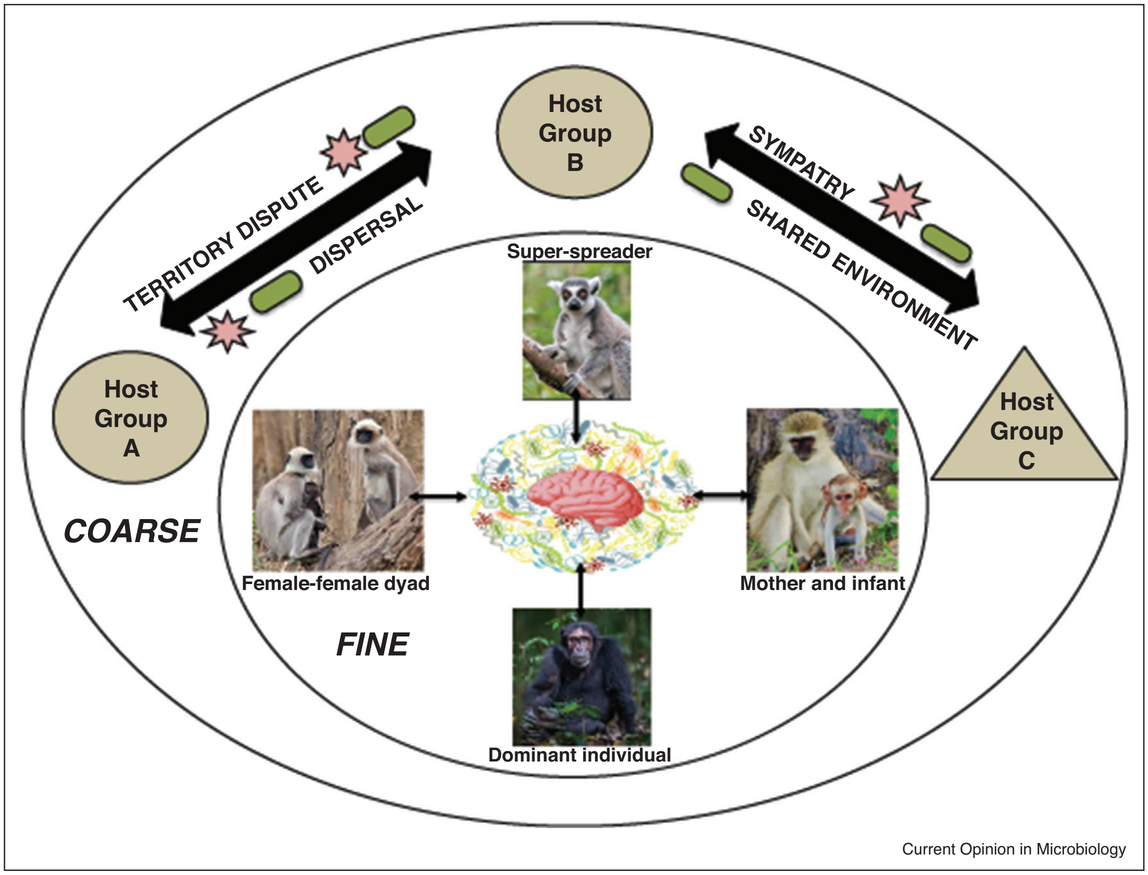
Group living is widespread in animals and is thought to promote sociality and increase fitness through mechanisms like reduced predation and increased reproduction [1,2]. It can also provide a pathway for microbial transmission. While pathogenic microbial transmission is well studied [3,4], far less is known about how sociality promotes the transmission of commensal or mutualistic microbes. We suggest non-human primates (NHPs) as models to study the social transmission of microbes due to their high sociality, wide range of group and dominance structures, and diverse intra-group and inter-group interactions. Although NHP social interactions are well characterized, applications to the microbiome are currently understudied, especially at the interface of sociality and microbial sharing. Importantly, the diversity of NHP social structures can provide evolutionary frameworks to model sociality and microbial transmission in humans. Here, we first examine the evolution of host-microbe interactions in NHPs and then consider how elements of primate sociality can impact the social transmission of microbes.

Sociality and microbial transmission

Microbes provide essential 'ecosystem services' for hosts, including maintaining homeostasis in the digestive tract, providing energy, and regulating the immune system [5,6]. Although vertical transmission from parent to offspring may seed initial gut microbiome development, horizontal transmission from the abiotic and biotic environment provides a crucial route for microbial exposure. In mammals, a major component of horizontal microbial transmission occurs between conspecifics during social interactions. NHPs are extremely social compared to other animals, making them an ideal model for analyzing horizontal microbial sharing. Although challenges exist when working with NHPs, including obtaining samples other than feces and urine, acquiring longitudinal samples from known individuals, accessing samples from infants, and collecting robust contextual data describing social and physical environments, long-term research projects exist for many NHP species and can provide the necessary infrastructure to overcome these challenges (Figure 1).

While microbial transmission due to sociality has traditionally been viewed as a risk for pathogen exposure, it may also be essential to host health if it facilitates the acquisition of beneficial microbes, particularly those that might not be gained through other mechanisms [2]. Given that most NHPs live in groups that facilitate almost constant social interactions, it is relevant to consider the potential microbial benefits that may be associated with group living. First, microbial sharing between conspecifics can create a shared microbial metacommunity, where microbial dispersal across group members promotes microbial species richness within and between individuals [7,8••]. This metacommunity can influence conspecific recognition and bonding, group-specific scent marks, and immune synchronization [2,9–14]—all of which affect host health, behavior, and fitness. Additionally, Moeller *et al.* [15] suggest microbial metacommunities may preserve microbial diversity by decreasing stochastic bottleneck extinctions that could occur in a system with solely vertical transmission. Elevated

Figure 1



Current Opinion in Microbiology

Nested scales of microbe-environment-host interactions. Microbes influence host physiology and behavior, which may impact patterns of *fine* social interactions between individuals. These interactions are dictated by individual sociality and behavior, including mating, grooming, and caring for dependent offspring, which directly influence microbial transmission. At the level of *coarse* social interactions, group-level dynamics, such as dispersal, territory dispute, and living in sympatry, drive patterns of microbial transmission between groups of both the same and different species, as indicted by the host group shapes. Shared environments may also be important mechanisms of transmission. Image credits: https://learn.genetics.utah.edu/content/microbiome/intro/; https://www.medicalnewstoday.com/articles/324998.php; Sue Roehl; Sandeep Gangadharan; Bas Versteeg; Will Burrard-Lucas.

microbial diversity is a proxy for host health, as it increases resilience to community perturbations and preserves functional capacity in hosts [16]. Therefore, mechanisms to maintain microbial diversity are likely under selection pressure.

Because of the potential benefits of horizontal microbial transmission, suites of social behaviors may have evolved to buffer against transmission of pathogenic microbes while facilitating sharing of beneficial ones [2,14,17,18]. Though limited empirical data exist to support this hypothesis, many primate behaviors could serve these functions. For example, partner choice can promote beneficial microbial transmission while simultaneously restricting pathogen transmission (i.e. avoiding sick individuals) [19,20]. Similarly, mothers maintain close contact with offspring as their immune systems develop in the first years of life. In addition to protecting against pathogen exposure during this sensitive period, parent-offspring microbial transmission may serve as a component of social immunity [21–23].

Of course, a bidirectional relationship exists between hosts and microbes. While primate behaviors transmit microbes, microbes can modify certain host behaviors. For instance, microbes can influence host chemical secretions that drive social communication, like scent-marking in lemurs [12,24]. Similarly, microbes, like *Lactobacillus*, impact host anxiety and aggression via the gut-brain axis, suggesting a route for influencing host fitness through decision-making and affiliative behavior [17,25]. If microbes influence their own transmission by modifying host behaviors, then host social interactions may represent an adaptive route through which microbes colonize new host environments [17]. Certain anaerobic and spore-forming microbes are less likely to persist outside of a host and may rely on host sociality for transmission [24,26]. For example, anaerobic microbial taxa in phylum *Actinobacteria*, families *Bifidobacteriaceae*, *Coriobacteriaceae*, and *Veillonellaceae*, and genus *Bifidobacterium* are associated with social structures in savannah baboons, suggesting they may depend on social transmission routes [26]. Whether or not microbes are driving these host behaviors remains to be seen. A recent study suggested that microbes would benefit from influencing host behavior only when they persist at high abundances and/or when there is strong selection for transmission [27]—conditions which most gut microbes do not meet. However, while the extent of this relationship has yet to be elucidated, it is fascinating to consider that the evolution of host social behavior may represent fitness benefits for both hosts and microbes.

NHPs as models for understanding microbial social transmission

More studies on complex social systems are required to fully understand the importance of differential social interactions for microbial transmission, implications for host biology, and potential impact on the evolution of sociality. Since NHPs display a diversity of complex social systems, they provide opportunities to explore the reciprocity between sociality and microbial transmission in the context of host health, ecology, and evolution. NHP social interactions range from *fine* (between individuals of the same group) to *coarse* (between groups or species) [24]. *Fine* social interactions likely drive horizontal microbial transmission between group members, where opportunities are dictated first by group structure and membership. Primate societies range from relatively solitary individuals that interact sporadically, like aye–ayes [28], to small, monogamous, pair-bonded groups of titi monkeys [29], to multi-male, multi-female fission–fusion groups, like chimpanzees [30], and finally to large, multi-level social organizations, like hamadryas baboons [31]. These distinct group structures drive intragroup sociality, likely influencing microbial sharing between conspecifics and shaping individual microbiomes.

Evidence of these dynamics is starting to appear in the literature. Frequent social interactions promote gut microbial species richness in multiple NHPs [15,26,32••]. In Verreaux's sifaka, individual sociality is positively associated with higher microbial diversity [12]. Baboons that spend more time grooming display similar microbial profiles [26], and rhesus macaques with higher huddling frequencies demonstrate an increased likelihood of *Escherichia coli* transmission [33]. Position within the social network, a proxy for individual sociality, can predict an individual's microbiota profile in red-bellied lemurs [34•]. Similarly, repeated social interactions in young rhesus macaques during weaning yield gut microbial homogenization [35]. Thus, microbial similarity across individuals can indicate the strength of social bonds and group cohesion [20].

Certain subgroups of individuals may also be more likely to engage in specific inter-individual interactions that drive microbial exchange, biasing the likelihood of microbial transmission. For example, male-dominated social interactions like sexual encounters may lead to different disease transmission events compared to female-dominated interactions [36]. Alternatively, some subgroups of individuals may engage in social behaviors more frequently than others. Female humans and NHPs are typically more social than males, suggesting female sociality as a predictor of microbial transmission [32••]. A study in humans in Fiji found that women harbor microbial strains that are more similar to those of their social contacts, compared to men and their contacts [37]. Likewise, *Alouatta caraya* and *Alouatta pigra* adult female dyads with increased physical contact have more comparable gut microbiota, in contrast to female–male and male–male dyads [17,32••]. Furthermore, while empirical data describing microbial transmission and host physiology are missing, juveniles are more social than adults, which may be an adaptive, immune-related behavior that promotes increased colonization by beneficial microbes. A specialized example of this interaction is maternal care during the first years of life, which creates opportunities for microbial transmission between mothers and infants and may serve as primary microbial colonization events in infants. These individuals with frequent social interactions can serve as 'super spreaders' and contribute disproportionately to the dissemination of microbes across the group [12,38]. Future studies should further assess the impact of these and other social interactions, including mating and juvenile play, on microbial transmission and link *fine* social interactions to host health and fitness.

Finally, in hierarchical societies, dominance structures may influence patterns of microbial transmission. Dominant adults at the center of the social network experience increased numbers of grooming partners as well as overall physical contact with and proximity to conspecifics. In addition to providing other health benefits [38–41], this central position may expose dominant individuals to microbial transmission events important for health outcomes. In this context, it is also important to consider the likely role of sex differences in microbial transmission. For example, in Japanese macaques, dominant females engage in high levels of social contact, which can bias microbial transmission toward these individuals [42]. In contrast, social interactions in egalitarian societies, such as in stumptail macaques, may lead to more symmetrical microbial transmission across sexes and the group [43].

Given the range of interactions between microbes and host biology, microbial transmission at the *fine* scale may be a critical component of NHP health, ecology, and evolution. Moving forward, it is crucial to identify which microbial taxa are most likely to be shared among group members, how those taxa influence host biology, and which group-level social patterns serve as adaptive routes for the transmission of these taxa [12]. While existing data provide an important foundation, they represent only a subset of the diversity of NHP species and social interactions. Therefore, much work remains to be done.

Scaling up from *fine* interactions, substantial gaps also remain in our understanding of how *coarse* social interactions that occur across groups of the same or different species contribute to microbial metacommunity traits in host populations. Group membership is a stronger predictor of shared microbiota than kinship or diet across the Primate order, including in baboons, chimpanzees, red-bellied lemurs, Verreaux's sifaka, and geladas [12,26,34•,44–46]. Therefore, interactions among conspecific groups due to territory overlap and individual dispersal are likely to result in meaningful microbial shifts for both individuals and groups. For example, the gut microbiomes of immigrant males in the well-studied Amboseli baboon cohort were found to resemble those of long-term group members [47]. Similarly, a fission event in a group of black and white colobus monkeys resulted in two groups with distinct group microbial profiles within one year [48•]. However, the dose-response relationship between time spent in the group and gut microbiome similarity suggests that microbial turnover can take time. Longitudinal data from multiple groups of known individuals will be critical for exploring these dynamics further.

Moreover, as described for *fine* interactions, certain subgroups that engage in frequent *coarse* interactions may be more likely to share microbes. For example, sex-based philopatry and dispersal across groups may influence microbial transmission across groups. Balasubramaniam *et al.* [33] hypothesize that dispersing males of many species, including grey-cheeked mangabeys [49] and African elephants [50], act as 'microbial transmitters' between groups. Males who actively defend home ranges, like chimpanzees and slender lorises, may also experience differential exposure to microbial transmission, although this has yet to be explored in the literature. Understanding these dynamics, as well as how they relate to *fine* scale social dynamics, will be important to further describe the complexity of microbial social transmission. Since these patterns are widespread across mammals, exploring sex-based movement and behavior in NHPs can lead to a better understanding of microbial dynamics in other group-living animals.

Lastly, it is important to note that a shared environment mediates social interactions at the *coarse* level, creating opportunities for horizontal transmission in the absence of direct physical contact between individuals. In this context, the environment, including soil and water, can be considered a 'host' that harbors its own microbiome and acts as a reservoir for microbes to colonize other hosts. Direct physical contact between the skin and the environment, for example, may transmit microbes not only to the skin, but also to the mouth and gut through consumption of food that was in contact with skin [51]. In humans, shared spaces within the 'built environment' facilitate microbial transmission across individuals [51–53]. Additionally, Moeller *et al.* [54] found that chimpanzees and gorillas living in sympatry in equatorial Africa have similar gut microbial community composition, with chimpanzee gut microbiomes converging on the phylotypes of the gorilla gut despite distinct diets and no physical contact. However, given that a study of nine different wild primate species living in sympatry in Cote d'Ivoire found that each species harbors a distinct gut microbiome despite their shared environment [55•], further work is needed to determine the drivers of microbial acquisition from the environment as well as persistence in hosts. These data not only will improve our knowledge of microbial transmission routes at varying ecological scales and associated influences on host biology, but they will also inform our understanding of inter-community dynamics, including zoonotic pathogen transmission at human-animal interfaces.

Conclusion

The spectrum of interactions within and between social groups across the primate phylogeny results in differential opportunities for microbial transmission. Therefore, it is important to move beyond descriptive analyses of social interactions and general microbial similarity and identify specific behaviors that drive social microbial transmission. Studies should also explore differential transmission frequency patterns of particular microbial taxa. Understanding these dynamics is important for the field of primate ecology since it can reveal socio-ecological drivers of host fitness and guide conservation practices. Additionally, assessing the mechanisms of microbial transmission in primates may have implications for better understanding the behavior, health, and evolution of other group-living species. Finally, due to the diversity of their social systems, NHPs can also effectively model the behavioral complexity and evolutionary context of human-microbe interactions as well as the role that sociality played in shaping the human microbiome.

Despite the clear utility of this approach, key questions about the interplay between sociality and microbial transmission remain unanswered. For example, does larger group size correspond to more diverse microbes cycling among individuals, potentially leading to more host benefits? If so, how are the costs and benefits of group size balanced? Additional questions emerge from generational microbial transmission through matrilineal or patrilineal social structure and the effect of allocare on infant microbial transmission and colonization. Although samples from wild infant NHPs are difficult to obtain, it can be accomplished in some circumstances. Finally, there is a need for longitudinal microbiome data in both humans and NHPs. The majority of the current literature offers snapshots into gut microbiome structure but is limited in its application to understanding complex temporal dynamics [56]. Given that long-term studies of NHP behavior and physiology are relatively common, these data should be relatively easy to obtain. Interdisciplinary collaborations between microbiome scientists and primatologists can capitalize on this resource to rapidly advance this area.

Future studies on the influence of the shared environment on microbial communities should also incorporate the skin microbiome. Since the skin is constantly exposed to the outside environment, it likely reflects patterns of host behavior and movement and may facilitate the transfer of microbes from the environment (including conspecifics) into an individual's gut. While research into the skin microbiome is gaining traction in humans [57,58•,59,60], challenges still exist in investigating the skin microbiome of NHPs, particularly in the wild, since sampling is mostly limited to non-invasive practices. Nevertheless, sedation of wild NHPs does occur, and more innovative solutions are likely to emerge as interest in these questions grows.

The NHP field is currently equipped with numerous study sites, datasets, and researchers, all of which can be leveraged to address outstanding questions regarding host sociality and the microbiome. Although only a handful NHP researchers currently focus on this topic, interest is quickly growing. Future interdisciplinary research with an evolutionary perspective will strengthen our understanding of the interplay between sociality and microbial transmission, and its impacts on host biology and health, for NHPs, humans, and mammals more generally.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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