JOURNAL OF
AVIAN BIOLOGY

Mini-review

Gut microbiome–diet interactions in wild birds

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Journal of Avian Biology
2025: e03456
doi: 10.1002/jav.03456
Subject Editor: Suvi Ruuskanen
Editor-in-Chief: Staffan Bensch
Accepted 3 August 2025

Birds show global declines, and understanding the relationship between avian diet and fitness can both answer basic questions in physiological ecology and inform conservation efforts. Diet-induced changes to the gut microbiome, the collection of microorganisms and their functional genes and metabolites inside the gut, may be of particular importance to avian fitness as the gut microbiome provides a suite of beneficial roles for nutrition and immunity of the host. Furthermore, evidence is growing that the gut microbiome may impact animals' diet choices, which could have cascading impacts on avian fitness. Sequencing technologies allow both diet and gut microbial composition and diversity to be characterized from the same fecal sample, creating ripe opportunities to explore diet–microbiome relationships. In this mini-review we summarize the existing literature on the effect of diet category, diet shifts, and dietary diversity on the gut microbiome, and the potential for the gut microbiome to serve as a modulator of diet choice in wild birds. We list open questions in the field of avian diet–microbiome interactions and provide methodology considerations for designing studies to sample both diet and gut microbiomes. This mini-review provides a framework for understanding the reciprocal relationship between diet and gut microbiota in wild birds.

Keywords: diet, dietary diversity, gut microbiome, microbial diversity

Introduction

Understanding the relationship between avian diet and fitness is increasingly important as birds experience marked global declines (Gaston et al. 2003, Inger et al. 2015, Rosenberg et al. 2019). The specific items or nutrients in a bird's diet can predict its health, survival, or reproductive success (Bidwell and Dawson 2005, Twining et al. 2016, Narango et al. 2018, Twining et al. 2018), and this can dictate management practices aimed at protecting species. Elucidating the mechanisms linking avian diet and fitness advances both our basic understanding of physiological ecology and our efforts to conserve bird species.

One mechanism through which diet could impact avian fitness is through the gut microbiome. The gut microbiome is the collection of microorganisms (e.g. bacteria,

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archaea, fungi, viruses, protozoa) and their collective genomes that reside in the gastrointestinal tract of the host. Before hatching, the avian gut microbiome may be established in ovo through transfer of maternal microbiota prior to shelling (Trevelline et al. 2018), or there may be no viable microbiome until hatching (Grond et al. 2017). After hatching, most gut microbiota are acquired through horizontal transmission from external sources such as the environment (e.g. nesting material; Diez-Méndez et al. 2023) and diet (Bodawatta et al. 2021a). Due to birds' closed, continuous gastrointestinal tract from mouth to cloaca, diet items consumed by the host provide the main source of nutrients used for gut microbial growth and survival (Pan and Yu 2014), though some microbiota may consume other microbes within the gut or feed on the mucus of the host's intestinal lining, as evidenced in mammals (Desai et al. 2016). Low signals of phylosymbiosis in avian gut microbiomes (i.e. when closely related species have more similar microbiome compositions) provide further evidence that diet is one of the main contributors to microbial composition in birds (but see Trevelline et al. 2020 for other contributing factors to low phylosymbiosis, and Grond et al. 2018 for a review of all intrinsic and extrinsic factors contributing to avian gut microbiome).

Though some microbial members may be harmful (Benskin et al. 2009), the avian gut microbiome generally provides many beneficial functions to the host, including nutrient extraction (Stanley et al. 2013), immune system training (Knutie 2020), metabolism of toxic secondary plant compounds in host diet (Gunasekaran et al. 2021), and production of vitamins and amino acids that could supplement host dietary intake (Lin et al. 2017). Some studies have found direct links between aspects of the gut microbiome and avian host fitness. For example, specific microbial compositions are associated with decreased survival in adult Seychelles warblers *Acrocephalus sechellensis* (Worsley et al. 2021), and decreased diversity and increased prevalence of potentially pathogenic microbial taxa are related to mortality in juvenile ostriches *Struthio camelus* (Videvall et al. 2020).

Previous studies have found relationships between diet and host fitness and, separately, the gut microbiome and host fitness (above); however, only recently have studies begun to investigate the interplay between diet and microbiome in relation to host fitness. For example, in northern cardinals *Cardinalis cardinalis* microbial alpha diversity is positively correlated with beak and back feather coloration, which are sexually selected traits acquired through dietary carotenoids (Slevin et al. 2025). Disentangling how diet can influence the gut microbiome and vice versa is essential to understand avian physiology, behavior, and fitness, and will have subsequent implications for connected disciplines such as conservation and management and evolutionary biology.

Diet–microbiome interactions have been extensively studied in foregut/hindgut fermenting mammals and, more recently, wild mammals with diverse diets (Weinstein et al. 2021, Stapleton et al. 2024). This work was then extended to birds with fermentation chambers such as hoatzins *Opisthocomus hoazin* (Godoy-Vitorino et al. 2008) and emus *Dromaius novaehollandiae* (Herd and Dawson 1984). Birds exhibit lower degrees of phylosymbiosis compared to mammals but, interestingly, birds have similar phylosymbiosis levels to bats, possibly due to convergent evolution of adaptations in their gut to minimize weight (Song et al. 2020). The short length of the intestinal tract in birds suggests the possibility that birds may have evolved to outsource certain digestive functions to microbes (Song et al. 2020).

There has been considerable work exploring diet and microbiomes in commercial poultry due to their economic importance (Pan and Yu 2013, De Cesare et al. 2019); diet–microbiome interactions in wild birds is still an emerging field possibly due to the logistical constraints of capturing wild birds and financial constraints of quantifying both diet and microbiome (Grond et al. 2018, Bodawatta et al. 2022, Matheen et al. 2022, Sun et al. 2022). Diet–microbiome interactions in poultry have been extensively reviewed elsewhere so we focus only on wild birds here. We are just beginning to uncover the roles microbes play in helping wild birds digest and assimilate nutrients from their diet (Kohl et al. 2016). The majority of studies have focused on the effect of diet on microbial communities (reviewed below). There is evidence in mammals that gut microbiota can modulate host diet choice (Trevelline and Kohl 2022), but the extent to which this relationship exists in birds remains unanswered.

In this mini-review, we explore the hypothesized bidirectional relationship between diet and gut microbiota in wild birds. We focus on different aspects of diet (diet category, temporal shifts in diet, and dietary diversity) and characteristics of gut microbiome (composition, diversity, and function) (Fig. 1, Table 1). We begin by reviewing evidence for the relationship between diet and microbiome, synthesizing study results via hypotheses (Table 2). The vast majority of work has focused on the effect of diet on microbiome; however, recent studies in mammals suggest that the gut microbiome may influence dietary choices (Trevelline and Kohl 2022). This side of the relationship has not yet been investigated in wild birds, so we explore possible pathways from the gut microbiome to diet (Fig. 1). We conclude with suggested future directions and methodological limitations and opportunities for the field of avian diet and gut microbiome interactions.

Effects of diet on gut microbiome

Diet category and gut microbiome

The general type of food consumed by a bird (hereafter, diet category; e.g. fish, fruits, grains, insects, meat, nectar, plants, or mixed, omnivorous diets) often predicts the specific microbial community found in its gut (Hird et al. 2014, Bodawatta et al. 2021a, 2022, Xiao et al. 2021, Wang et al. 2022, Ogasawara et al. 2023). Host phylogenetic relatedness can play a role in shaping microbial communities, but in some instances diet category can be an even stronger predictor than phylogenetic relatedness (Xiao et al. 2021, Wang et al. 2022; but see Bodawatta et al. 2022). For example, in New Guinean birds, gut microbial communities are primarily affected by host species, and are impacted to a lesser extent by host diet

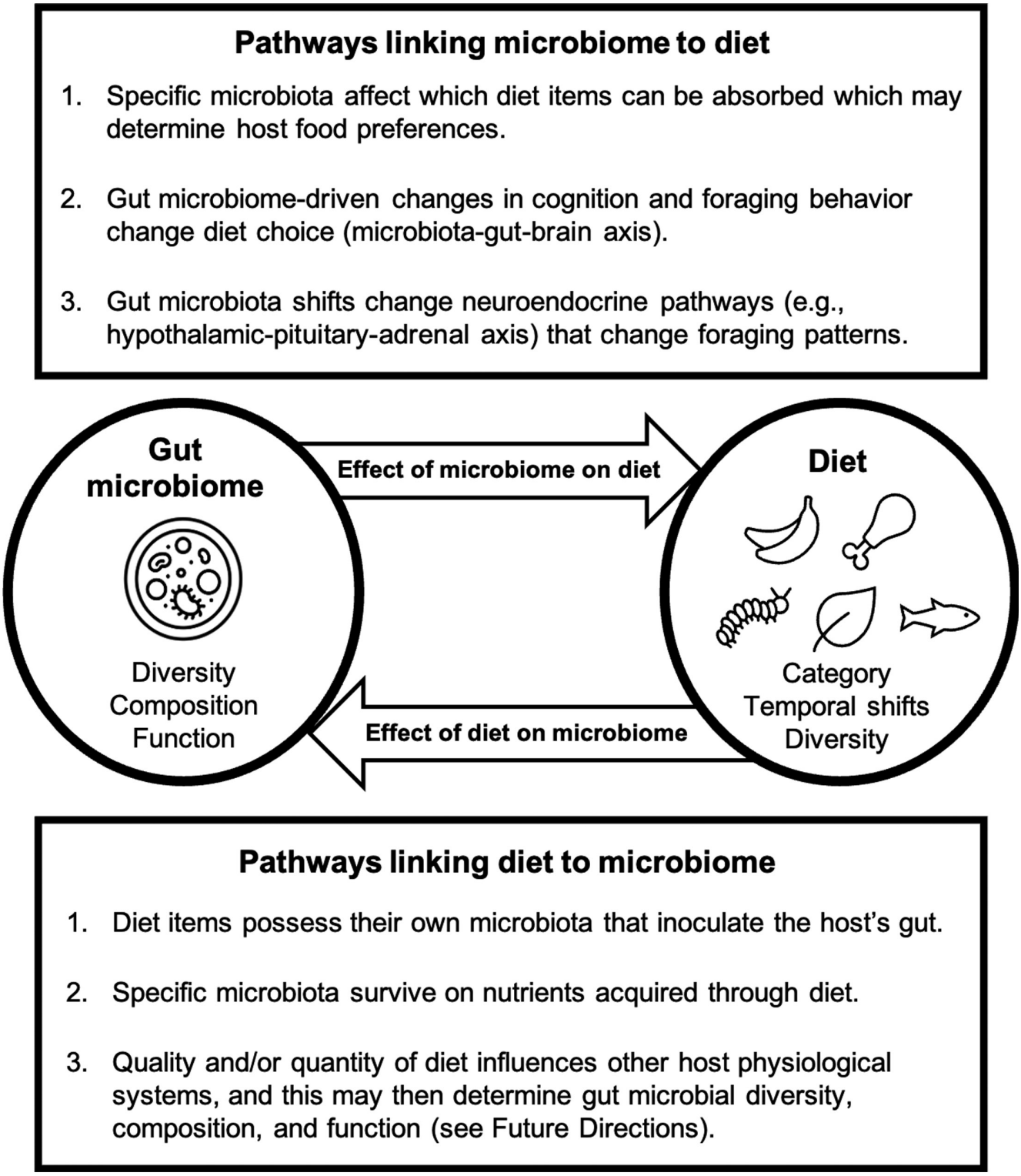

Figure 1. Hypothesized bidirectional pathways connecting the gut microbiome and diet in wild birds.

category (frugivore, insectivore, frugivore + insectivore, insectivore + nectarivore, or granivore), but host phylogeny does not predict gut microbial communities (Bodawatta et al. 2021a).

A striking example of the impact of diet category on gut microbial communities is the gut microbiome of the Galápagos vampire finch *Geospiza septentrionalis* (Michel et al. 2018). In a study of twelve species of Darwin's finches, all species

Table 1. Definitions for aspects of diet and gut microbiome discussed in this mini-review.

Term	Definition
Alpha diversity	Within-individual diversity. Example metrics include Shannon index, Chao1 index, Simpson index, Faith's phylogenetic diversity, and observed number of ASVs/species
Amplicon sequence variant (ASV)	Exact sequence variants that are classified at the single nucleotide level and not grouped together
Beta diversity	Variation in diversity between individuals or groups. Example metrics include Bray–Curtis dissimilarity, Jaccard distance, weighted/unweighted UniFrac, and Aitchison distance
Diet category	General or specialized type of food consumed by an animal. Examples include fish, fruits, grains, insects, meat, nectar, plants, or mixed (omnivorous)
Dietary diversity	Richness (presence/absence) and/or evenness (abundance) of diet items consumed by a host
Diet composition	The specific diet items consumed by an individual animal. Note that individual animals may be capable of consuming many types of foods, but their diet composition may be more limited depending on environmental factors
Evenness	Component of diversity that measures the abundance of each species, ASV, or OTU present in a sample. Example metrics include Shannon index (alpha diversity metric) and Bray–Curtis dissimilarity (beta diversity metric)
Microbial diversity	Richness (presence/absence) and/or evenness (abundance) of a defined microbiota or microbiome of a host
Microbial metagenome	All the microbial genetic material or DNA from a microbiome sample rather than sequencing a single gene/amplicon (e.g.: V4 region of the 16S rRNA gene)
Microbial metatranscriptome	All the microbial RNA from a microbiome sample that shows expression of genes
Microbiota	Collection of microorganisms in a defined space or environment. Examples include bacteria, archaea, fungi, viruses, and protists
Microbiome	All the microbiota and their collective genomes and functions within a defined space or environment
Microbiome composition	The taxonomic identities (phylum to species) of the gut microbial community members
Operational taxonomic unit (OTU)	A group of sequences that is clustered together based on a defined similarity threshold (e.g. 97–99%)
Richness	Component of diversity that measures the presence/absence of unique species, ASVs, or OTUs present in a sample. Example metrics include Chao1 (alpha diversity metric) and Jaccard distance (beta diversity metric)

(including insectivores and herbivores) demonstrate very similar core gut microbiomes except for the Darwin's finch that consumes blood, the Galápagos vampire finch. This species' gut microbiome contains bacteria that are highly uncommon or not present in other species, such as *Fusobacterium*, *Cetobacterium*, *Ureaplasma*, *Mucispirillum*, *Campylobacter*, and Clostridia (Michel et al. 2018), providing evidence that these bacteria may help the host digest nutrients found in blood. Predicted functional analyses of the vampire finch gut microbiome reveal genes that produce proteins involved in iron–sulfur reactions and sodium transport, which provides more evidence that these gut microbiota may allow the host to deal with the high iron and salt concentrations in blood (Song et al. 2019).

Diet category may also affect gut microbial alpha diversity and function. In migrating birds, omnivorous birds show the greatest gut microbial diversity, herbivorous birds show the second highest diversity, and carnivorous birds show the lowest (Wang et al. 2022). For birds in zoos and on farms in Guangzhou, China, granivores have lower alpha diversity of the gut microbiome compared to frugivores, carnivores, omnivores, and birds that eat corn and soy (Xiao et al. 2021). Functional metagenomic analyses also show that birds with diets high in plant-derived polysaccharides (frugivores, omnivores, and birds that eat corn and soy) are enriched in genes for starch and sucrose metabolism in comparison to carnivorous species (Xiao et al. 2021). The opposite is true for gut microbial diversity of birds kept in a zoo in Hokkaido, Japan: grain-fed birds have higher gut microbial diversity than meat-fed and fish-fed birds (Ogasawara et al. 2023). However, in birds in a Papua New Guinea rainforest, diet category typically does not predict gut microbiome alpha diversity (Bodawatta et al. 2022). Individuals within a species may vary greatly in the dietary items they actually consume; this may explain why species' diet categories do not show consistent relationships with microbial alpha diversity across studies, especially when some studies are performed on captive populations with controlled diets and others focus on wild populations.

Species with highly specialized diets may show distinct gut microbial communities, often (but not always) with limited alpha diversity (Dunbar et al. 2024). For example, the kakapo *Strigops habroptilus*, a highly endangered New Zealand parrot that consumes shoots and leaves, has low gut microbial diversity (Waite et al. 2012, West et al. 2023). The cecal microbiome of another herbivorous species, the greater sage-grouse *Centrocercus urophasianus*, is enriched in microbial genes associated with xenobiotic degradation and metabolism to degrade plant compounds (Kohl et al. 2016). Furthermore, New World vultures harbor low gut microbial diversity; their gut microbiomes are dominated by Clostridia and Fusobacteria, which are pathogenic to most other vertebrates and commonly found in soil and decaying carrion, but may help the vultures digest carrion (Roggenbuck et al. 2014). Dunbar et al. (2024) suggest that species with more specialized diets could have less diverse gut microbiomes due to more limited digestion pathways. Species with specialized diets may only need a few key gut microbial taxa that

Table 2. Proposed hypotheses for how different aspects of diet influence microbial composition, diversity, and function. For each hypothesis, the relevant studies reviewed in this mini-review are divided by whether they support or do not support the hypothesis.

Area of research: diet category and gut microbiome	
Hypothesis 1: diet category of a bird species predicts gut microbial composition	
Supports: Hird et al. (2014), Michel et al. (2018), Bodawatta et al. (2021a), Xiao et al. (2021), Bodawatta et al. (2022), Wang et al. (2022), Ogasawara et al. (2023)	Does not support: None
Hypothesis 2: diet category of a bird species predicts gut microbiome alpha diversity	
Supports: Xiao et al. (2021), Wang et al. (2022), Ogasawara et al. (2023)	Does not support: Bodawatta et al. (2022)
Hypothesis 3: diet category of a bird species predicts gut microbiome function	
Supports: Roggenbuck et al. (2014), Kohl et al. (2016), Zepeda Mendoza et al. (2018), Song et al. (2019), Xiao et al. (2021), Schmiedová et al. (2022)	Does not support: None
Hypothesis 4: specialists with less diverse diets than generalists will have less diverse gut microbiomes	
Supports: Waite et al. (2012), Roggenbuck et al. (2014), West et al. (2023)	Does not support: None
Hypothesis 5: individual variation in diet items consumed within a species predicts individual variation in microbial taxonomic composition	
Supports: Murray et al. (2020), Teyssier et al. (2020), Góngora et al. (2021), Mohr et al. (2022), Schmiedová et al. (2022), Jones et al. (2023), Ogasawara et al. (2023)	Does not support: Bodawatta et al. (2022)
Hypothesis 6: individual variation in diet item consumption within a species predicts individual variation in microbial alpha diversity	
Supports: Teyssier et al. (2020), Jones et al. (2023)	Does not support: Murray et al. (2020)
Area of research: temporal shifts in diet leading to shifts in microbiome	
Hypothesis 1: shifts in diet items consumed over time lead to shifts in gut microbial composition and/or alpha diversity	
Supports: Lewis et al. (2017), Davidson et al. (2020), Teyssier et al. (2020), Bodawatta et al. (2021b), Skeen et al. (2021), Trevelline et al. (2023)	Does not support: None
Hypothesis 2: shifts in diet items consumed over time lead to shifts in gut microbiome function	
Supports: Teyssier et al. (2020), Trevelline et al. (2023)	Does not support: None
Area of research: dietary diversity and microbial diversity	
Hypothesis 1: birds with more diverse diets will have greater gut microbial alpha diversity	
Supports: Houtz et al. (2023)	Does not support: Bodawatta et al. (2022), Baiz et al. (2023)

perform specific functions related to their diet. Functional analyses of vultures show that their gut microbiota contain genes for the production of antiparasitics and insecticides (Zepeda Mendoza et al. 2018) and tissue-degrading enzymes (Roggenbuck et al. 2014) that may aid adaptation to their carrion diets.

Notably, individuals within a species may be capable of consuming a broader range of diet items than they actually eat. This relates to the broader concept of fundamental versus realized niches: a species may be capable of using a broad range of resources, but individuals are ultimately limited in what they actually use due to factors like competition or predation (Greenberg 2016). Studies investigating the relationship between individual variation in diet and individual variation in microbiome help to further elucidate how and why individuals within the same diet category may show different gut microbial communities and levels of alpha diversity.

Researchers use a variety of methods to measure both diet and gut microbiome in the same wild individual. In non-experimental studies of wild birds, data on diet composition can be collected via classifying diet based on where birds are foraging, visual identification, fecal and regurgitated food DNA metabarcoding, and stable isotope analysis. Generally, regardless of the diet characterization method used, studies indicate that community composition in the gut microbiome covaries with individual diet composition (Murray et al. 2020, Góngora et al. 2021, Schmiedová et al. 2022, Jones et al. 2023; but see Bodawatta et al. 2022), and that individual variation in diet composition is also sometimes associated with individual variation in gut microbial alpha diversity (Jones et al. 2023; but see Murray et al. 2020). Experimental studies that directly manipulate the diets of captive wild birds also indicate that individual variation in diet composition predicts gut microbial composition (Teyssier et al. 2020, Mohr et al. 2022, Ogasawara et al. 2023) and gut microbial alpha diversity (Teyssier et al. 2020). More work is needed on how the specific nutrients of diet items impact the gut microbial community composition and gut microbial diversity of the host.

Temporal shifts in diet leading to shifts in microbiome

For the most part, the studies discussed so far consider bird diets at static timepoints. However, birds may shift their diets on daily or seasonal bases due to natural variation in food availability or varying nutritional needs during different life stages. For example, migratory birds often consume different types of food throughout their annual cycle due to shifting nutritional needs (Bairlein and Gwinner 1994, Podlesak et al. 2005, Gómez et al. 2018). Researchers also experimentally shift wild birds' diets in captivity. Studies in both free-living and captive wild birds demonstrate that dietary shifts are associated with gut microbial shifts.

Given their propensity to shift diets across their annual cycle, migratory birds provide a good model for exploring the relationship between shifts in diet and corresponding

gut microbial responses. Free-living songbirds stopping over during migration in the same location have gut microbial communities that become more similar over the course of stopover (Lewis et al. 2017), and blackpoll warblers *Setophaga striata* show similar remodelling of the gut microbiome across different migratory stages even when they are in different geographic localities (Trevelline et al. 2023). These shifts in gut microbial composition may be related to birds' consumption of similar dietary items when stopping over in the same location (Lewis et al. 2017), or birds shifting to new diets (for example, insectivory to frugivory) from breeding to stopover (Trevelline et al. 2023), though additional factors such as adaptive gut rebuilding likely also affect gut microbiome during stopover (Lewis et al. 2017). Furthermore, Kirtland's warblers *Setophaga kirtlandii* sampled on their wintering grounds and breeding grounds show distinct differences in microbial communities, likely due to differences in items consumed: Kirtland's warblers eat more fruit in the winter, and insect-rich diets on their breeding grounds (Skeen et al. 2021). Shifting from a protein-rich insectivorous diet to a carbohydrate-rich frugivorous diet may change gut microbial function, as staging blackpoll warblers consuming a frugivorous diet were enriched in bacterial metabolic pathways involved in sugar degradation (Trevelline et al. 2023).

In captive studies of wild birds, dietary shifts also result in gut microbial shifts, potentially due to less environmental microbial exposure or different microbial inocula from their captive diet (Florkowski et al. 2023). For example, captive great tits *Parus major* show distinct shifts in their microbial community structures from before to after diet manipulation (Bodawatta et al. 2021b). In a separate study of wild great tits brought into captivity, Davidson et al. (2020) also demonstrate that the shift from a wild diet to a captive diet of either seed or insects results in corresponding shifts in gut microbial community composition and alpha diversity. Urban-caught and rural-caught house sparrows *Passer domesticus* fed diets from their opposite habitats showed distinct shifts in their gut microbial alpha and beta diversity and taxonomic composition (Teyssier et al. 2020). These diet shifts also caused changes in gut microbial function, evidenced by increased lipid metabolism and xenobiotic degradation in rural-caught birds switched to the urban diet (Teyssier et al. 2020).

More broadly, it is essential to study the reciprocal relationship between diet and gut microbiome in wild systems because captivity can change the gut microbiome of wild organisms (McKenzie et al. 2017). Bringing wild animals into captivity most likely affects their gut microbiome through the shift to an artificial diet, and some dietary niches may be more affected by captivity than others (Frankel et al. 2019). Beyond dietary changes, different aspects of captivity such as increased proximity to or increased contact with humans, antibiotic treatments, and artificial enclosures which lack substrates with microbial inocula from natural environments could shift the microbiota of captive individuals (Houtz et al. 2021, Florkowski et al. 2023). However, captive studies could be paired with studies in wild conspecifics to rule out environmental effects on the host gut microbiota.

Dietary diversity and microbial diversity

In some wild birds, more diverse diets can lead to better fitness outcomes (Whitfield et al. 2009, Margalida et al. 2012, Serrano-Davies and Sanz 2017; but see Resano-Mayor et al. 2014, Lourenço et al. 2015). There is mixed evidence about whether high microbial diversity equates to increased host health/fitness in birds. Across hosts, a higher diversity of microbiota of different metabolic requirements or functions may promote more nutrient assimilation (Le Chatelier et al. 2013) and resist pathogen invasion in the gut (Buffie and Pamer 2013). However, gut microbial diversity is sometimes negatively associated with fitness; for example, there is a negative relationship between gut microbial diversity and body mass in nestlings of some bird species (great tits: Davidson et al. 2021, American kestrels *Falco sparverius*: Houtz et al. 2023), and body mass can be an indicator of post-fledging survival. This may be the case because an increased relative abundance of one or two key microbial community members may be more important than maintaining a high diversity overall. In migrating blackpoll warblers *Setophaga striata*, microbial alpha diversity decreases and a bacterium belonging to the family Enterobacteriaceae increases in relative abundance, which may be related to the metabolic needs of migrating birds (Trevelline et al. 2023).

It is intuitive to hypothesize that increased dietary diversity would lead to increased gut microbial diversity. Each diet item may possess its own unique microbiome which would inoculate the gut of the host (Fig. 1), though whether these dietary microbes become residents or are transient through the gut must be considered. Certain microbes may be excluded or incorporated into the host's microbiome based on physiological constraints of the host (e.g. stomach acids, gut physiology). Another mechanism could be that each microbial member has specific nutrient requirements (Fig. 1) so a more diverse diet is needed to sustain a more diverse microbial composition; however, functional redundancy of the microbiome would look like a more 'diverse' population even though members could be playing similar metabolic roles.

A few studies have investigated the relationship between dietary diversity and microbial diversity in wild birds (Bodawatta et al. 2022, Baiz et al. 2023, Houtz et al. 2023), but the question still remains a ripe area for future research. In American kestrel nestlings, there is a positive correlation between nest-level microbial alpha diversity and diet alpha diversity (i.e. diet and microbiome diversity averaged across all nestlings in a nest) (Houtz et al. 2023). However, Baiz et al. (2023) and Bodawatta et al. (2022) found little association between dietary and microbial diversity. Another factor that may be important to consider when investigating the relationship between dietary diversity and microbial diversity is diet quantity, based on results in Eastern bluebird *Sialia sialis* nestlings showing that food supplementation leads to greater gut microbial diversity (Knutie 2020). Given the conflicting evidence in the strength of association, more studies should measure both dietary and microbial diversity from individuals at the same time point (i.e. same fecal sample), and incorporate measures of food quantity, if possible.

Effects of gut microbiome on diet

The majority of studies on diet–microbiome interactions across vertebrate taxa have focused on the effect of diet on gut microbial composition, diversity, and functional capacity. This focus on one side of the diet–microbiome interaction raises the question whether changes in the gut microbiome can affect diet choice and foraging behavior of the host (Fig. 1). The gut microbiome could affect the absorption of nutrients, where two birds with the same diet might have different abilities to absorb, assimilate, and transport nutrients based on differences in gut microbiota. The presence or absence of specific gut microbiota may benefit or harm the host by aiding or preventing nutrient extraction from the diet (Liu et al. 2018), but the microbiota may promote their own fitness by eliciting host foraging behaviors that enrich the gut environment in nutrients on which they depend (Alcock et al. 2014). Trevelline and Kohl (2022) recently demonstrated microbiome-driven host diet choice in germ-free (i.e. lacking any microbes) mice colonized by microbiomes from wild rodents with varying natural feeding strategies. Based on the specific microbes they were colonized with, mice exhibited significant differences in their voluntary dietary selection of carbohydrates (Trevelline and Kohl 2022). Though this has not been experimentally demonstrated in wild birds, there is potential for changes in the avian gut microbiome to drive changes in cognition and foraging behavior that ultimately change diet choice.

Previous research has demonstrated links between the gut microbiome and cognitive performance in birds via the microbiota–gut–brain axis (i.e. communication between the gut microbiome and host brain/neuroendocrine system; Davidson et al. 2020, Slevin et al. 2020). Davidson et al. (2018) summarizes the feedback loop between microbial diversity and foraging behavior. A diverse gut microbiome may promote increased cognitive capacity, resulting in increased foraging success of diverse foods that maintain high microbial diversity. Conversely, low microbial diversity may lead to impaired foraging ability that further maintains low microbial diversity. It is also possible that a low diversity of microbiota may increase the host's foraging ability if the host has a specialized diet where a few microbiota are good at assimilating nutrients from their narrow diet. Importantly, diet–microbiome interactions are cyclic rather than unidirectional, as initial dietary diversity may establish the level of microbial diversity that supports different foraging behaviors that then reinforce microbial diversity.

Another mechanism through which the gut microbiome could impact diet choice is through its interaction with the hormonal stress response (Noguera et al. 2018, Houtz et al. 2022a). The specific pathways between the gut microbiome and hypothalamic–pituitary–adrenal (HPA) axis are reviewed in detail elsewhere (Morais et al. 2021), but shifts in gut microbial communities can communicate with the host neuroendocrine system by stimulating the vagus nerve or activating immune cells in the gut. Numerous abiotic and biotic factors such as temperature (Sepulveda and Moeller 2020) or introduction of invasive species (Martignoni and Kolodny 2024) could directly change the microbiome, which may have cascading effects on diet through changes in foraging ability and subsequently diet of the host. Stressors such as noise pollution (Berlow et al. 2022), artificial light at night (Malik et al. 2020), and landscape change via urbanization (Berlow et al. 2021) have all been demonstrated to have significant effects on avian gut microbiomes. These stress-induced changes in the gut microbiome could lead to elevated levels of glucocorticoid hormones, the central regulators of the vertebrate hormonal stress response (Crumeyrolle-Arias et al. 2014). Increased glucocorticoid levels can result in changes in foraging behavior including dietary choice (Teegarden and Bale 2008) and foraging frequency (Lohmus et al. 2006, Crossin et al. 2012). It is possible that stressors cause changes in glucocorticoid levels first that then have downstream effects on the gut microbiome; or that elevations in glucocorticoids influence foraging behavior and dietary choice independent of any changes in microbiome. However, experimental evidence suggests that the microbiota–gut–brain axis is bidirectional (Houtz et al. 2022a), where changes in the gut microbiome could elicit changes in diet directly via changes in cognition/foraging behavior or indirectly via changes in hormones (e.g. glucocorticoids) that influence foraging behavior.

Future directions and limitations

Broadly, while many studies characterize gut microbiome in great detail, methods for characterizing diet often prevent the same specificity. For example, if we assume that birds foraging in the same area are eating the same diet items from the same substrates (e.g. ground, vegetation, water), we fail to capture the individual variation in food selection and foraging location that may be essential for fully understanding the relationship between diet and gut microbiome.

DNA extracted from a single fecal sample can be used for both diet and microbiome analyses. Diet and microbiome amplicon sequencing will require different primer sets (for example, primers for the CO1 gene for animal-based diets and primers for the 16S gene for microbiome), but they can be sequenced on the same lane (Fig. 2). Limited studies have made use of fecal DNA extracts for both microbiome and diet (but see Schmiedová et al. 2022), yet there is great potential for further discoveries about the relationship between gut microbiome and diet with just a single sample collected from an individual. Investigations of the relationship between diet and microbiome often suffer from low sample sizes; fecal samples could solve this problem, as feces can be collected with low additional time and financial investment beyond what is already needed for capturing wild birds (Knutie and Gotanda 2018).

There are limitations to this metabarcoding approach, and researchers must consider the costs and benefits for different methods depending on their study species and research question. 16S rRNA sequencing cannot distinguish between living and dead microbiota so it is possible that dead remnant DNA in the gut of the host could give a false positive as an assumed living part of the gut microbiome. The 16S gene is also found in the mitochondria of eukaryotes so researchers

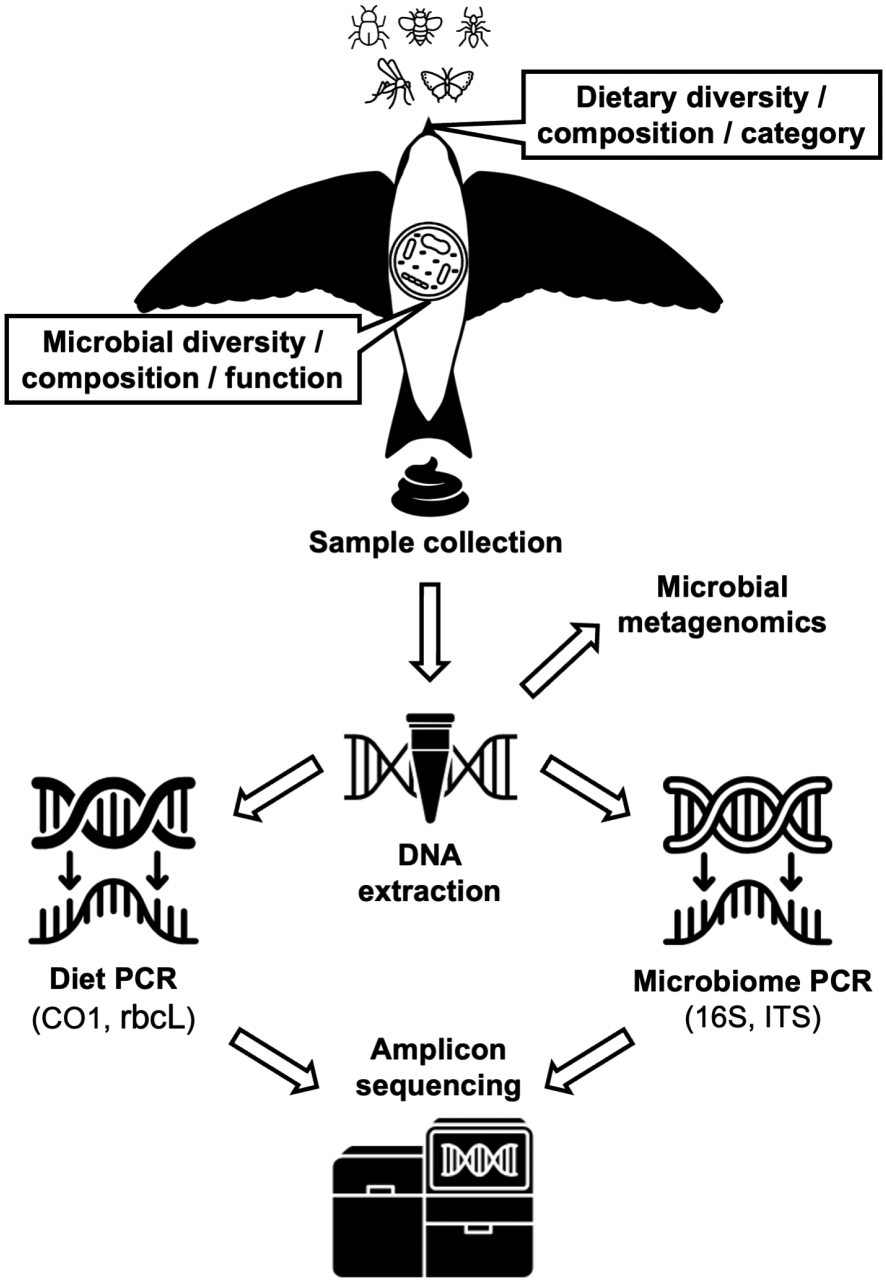

Figure 2. Proposed methodology of DNA extraction, PCR, and amplicon sequencing to characterize aspects of avian diet (target genes: CO1 for animal-based diets; rbcL for plant-based diets) and gut microbiome (target genes: 16S for bacteria; ITS for fungi) from the same fecal sample. Researchers can also use the same DNA extract for microbial metagenomics, and they can perform an RNA extraction on the same fecal sample for transcriptomics analysis. Image attribution from PhyloPic (CC0 1.0 Universal) includes: bird silhouette (*Tachycineta bicolor*). Image attributions from the Noun Project (CC BY 3.0) include: gut microbiome (Soorya Tee), fecal sample (ainul muttaqin), DNA extraction tube (Irfan ms), black and white DNA for PCR (Irfan ms), and sequencer (Maulina Vitria Ulfa).

must filter out this DNA to only include microbial DNA. Some studies investigating the effects of diet on the functional capacity of the avian gut microbiome have used the program Phylogenetic Investigation of Communities by Reconstruction of Unobserved States (PiCRUSt2; Song et al. 2019, Teyssier et al. 2020, Schmiedová et al. 2022), which predicts the functional potential of a bacterial community based on marker gene sequencing profiles (e.g. 16S rRNA gene; Douglas et al. 2020). PiCRUSt2 functional predictions from 16S rRNA sequences only captures a small part of the microbial genome and functional capacity, whereas metagenomic and metatranscriptomic analyses would reveal the full functional capacity of the gut microbiome and how these functions change in response to diet. The ability to sequence diet and microbiome samples on the same lane is dependent on the sequencing platform, sample sizes, sequencing depth,

number of markers, etc. For example, from the diet perspective, omnivorous species will require different primer sets to detect plant versus animal diet items (e.g. *g-h* primers for plants: Hollingsworth et al. 2011, *ANML* primers for animals: Forsman et al. 2022; Fig. 2). DNA metabarcoding also has inherent biases; for example, this method identifies just the food items consumed most recently (Thuo et al. 2019), and an animal's digestive tract may digest the DNA of certain diet items more than others (Deagle and Tollit 2007). Therefore, diet characterizations can be improved when metabarcoding is coupled with additional methods, for example, stable isotope analysis (Hoenig et al. 2022).

For gut microbiome characterization, researchers must weigh the level of invasiveness of the sampling method with the specific region of the gut they seek to characterize. The least invasive methods are feces and cloacal swabs. Feces may be representative of the entire gut tract as the fecal material may pick up microbes as it moves through each section; alternatively, fecal material may be more representative of the large intestine where it is stored (Videvall et al. 2018). However, wild birds do not always defecate during capture and handling, meaning that fecal samples are not guaranteed. Cloacal swabs are the most reliable sampling method but could only be representative of the large intestine (Berlow et al. 2020). Lethal sampling allows characterization of microbial composition across gut tract regions (i.e. proventriculus, small intestine, large intestine, ceca) (Grond et al. 2020, Houtz et al. 2022b).

Most studies have focused on descriptive diet–microbiome relationships; thus, there is a need for experimental manipulations of either side of the relationship. To dysregulate the gut microbiome, researchers could administer broad-spectrum or more targeted antibiotics; however, antibiotics can have off-target effects on host physiology that could influence foraging behavior. Conversely, species-specific probiotics could be acquired from cultured isolates of fecal samples that could be fed back to the bird. The most robust method would be using germ-free (i.e. sterile or completely lacking microbes) or gnotobiotic (i.e. all microbial inhabitants are known) birds to ask questions about the role of specific food items in microbial inoculation of avian hosts. Many methods can be used to manipulate diet effects on the gut microbiome including food supplementation, food limitation, or food sterilization (i.e. to test the effect of food-associated microbes on host gut microbiota).

The field of avian diet–microbiome interactions is ripe with opportunity for expansion. Questions that need to be addressed include:

1. **How fast does a change in diet lead to a change in the gut microbiome?** In humans, diet-induced change in the gut microbiome can be detected within 24 hours (David et al. 2014). How does variation in gut passage time among bird species influence this relationship? Another important question to consider is how long DNA from dead microbes remains detectable in the host gut (e.g. between intestinal villi).
2. **How does diet nutrient content impact gut microbial composition, diversity, and function?** Twining et al. (2016) found that food quality (i.e. specific macronutrients) is more important to the growth of aerially insectivorous birds than food quantity. Could specific macronutrients also be essential for promoting certain microbial communities or functions that are important for host health? Conversely, secondary plant compounds from the host diet could be toxic to some microbial members.
3. **Do microbiota in or on food become incorporated in the gut microbiome of the consumer?** Or does diet mainly shape the gut microbiome by providing nutrients that promote specific microbial membership? Researchers could investigate this question by fluorescently labeling bacteria derived from diet items and following the labeled bacteria through the gut of the consumer to assess if it is incorporated into the host gut microbiome (Cheng et al. 2018).
4. **Does the relationship between dietary diversity and microbial diversity differ across individuals and across contexts?** Only limited studies have started to investigate the relationship between dietary diversity and microbial diversity (Bodawatta et al. 2022, Baiz et al. 2023, Houtz et al. 2023). More research is needed to elucidate how this relationship may vary by population, species, sex, age, geographic location, and sampling method.
5. **How does diet quality or quantity impact other host physiological traits that could determine membership of the microbiome?** For example, tree swallow nestlings fed a diet high in long-chain polyunsaturated fatty acids (LCPUFA) had increased immunocompetence (measured via a phytohaemagglutinin-induced immune response) compared to those on low-LCPUFA diets regardless of diet quantity (Twining et al. 2016). This aspect of the cell-mediated immune system can have downstream effects on gut microbial composition of nestling birds (Kreisinger et al. 2018). Determining causality and directionality in this type of trifold relationship may prove difficult, but could offer important insight into organismal processes in wild systems.

Both diet and microbiome play important roles in avian health, survival, and reproductive success. Additionally, both can be deeply impacted by shifts in birds' environments. The role of the gut microbiome (Trevelline et al. 2019) and diet (Ewen et al. 2015) have been considered in species conservation efforts separately, but researchers must consider their interactions. As we continue to learn more about the reciprocal relationship between diet and microbiome, we will better understand and predict avian fitness, especially in a changing environment.

Acknowledgements – We thank the editor and two reviewers for very helpful comments that strengthened the manuscript.

Author contributions

Jennifer J. Uehling: Conceptualization (equal); Investigation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Jennifer L. Houtz**: Conceptualization (equal); Investigation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/jav.03456.

Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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