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# Stabilization and optimization of host-microbe-environment interactions as a potential reason for the behavior of natal philopatry

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## Abstract

Many animals engage in a behavior known as natal philopatry, where after sexual maturity they return to their own birthplaces for subsequent reproduction. There are many proposed ultimate factors that may underlie the evolution of natal philopatry, such as genetic optimization, suitable living conditions, and friendly neighbors, which can improve the survival rates of offspring. However, here we propose that a key factor that has been overlooked could be the colonization of gut microbiota during early life and the effects these microorganisms have on host performance and fitness. In addition to the bacteria transmitted from the mother to offspring, microbes from the surrounding environment also account for a large proportion of the developing gut microbiome. While it was long believed that microbial species all have global distributions, we now know that there are substantial geographic differences and dispersal limitations to environmental microbes. The establishment of gut microbiota during early life has enormous impacts on animal development, including energy metabolism, training of the immune system, and cognitive development. Moreover, these microbial effects scale to influence animal performance and fitness, raising the possibility for natural selection to act on the integrated combination of gut microbial communities and host genetics (i.e. the holobiont). Therefore, in this paper, we propose a hypothesis: that optimization of host-microbe-environment interactions represents a potentially important yet overlooked reason for natal philopatry. Microbiota obtained by natal philopatry could help animals adapt to the environment and improve the survival rates of their young. We propose future directions to test these ideas, and the implications that this hypothesis has for our understanding of host-microbe interactions.

## Introduction

In nature, many species with long migration distances display some degree of natal philopatry, or returning to their birthplace to breed the next generation [1, 2]. By means of this activity, animals can meet the environmental conditions they need during a specific period of life, likely resulting in higher survival and fitness of individuals [3–5]. However, the ultimate mechanisms underlying the evolution of natal philopatry are still poorly

understood. There has been a recently renewed appreciation for the role that host-associated microbes play in the performance and fitness of wild animals [6–9], including aspects of animal behaviors [10]. In this perspective article, we propose a potential role for these interactions to play in the evolution of natal philopatry. Specifically, we argue that by parents returning to natal habitats to breed, new offspring will acquire the optimal microbiome for their own physiological performance and fitness. We recognize that this idea is largely speculative but feel that it represents an exciting area for future research.

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Natal philopatry is a life-history strategy where animals locate and return to reproduce at the same geographic location in which they were born [11]. An equivalent term, “natal homing”, was first used when describing the migratory and breeding habits of sea turtles [12]. In addition to sea turtles and well-known groups such as songbirds and salmon, many other animal groups engage in natal philopatry (Table 1). The prevalence and taxonomic distribution of natal philopatry has been reviewed elsewhere for mammals [30] and birds [31, 32].

In recent decades, there has been a renewed appreciation for the fact that animals evolved in a world already dominated by microbes [33]. Therefore, many physiological processes in animals are intertwined with the action of microbial symbionts. Host-associated microbial communities have a number of impacts on their hosts, such as assisting with digestion or nutrient synthesis [34], providing protection against pathogens [35], aiding in the development of the immune system [36], and determining life history traits [37]. The hologenomic theory of evolution considers the collection of host and microbial genomes—known as ‘the holobiont’—a biological unit of organization upon which natural selection can act [38, 39]. There are numerous examples of connections between hologenomic evolution and aspects of animal behavior [10]. Here, we propose that microorganisms present in the natal habitat may be more suitable or beneficial for offspring, and thus returning to the natal habitat for reproduction may provide a fitness benefit to animals. We set up the rationale for this hypothesis by first reviewing the basics of natal philopatry, and then discussing how host-microbe interactions fit within these existing theories.

### **Mechanisms for Natal Philopatry**

How do animals locate their birthplaces to reproduce and generate offspring? Several proximate mechanisms for natal philopatry have been proposed. Early work on homing in turtles hypothesized that this behavior was proximately driven through “social facilitation”, where first-time breeders follow experienced females to a nesting beach, and having had a “favorable” breeding experience, fix on that site for future nesting [2, 40]. Related, Nordeng et al. (1977) proposed a “pheromone hypothesis”, where anadromous salmon might produce population-specific odors which guide them in homing migration [41]. However, imprinting on the natal site itself seems to be the most accepted mechanism underlying this behavior. Genetic analysis of natal philopatry in sea turtles is quite consistent with natal homing expectations and indicate that social facilitation to non-natal sites is uncommon [42]. There is some evidence sea turtles may imprint on the geomagnetic features of their natal beaches to return to these sites for

reproduction [43]. Additionally, although definitive evidence is lacking, it is widely assumed that Pacific salmon imprint on key features of their nesting region, like the chemical profile of the beach or surrounding waters, during development, and then use this information to return as adults [44].

While these hypotheses explain the proximate mechanisms of how animals are able to locate their natal sites, the evolutionary reasons, or ultimate mechanisms, for natal philopatry are still poorly understood. Below we briefly outline the current theories of the ultimate mechanisms for natal philopatry. For example, the advantage of local knowledge may enable animals to optimally exploit the resources of the area and to successfully defend their territories against competitors [45, 46]. Thus, over many generations and through natural selection, populations would become adapted to the conditions prevailing in their natal habitat [45, 46]. Indeed, individual Collard Flycatchers that are more philopatric exhibit higher reproductive fitness than those that disperse over larger distances [47]. Similarly, philopatric individuals of the Great Reed Warbler exhibit higher lifetime fitness when compared to immigrant individuals [5].

### **Reasons for animal’s natal philopatry**

#### **Evolutionary and genetic optimization**

The distance that young animals disperse from their place of origin before breeding has important implications for the extent of inbreeding and for the genetic structure of populations. Indeed, natal philopatry tends to result in high relatedness among individuals at a particular site [48, 49]. It has been proposed that natal philopatry may actually promote an optimal rate of inbreeding. While inbreeding is often viewed as detrimental due to the increased fixation of deleterious alleles, it can also offer benefits if alleles at various loci across the genome interact with each other in a beneficial manner. Thus, optimal inbreeding can reduce the costs of meiosis and recombination by preserving these interactions [50]. Such genetic optimization could be especially important for local adaptation associated with philopatry. For example, Coho salmon (*Oncorhynchus kisutch*) from more interior streams have greater swimming stamina as an adaptation to the longer migration distances [51]. It has previously been argued that gene flow between populations may erode these local adaptations [52]. Further, given that complex traits and adaptations are likely polygenic, maintenance of interacting alleles could also be important [53]. These genetic mechanisms could underlie the evolutionary benefits of natal homing behaviors.

#### **Suitable environmental factors**

Animals may also return to their birthplace for reproduction because these natal environments are most

**Table 1** Examples of natal philopatry**Insects**

- The spotted darter dragonfly (*Sympetrum depressiusculum*) exhibits strong philopatry to their natal ponds [13].
- The lesser marbled fritillary butterfly (*Brenthis ino*) returns to natal sites [14].

**Fish**

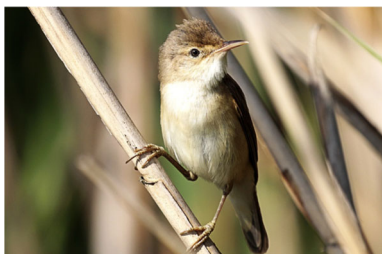
- Numerous species of salmonids (salmon, trout, char, etc.) migrate back to natal sites for spawning [15].
- In marine weakfish (*Cynoscion regalis*), spawning site fidelity ranges from 60 to 81% [16].
- Several shark species exhibit philopatric behavior [17].

**Amphibians**

- In marbled salamanders (*Ambystoma opacum*), roughly 90% of individuals return to their natal ponds for breeding [18].
- Several anuran species (frogs and toads) exhibit strong philopatry to their natal ponds [19–21].

**Reptiles**

- Both male and female green sea turtle (*Chelonia mydas*) return to natal rookeries to breed [22, 23].
- Female pine snakes (*Pituophis melanoleucus*) repeatedly return to nesting sites [24].

**Birds**

- Great Reed Warblers (*Acrocephalus arundinaceus*) exhibit limited dispersal, and remain in their natal habitats [25].
- The Wandering Albatross (*Diomedea exulans*) exhibits high philopatry, where 70-92% of individuals breed at natal sites [26].

**Mammals**

- Bottlenose dolphins (*Tursiops truncatus*) return to breed in their natal habitats well into adulthood [27].
- In the brown long-eared bat (*Plecotus auritus*), both sexes exhibit philopatry to natal roosts [28].
- Female Antarctic fur seals (*Arctocephalus gazella*) return to breed within a few meters of their own birth site [29].

suitable for the growth and development of their young, including suitable temperature, abundant food resources, low abundances of predators, and nesting sites with superior geographical location. For example, female Pine snakes (*Pituophis melanoleucus*) show a high degree of nest site philopatry because it promotes location of sites that provide suitable temperature conditions [54]. Temperate zone bat species are believed to form summer maternity colonies to provide the appropriate thermal conditions for the growth and survival of their offspring [55]. Natal philopatry in bannertailed kangaroo rats (*Dipodomys spectabilis*) may be a means of providing juveniles with access to essential resources, such as food caches and large complex burrow systems, that are not readily available outside natal home ranges [56]. Overall, by returning to the same site for reproduction each year, individuals can be assured of the suitable environmental conditions to support growth, maturation, and survival of their young.

#### **Maintaining social networks**

Natal homing can help animals establish familiar community structure and reduce resource competition. In Antarctic fur seals (*Arctocephalus gazella*), adults of both sexes return to within a few meters of the breeding sites that were held in previous years [57]. Such behavior could potentially be adaptive in a crowded and highly competitive environment, perhaps by facilitating the re-occupation of previously held territories [58] or by creating stable neighborhood networks in which overall levels of conflict are minimized [59].

Beyond reducing competition, natal philopatry may help to maintain familiar social networks. For bottlenose dolphins (*Tursiops truncatus*), philopatry offers the benefits of familiar social networks and foraging habitats [60]. Additionally, it is thought that natal philopatry in Brown long-eared bats (*Plecotus auritus*) could be driven by the social benefits of associating with familiar individuals [28]. Thus, homing behavior may serve as a mechanism to sort and distribute animals, and in the process may maintain social benefits or decrease intraspecific competition for resources.

#### **Another potential reason for natal philopatry: host-microbe-environment interactions**

The fact that animals evolved in a world already dominated by microbes [33] opens the possibility for microbial involvement in the processes of natal philopatry. First, microbes could play a role in the proximate mechanisms of animals locating their natal sites. While many animals imprint on the geomagnetic features of their natal sites [43], we have a poor understanding of how animals sense and respond to magnetic fields, including the fact that bona fide animal magnetoreceptors have

still not been identified [61]. It has recently been proposed that symbiotic magnetotactic bacteria could contribute to these capabilities [62]. For example, host-associated magnetotactic bacteria may aggregate based on the geomagnetic field and provide signals to their hosts [62]. Additionally, microbes may be involved in the location of natal sites using chemical cues given the large repertoire of volatile compounds they produce, which are also involved in inter-kingdom interactions [63]. For example, microbes create volatile compounds that may be used for inter-host communication, such as on the scent glands of hyenas [64] or the uropygial glands of birds [65]. Some soil bacteria also generate volatile compounds that attract small invertebrates (springtails), which then feed on the bacteria and mediate the dispersal of bacterial spores [66]. Therefore, it could be that local environmental microbes produce volatile compounds to act as proximate signals for the location of natal sites.

Beyond the location of natal sites, we propose that acquiring the optimal composition and structure of microorganisms may also be a reason why animals return to their birthplace for reproduction. Analogous to the ultimate factors previously proposed for the evolution of natal philopatry (Evolutionary and genetic optimization, Suitable environmental factors, and Maintaining social networks), we propose that host-microbe interactions during early life could be involved in (i) evolutionary and hologenomic optimization, (ii) acclimating to local environmental conditions and (iii) the social benefits of natal philopatry. While the connections between natal philopatry and microbial ecology have not been thoroughly investigated, we present a series of studies that provide interesting data supporting this hypothesis.

#### **Evolutionary and hologenomic optimization**

Our understanding of the evolutionary importance of host-microbe interactions is rapidly increasing. Host-microbe interactions have the capacity to affect many aspects of host performance and fitness [67]. Numerous studies across animal taxa have demonstrated that there are optimal combinations between host genetics and associated microbial communities, such that inoculating animals with the microbial communities from heterologous host species reduces performance and fitness [9, 68–70]. For example, individuals of *Peromyscus polionotus* inoculated with the microbes from other *Peromyscus* species exhibit decreased rates of food digestibility [9]. Additionally, both *Drosophila* flies, *Nasonia* wasps, and *Caenorhabditis* worms exhibit decreased fitness when inoculated with the microbiomes of congener hosts [9, 68–70]. Last, animals that are the hybrids of two species often suffer from incompatibilities between the host genome and the microbiome, leading to detrimental effects,

such as gut inflammation or lethality [71, 72]. Thus, it is increasingly being recognized that we must expand our view of biological interactions to be a combination of  $\text{Genome}_{\text{Host}} \times \text{Genome}_{\text{Microbial}} \times \text{Environment}$  interactions [38, 73]. For wild animals, ensuring that offspring associate with the proper microbial community in early life (described more in the sections below) could have large fitness consequences for reproducing animals.

These microbial associations can be especially important during early life [74]. Animals exhibit developmental windows during which microbial interactions are especially crucial [75]. For example, disruption of the microbiome in larval zebrafish can cause lasting changes to behavior and neurodevelopment [76]. Similarly, tadpoles reared under depleted microbial conditions exhibit increased susceptibility to later parasitic [77] and viral infections [78]. Moreover, early associations with particular microbes in early life can also influence the ability for subsequent microbes to take hold, a process known as priority effects or historical contingency [79]. Therefore, exposure to early environmental microbes could have life-long impacts on what other microbes are able to colonize animals. Given the effects that microbes can have on host digestion [34], protection against pathogens [35], the development of the immune system [36], associating with the proper microbial communities in early life has the potential to yield lifelong fitness effects.

#### Microbes as environmental factors

How then, do animals obtain their microbiome? Starting at birth or hatching, the microbiota develops from a simple, unstable community into a complex and climax community [74]. While a portion of the microbiome is vertically transmitted [80], a number of environmental microbes are also important early colonizers [81]. For example, some animal species predominantly acquire host-associated microbial communities from the environment each new generation, such as stinkbugs [82] and bioluminescent squid [83]. Studies in tadpoles [84] and several fish species [85, 86] demonstrate that the gut microbiota largely reflects those microbes present in their surrounding environments. In nest-building species, such as birds, the characteristics and environmental microbiome of nesting material can influence the composition of their offspring's microbiome [87, 88]. Experimental research on laboratory mice [89] and wild *Peromyscus* mice [90] have also demonstrated that the gut microbiome of mammals can be determined by their juvenile environment. Thus, the microbiome of the surrounding environment could have important implications for the assembly of host-associated communities.

Additionally, environmental microbial populations exhibit substantial spatial heterogeneity across the landscape. While it had long been assumed that “everything

is everywhere” [91], recent studies demonstrate that both terrestrial and aquatic microbial communities exhibit considerable biogeographic trends, resulting in heterogeneity of microbial diversity and community structure over geographic space [92, 93]. This spatial heterogeneity may contribute to the well-documented effects of geography on host-associated microbial communities [94]. For example, when comparing the gut microbial communities wild mice obtained from across France and Germany, results showed that patterns of microbiota diversity were principally explained by the geographical location of the mice, with weaker effects due to the genetic distance [95]. Other work has found that sympatric populations of gorillas and chimpanzees share more bacterial taxa than gorillas and chimps from disparate regions, suggesting a potential of limits to microbial dispersal [96]. The cloacal microbiota of fledgling greater flamingos (*Phoenicopterus roseus*) varied substantially across nine breeding sites, suggesting that local environments harbor distinct microbial communities [97].

The geographic variation in environmental microbes may carry “signatures” relating to characteristics of the local environment. For example, over large geographic scales the biogeographic distribution of soil microbes is driven by temperature [98, 99]. Host-microbe interactions have been implicated in thermal physiology of hosts [100] and their adaptations to local climate [101]. Thus, it could be that animals acquire environmental microbes that are adapted to certain aspects of the local environment (temperature, frequency of disturbance, etc.), and thereby convey related physiological benefits to their hosts. However, it should be noted that we still have a poor understanding of the spatial heterogeneity of environmental microbes on spatial scales that may be ecologically relevant to natal philopatry. For example, in a study of philopatric songbirds, a dispersal distance of roughly 1000 m from the natal habitat yielded lower fitness [47], while studies investigating site-specific avian microbial communities typically use greater spatial distances between sites [97, 102].

#### Microbes as a social benefit

Analogous to how natal philopatry may yield the social benefits through cooperation or reduced competition, there may be microbial benefits to living together [103]. The behavior of allo-coprophy, where offspring consume the feces of adult individuals, including unrelated individuals, has been recorded in insects [104], reptiles [105, 106], birds [107], and mammals [108, 109]. This behavior can be important for juveniles to become inoculated with a microbial community. For example, cockroaches regularly consume feces of conspecifics, and doing so results in colonization of the gut and enhanced growth and tissue development [110]. Similarly, green

iguanas regularly consume the feces of adult individuals [105], and doing so increases their ability to digest plant material and improves growth rates [111].

Even if not a principal source of microbial inoculation, group living has also been demonstrated to result in microbial sharing between individuals. Numerous social or gregarious insect species transmit some beneficial microbes between individuals [112–114]. In baboons, the degree of social interactions between individuals can explain a significant portion of microbial sharing [115]. Additionally, dispersal of individuals to join unrelated groups can result in acquisition of new microbial communities, and individuals that engage in more grooming behavior share similar microbial communities [116]. Similarly, affiliative behaviors between unrelated individuals of feral horses correlate with similarities in gut microbial community structure [117]. Thus, returning to the natal site for breeding may expose offspring to a social network and associated microbial symbionts that may be acquired through social transmission.

### Caveats

It is important to acknowledge that our framework also has caveats. First, while natal philopatry is a relatively common behavior across animal taxa (Table 1), studies of this behavior may suffer from a reporting bias towards those that exhibit philopatry or are easier to study [32]. Second, natal philopatry is not always an adaptive behavior. In contrast to studies cited earlier, a study of Western gulls showed that philopatric individuals had lower survival and reproductive fitness, leading to a conclusion that the benefits of this life history strategy may vary temporally and spatially [118]. Similarly, the benefits of microbial interactions may also be variable across space and time. Related, our framework is largely rationalized by philopatry promoting the stabilization of environment-host-microbe interactions. However, novel microbial communities are thought to be a route by which animals may gain enhanced capabilities and adapt to novel environments [119]. Therefore, there may be some benefits to animals dispersing to new habitats for reproduction, which may lead to the acquisition of novel microbes in offspring. Such benefits could underlie the observed variability in the degree of site fidelity across individuals. Overall, more studies are needed to test ideas of our framework in a broad array of systems.

### Future directions

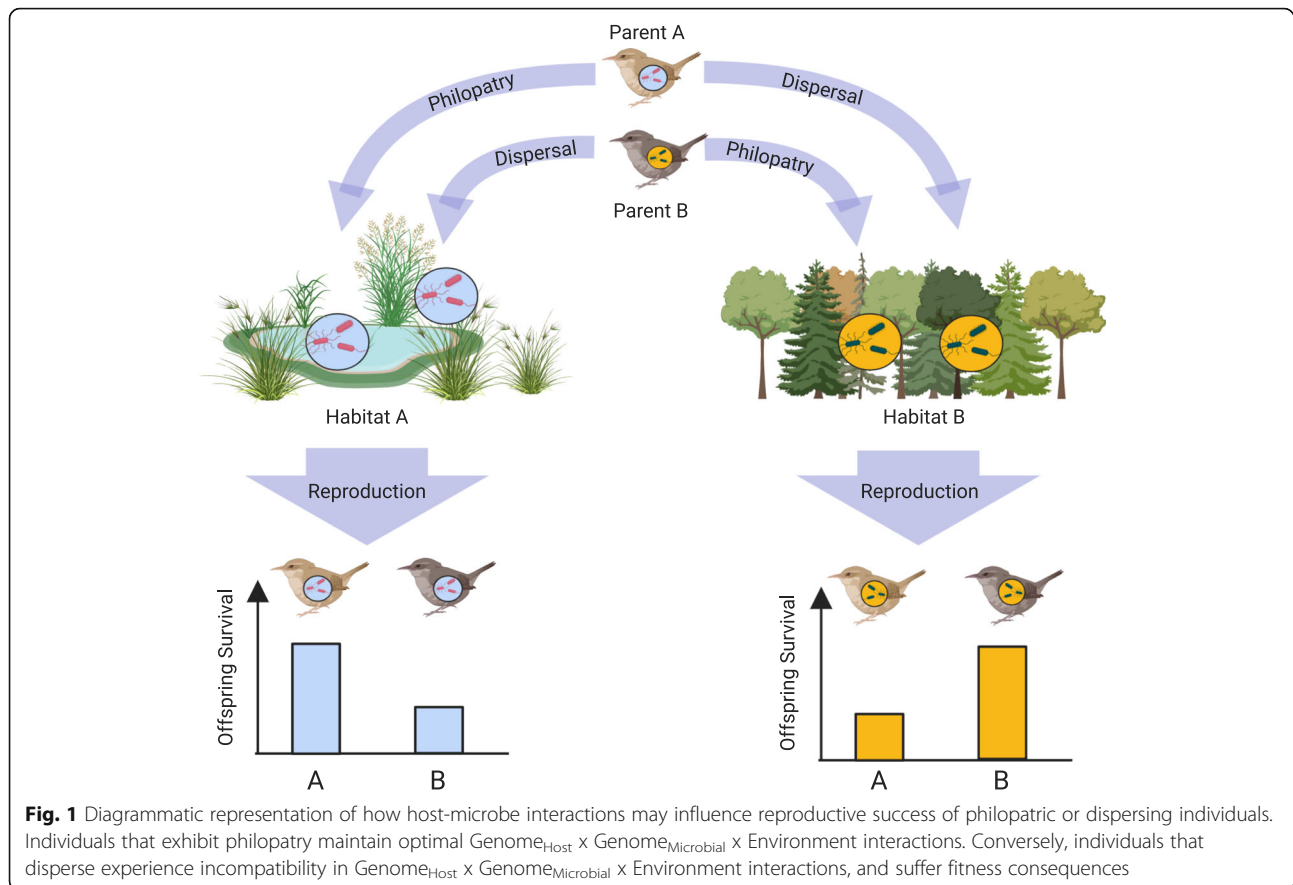
With these research findings and caveats in mind, we propose a conceptual framework by which environmental acquisition of microbes and associated fitness benefits may contribute to the evolution of natal philopatry (Fig. 1). Here, individuals that exhibit philopatry return to their birthplace for reproduction, and thus their offspring

acquire the optimal microbial communities during early life and exhibit improved performance and survival. Conversely, offspring of individuals that had dispersed for reproduction have a mismatch between host genetics and microbial genetics, and the environment. Such sub-optimal matching may result in decreased performance and fitness of offspring in these environments. Such fitness consequences may yield evolution in behavioral traits, such as natal homing, especially since natural selection is thought to act strongly on behavior [120], and behavioral traits are evolutionarily labile [121]. Through these processes, host-microbe interactions and the resulting fitness benefits could act as ultimate factors underlying the evolution of natal philopatry.

However, we again recognize that our framework is highly speculative. Future observational, comparative, and experimental work could help to address these ideas and large open questions that remain in this framework. First, a thorough understanding of the basic microbial ecology of animal systems that engage in natal philopatry is still lacking. Overall, microbiome research has been largely biased towards model systems and biomedical studies [122–124]. In many wild systems we still lack thorough knowledge on the routes of microbial acquisition, microbial sharing, and the effects of microbial communities on performance and fitness. Therefore, researchers should employ current techniques for inventorying the taxonomic composition and functions of microbial communities [125] and integrating these techniques with questions of integrative and comparative biology [125, 126]. Additionally, as mentioned above, we have poor understanding of the resolution of spatial heterogeneity in microbial communities, especially on scales relevant to animal ecology.

Another large question relates to the concept  $\text{Genome}_{\text{Host}} \times \text{Genome}_{\text{Microbial}} \times \text{Environment}$  interactions, and which of these interactions are most important in determining performance and fitness. Classical work to test  $\text{Genome} \times \text{Environment}$  interactions, such as common garden or transplant experiments, have largely conflated the aspects of  $\text{Genome}_{\text{Host}}$  and  $\text{Genome}_{\text{Microbial}}$ . Additionally, existing work on  $\text{Genome}_{\text{Host}} \times \text{Genome}_{\text{Microbial}}$  interactions have largely ignored environmental variables, as they have been conducted in captivity under constant conditions [9, 68–70]. Thus, to our knowledge, full tests of  $\text{Genome}_{\text{Host}} \times \text{Genome}_{\text{Microbial}} \times \text{Environment}$  interactions remain lacking. In the future, a combination of controlled microbial inoculations during early life followed by exposure to varying environments would benefit the framework presented in this article, as well as the greater field of host-microbe interactions.

We predict that manipulative experiments will provide powerful approaches to disentangle the effects of



genetics, location, and the microbiome on breeding success. Some groups have used cross-fostering approaches in nestling birds to demonstrate that the local environment determines the membership of their gut microbiome [127]. Similar approaches could be taken in philopatric species. Additionally, controlled experimental studies in the laboratory could be useful. Several studies have manipulated environmental microbial communities in the lab to investigate their effects on animal performance [77, 128]. Similar approaches could be used with multiple environmental microbial sources. Following such microbial manipulations, researchers could release animals into experimental field sites and track performance and fitness. For example, researchers have used controlled environmental mesocosms to track the population dynamics of released lizards [129], voles [130], fish [131] and invertebrates [132]. Combining experimental microbial manipulations with mesocosm approaches will be a necessary next step in testing aspects of our conceptual framework.

Overall, it is becoming more and more clear that microbial partnerships influence many aspects of animal life-history and revealing a role for these partnerships in the enigmatic behavior of natal philopatry could have numerous implications. First, testing whether microbial

interactions play a role in the evolution of natal philopatry will greatly enhance our understanding of hologenomic evolution [38], including the evolution of animal behavior [10]. Additionally, understanding the proximate and ultimate causes of natal philopatry has conservation implications to ensure successful breeding [13, 133]. Similarly, host-microbe interactions have the potential to influence conservation efforts [8], and thus understanding the role of microbes in early life success could help to shape and prioritize breeding sites and captive breeding efforts.

### Conclusion

This article highlights the potential for host-microbe interactions to underly the evolution of natal philopatry. Numerous studies have demonstrated the importance of environmental microbes in colonizing animal hosts, and the effect of specific host-microbe associations on animal performance. Thus, we argue that the combination of these factors may lead animals to return to natal sites for breeding to ensure that their offspring acquire the optimal microbiome.

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**Authors' contributions**

T.B.B. and K.D.K. worked together to write this manuscript. The authors read and approved the final manuscript.

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The authors declare that they have no competing interests.

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