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Mini review

Migratory microbiomes: the role of the gut microbiome in bird migration eco-physiology

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Long-distance bird migration is one of the most metabolically and immunologically challenging feats in the animal kingdom, with birds often needing to double their weight in a matter of days and facing increased exposure to novel pathogens. The physiological and behavioural adaptations required to survive such journeys may be facilitated by the gut microbiome, a diverse community of symbiotic microbes that produce rare nutrients, fatty acids, and immune compounds that can confer rapid physiological adaptations to changing environmental conditions. However, the causal role of the gut microbiome in regulating migration physiology remains a mystery. In this review, we synthesize current knowledge of gut microbiome composition and function during migration, outline possible mechanisms by which changes in the gut microbiome could benefit migrants, and identify future research priorities. We find that active migration is usually associated with reduced diversity of the gut microbiome and with the expansion of several study-specific taxa. Additionally, some microbial traits have been found to correlate with host condition and fat deposits during migration. However, there remains little understanding of how changes in the gut microbiome during migration relate to most physiological parameters, the molecular mechanisms linking the gut microbiome to host physiology during migration, or the underlying ecological, dietary, and intrinsic drivers of gut microbiome changes across the migratory cycle. Our review draws from examples across non-migratory systems to explore how gut microbiomes could adaptively regulate physiological traits relevant to migration. We highlight the need for studies that connect gut and circulating metabolites and for experimental studies that test the underlying drivers of gut microbial and metabolite dynamics in controlled settings. Given its diverse physiological demands and ubiquity, bird migration presents an excellent model system to investigate the adaptive potential of the gut microbiome in natural populations.

Keywords: gut microbiomes, host-associated microbiomes, immunity, metabolism, migration

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Introduction

Migration is a common strategy in birds to cope with seasonality (Fudickar et al. 2021). Despite the widespread occurrence of this behaviour, it poses significant challenges to migrants, from navigating long-distance flights to finding food across diverse and unfamiliar environments (Hederströn 2008). Indeed, migration is the most dangerous event of the year for most migratory birds, demonstrated by relatively high mortality during migration compared to other periods (Newton 2024). Overcoming these challenges requires highly specialised physiological adaptations (Hederströn 2008, Piersma and van Gils 2011), such as the ability to rapidly build up fat reserves adjusting to changes in nutritional landscapes (Lindström and Piersma 1993, Price 2010). Migrants also face considerable immunological challenges during migration, most notably being able to regulate the trade-off between pathogen defence and costly immune responses (Nebel et al. 2012, Eikenaar and Hegemann 2016, O'Connor et al. 2018) during increased exposure to novel pathogens (Figuerola and Green 2000, Leung and Koprivnikar 2016, Poulin and de Angeli Dutra 2021). Many of these physiological adaptions of migrants require extreme phenotypic flexibility as individuals switch between migratory stages, ecosystems, and latitudes.

One way animals can mediate adaptive plastic responses to environmental changes is through interactions with the gut microbiome (Alberdi et al. 2016), the resident community of micro-organisms, including bacteria, Archaea, viruses, fungi and cellular eukaryotes that live in the digestive tract of animals. The gut microbiome plays a multi-functional role by releasing nutrients from food, generating metabolites that interact with the host to regulate physiological signalling cascades, and by controlling the proliferation of potentially pathogenic microbes (Thaiss et al. 2016, Brooks et al. 2021, Somers et al. 2024). Moreover, the gut microbiome is highly flexible and sensitive to gut conditions, making it an effective sentinel for environmental changes (e.g. diet switches; Bodawatta et al. 2021). This flexibility has led to the proposal that the gut microbiome can confer rapid ecological adaptations to novel conditions (Alberdi et al. 2016), such as those regularly faced by migrants. Whilst migration is a predictable phenomenon, local environmental conditions along migratory routes can be highly unpredictable and may require rapid physiological adaptations. The remodelling of the gut microbiome across migratory journeys, which can occur very rapidly (Risely et al. 2017), could confer optimized regulation of physiological traits, including nutrition and fat deposition (Trevelline et al. 2023), to match both the physiological demands of migration and local conditions.

Active migration has repeatedly been associated with altered gut microbial composition and diversity across migratory species (Risely et al. 2018, Skeen et al. 2021, Thie et al. 2022, Trevelline et al. 2023). Although some trends, such as reduced diversity during migration (Skeen et al. 2023) are beginning to emerge, the physiological impacts of these changes, the molecular mechanisms, and their environmental and intrinsic drivers remain poorly understood. Like hibernation, a metabolically challenging state that is facilitated by adaptive changes to the microbiome (Sommer et al. 2016, Regan et al. 2022), migration can act as a powerful model system to test the adaptive – or maladaptive – potential of the gut microbiome under physiological stress. Given migratory birds are particularly sensitive to habitat loss and climate change (Bairlein 2016, van Gils et al. 2016, Hallworth et al. 2021), this system also provides opportunities to understand how gut microbiome disruption during migration, for example through sub-optimal diets, may negate or reverse any adaptive benefits of migratory microbiomes (Marsh et al. 2024).

In this review, we examine the state of knowledge of the gut microbiome during migration and distil the mechanistic pathways by which the gut microbiomes may regulate physiology during migration, with a focus on the link between the bacterial microbiome and host metabolism and immunity (Fig. 1). We aim to 1) provide a basic overview of the avian gut microbiome and review current knowledge of its composition, dynamics, and function in migratory birds; 2) highlight known mechanistic pathways by which the gut microbiome regulates physiological traits relevant to migration; 3) identify key gaps of knowledge in our understanding of the role of gut microbiomes in bird migration, and offer a methodological roadmap with suggested experimental designs to tackle key questions.

The composition and ecology of the avian gut microbiome

The avian gut microbiome fundamentally differs from other gut microbial communities found in most mammals, fish, and reptiles (Song et al. 2020). The gut microbiome tends to be made up of gut specialists adapted to anaerobic conditions, and is usually dominated by the bacterial phyla Bacteroides, Firmicutes, and Pseudomonadota (formerly Proteobacteria). Bird microbiomes, along with bat microbiomes, are unusual in that they tend to be less diverse, have notably low proportion of Bacteroides and a higher proportion of Pseudomonadota compared to other vertebrates (Song et al. 2020, Matheen et al. 2022). The reason for this is unclear, but is proposed to be related to adaptations to flight (Song et al. 2020, Bodawatta et al. 2022). If true, this suggests active flight, and potentially sustained flights during migration, imposes a strong selective force on the gut microbiome.

Birds also lack a strong co-evolutionary signal in their gut microbiome, unlike mammals whose gut microbiomes suggest a tight co-evolutionary relationship with their hosts (Groussin et al. 2017). This has led to the suggestion that birds are less functionally reliant on their gut microbiomes than mammals (Song et al. 2020). Nevertheless, variation in the gut microbiome has been linked to survival and fitness correlates in birds (Davidson et al. 2021, Worsley et al. 2021, Somers et al. 2024). Moreover, some gut microbes are maternally transferred via the egg (Trevelline et al. 2018), through

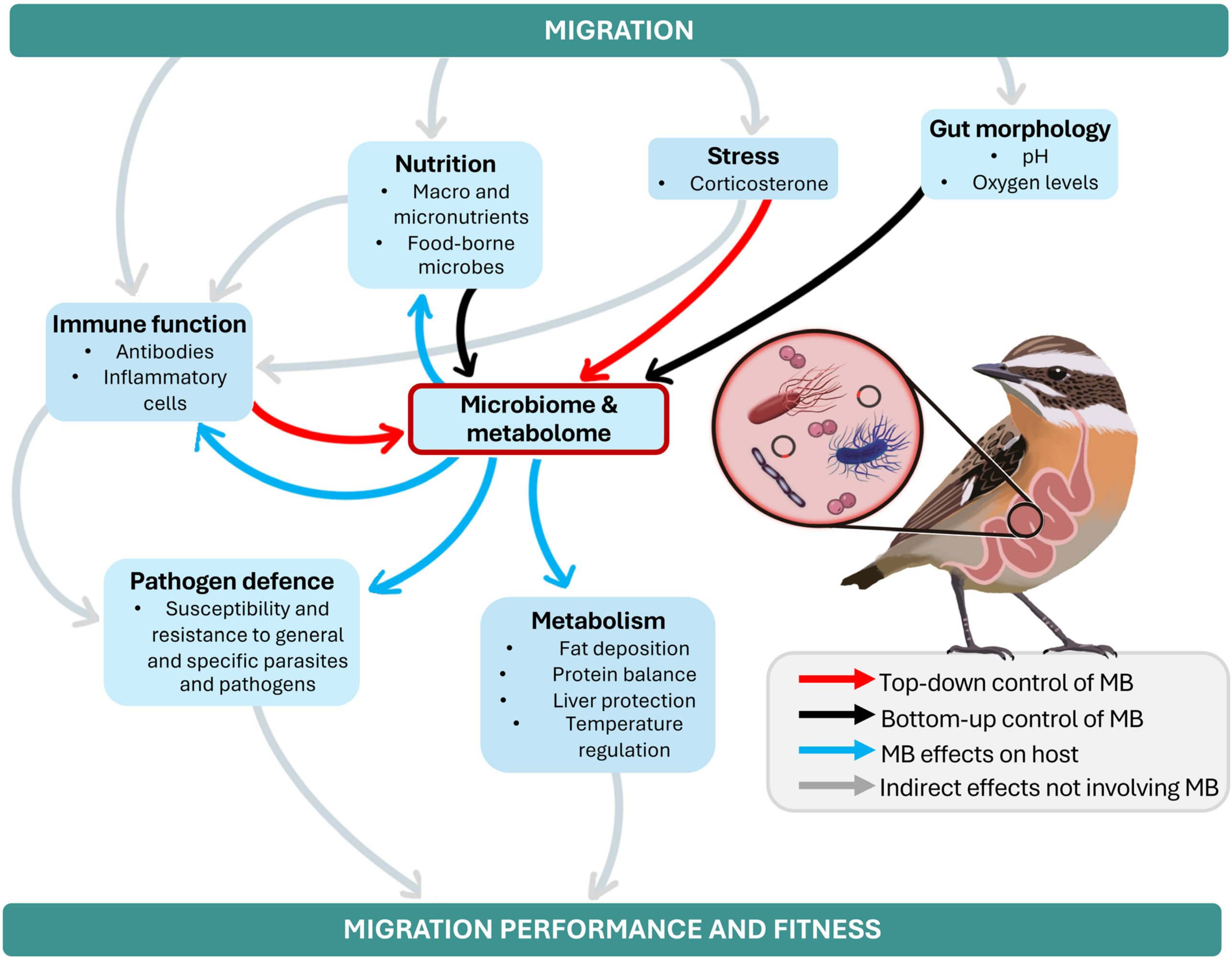


Figure 1. Conceptual summary outlining potential mechanistic links between migration, gut the microbiome ('MB'), and migration performance, including variables likely to drive individual variation of gut microbiomes and its impact on (some of) host physiological parameters relevant to migration (metabolism [i.e. energetics] and immunity).

salivary transfer during feeding (Chen et al. 2020), or through coprophagy (Videvall et al. 2023), together suggesting some level of vertical transfer and potential for co-evolution in at least some clades. The majority of the gut microbiome is however acquired through recruitment from the environment and diet (Chen et al. 2020, Diez-Méndez et al. 2023), which, for migratory species, changes dramatically across the year. Previous studies suggest that gut microbiome composition can rapidly vary after changes in environmental conditions within migratory journeys (Grond et al. 2023).

Links between migration and gut microbiome composition

Several studies have now investigated how the taxonomic composition of the gut microbiome changes during migration (Table 1 for overview of studies). These studies have compared the composition of the gut microbiome of migratory species against non-migratory sister taxa (Turjeman et al. 2020; or between migratory and non-migratory individuals of the same species in the same location Risely et al. 2018) or have compared the gut microbiome of migratory species across different stages (i.e. breeding, migration, non-breeding; Skeen et al. 2021, Trevelline et al. 2023) (Table 1). However, no study to date has compared the gut microbiome across the full annual cycle, given the challenging nature of this task.

Broadly speaking, these studies have demonstrated that the gut microbiome composition of migrants can substantially differ between breeding, non-breeding, and migration periods, and that these changes occur within individuals. In a recent study, Schmiedová and colleagues compared the gut microbiome composition of two migratory species, the garden warbler *Sylvia borin* and the willow warbler *Phylloscopus trochilus* with resident birds at both the breeding and non-breeding grounds (Schmiedová et al. 2023). Their data indicates that the gut microbiome of migratory individuals changes to resemble the gut microbiome of the resident bird

Table 1. Summary of studies that have examined the link between migratory traits and and the gut microbiome. Studies that attempted to link gut microbiome variation to functional traits associated with migration are highlighted in grey. Studies presented un reversed chronological and alphabetical order.

Study species	Study design	Main findings	Reference
Ruddy turnstone *Arenaria interpres*	Gut microbiota composition and function assessed at different time points after arrival to staging site	• Increase in alpha diversity with time after arrival at staging site • Abundance of *Vibrio* and *Flavobacterium* associated with changes in weight • Differences in functional gene community of individuals across weight categories • Expression of metabolic genes of polyunsaturated fatty acids associated with weight gain	Grond et al. 2023
Red-headed bunting *Emberiza bruniceps*	Experimental comparison of microbiome and serum metabolites across migratory and non-migratory periods	• Indication of changes in the gut microbiome caused by migratory phenotype • Suggestive study of a link between changes in gut microbiome and blood metabolites associated with migratory behaviour; however, direct link not shown	Gupta et al. 2023
Brent goose *Branta bernicla hrota*	Link to body mass gain during spring staging	• Variation in gut microbiome composition explained by foraging phenotype at a staging site during spring migration • Individual stability in gut microbiome alpha and beta diversity also linked to foraging phenotype • Foraging phenotype, not gut microbiome variation directly, linked to body mass gain during spring staging	Jones et al. 2023
Garden warbler *Sylvia borin* and willow warbler *Phylloscopus trochilus*	Comparison of breeding and wintering periods against resident species at wintering and breeding grounds	• Drastic changes in gut microbiome composition between breeding and wintering grounds • Breeding ground gut microbiome composition resembled that of resident species at breeding grounds • Wintering ground gut microbiome composition resembled that of resident species at wintering grounds • *Staphylococcus* and *Serratia* the two genera with largest changes between breeding and wintering	Schmiedová et al. 2023
Catharus thrushes	Comparison of spring migration, breeding and autumn migration	• Reduced alpha diversity during migration • Five most differentially abundant genera in spring migratory individuals (compared to breeding): 67–14, *Lysobacter, Babeliales,* Nannocystaceae, *Ralstonia* • Five most differentially abundant genera in autumn migratory individuals (compared to breeding): 67–14, *Ralstonia,* Nannocystaceae, *Babeliales, Bacillus*	Skeen et al. 2023
Blackpoll warbler *Setophaga striata*	Comparison of breeding, stopover and staging sites in autumn migration; link to function and body condition	• Reduction in alpha diversity and increased similarity across migration • Reduction in the relative abundance of Firmicutes along migratory route • Increase in the relative abundance of Proteobacteria along migratory route • Enterobacteriaceae family increased along migratory route • Gut microbiota metabolic profile in stopping over and staging individuals enriched by pathways involved in vitamin, amino acid and fatty acid biosynthesis, carbohydrate degradation and homolactic fermentation of carbohydrates to the short-chain fatty acid lactate.	Trevelline et al. 2023
Canada goose *Branta canadensis*	Comparison of migratory and resident populations	• Reduced alpha diversity in migratory individuals • Most differentially abundant genera in migratory individuals: *Epulopiscium*, *Cellulosilyticum*, *Terrisporobacter*, *Turicibacter* • Firmicutes more abundant in migrants • Resident populations living in urban area, which might confound the comparison between migratory and resident individuals	Obrochta et al. 2022
Steppe buzzard *Buteo buteo vulpinus*	Link between microbiota and body condition during migration	• Early spring arrival to stopover site associated with increased gut microbiome alpha diversity • Body condition at stopover arrival negatively associated with the relative abundance of Escherichia–Shigella • Relative abundance of several gut bacterial taxa associated with time of arrival at stopover sites, suggesting a link between migratory phenotype and gut microbiome composition	Thie et al. 2022

(*Continued*)

Table 1. Continued.

Study species	Study design	Main findings	Reference
Eurasian reed warbler *Acrocephalus scirpaceus*	Experimental effect of antibiotics on migratory restlessness orientation	• Suggestive evidence of disrupted orientation after treatment with antibiotics • Results might be linked to magnetic reception	Werber et al. 2022
Hooded crane *Grus monacha*	Comparison of fungal microbiome between wintering and stopover period	• Decrease in fungal gut microbiome alpha diversity at stopover sites (in spring and autumn migration) compared to wintering grounds • Increased *Zygomycota* and *Rozellomycota* in wintering grounds compared to spring and autumn stopover sites • Increased abundance of potentially pathogenic taxa in wintering grounds compared to stopover sites during spring migration	Mahtab et al. 2021
Kirtland's warbler *Setophaga kirtlandii*	Comparison of wintering and breeding periods using longitudinal and cross-sectional sampling	• Re-sampling of individuals at breeding and wintering ground • Indication of gut microbiota diversity increases after arrival to breeding grounds • Gut microbiota diversity higher at wintering grounds than breeding grounds (but note a potential effect of time after arrival) • 28 amplicon sequence variants with similar abundances across time periods suggesting a core gut microbiota	Skeen et al. 2021
Barn swallow *Hirundo rustica*	Comparison of migratory and resident subspecies	• Differences in beta diversity, but not alpha diversity, between migratory and resident individuals • Found significantly greater abundance of the genera *Catellicoccus*, *Clostridium* sensu stricto 1, *Citrobacter*, *Corynebacterium*, *Fusobacterium*, *Lactobacillus*, *Leuconostoc*, *Mycoplasma*, *Romboutsia*, *Staphylococcus* and *Turicibacter* in migrants compared to residents • Firmicutes more abundant in migrants	Turjeman et al. 2020
Hooded crane *Grus monacha*	Comparison of bacterial gut microbiome between wintering and migration periods	• Decrease in bacterial gut microbiome alpha diversity at stopover sites (in spring and autumn migration) compared to wintering grounds • Differences in the relative abundance of *Lactobacillus* and *Alphaproteobacteria* detected between wintering and stopover periods	Zhang et al. 2020a
Curlew sandpiper *Calidris ferruginea* and red-necked stint *Calidris ruficollis*	Comparison of migrating and non-migrating cohorts of same species	• Migrants show higher abundances of Actinobacteria than residents • *Corynebacterium* particularly abundant in migrants compared to resident individuals across species and sites • Excluding differences in *Corynebacterium*, only weak effects of migratory status on gut microbiota composition • Differences in gut microbiota composition between migrants and residents tended to decrease with longer intervals between arrival and sampling for migratory individuals	Risely et al. 2018
Swainson's thrush *Catharus ustulatus*, wood thrush *Hylocichla mustelina*, and gray catbird *Dumetella carolinensis*	Gut microbiota composition assessed at different time points after arrival to stopover site	• Re-sampling of individuals at breeding and wintering grounds • Inter-species differences in gut microbiota community decrease after arrival to stopover site • Limited sample size	Lewis et al. 2017
Swainson's thrush *Catharus ustulatus* and grey catbird *Dumetella carolinensis*	Comparison of spring and autumn migrants at a stopover site; Link to body condition during migration	• Large changes in gut microbiota composition between spring and fall migrants, but unclear whether those changes are associated to migration per se • No gut microbial taxa associated with body condition at a stopover site in spring or fall migration	Lewis et al. 2016

community, both at the breeding and non-breeding grounds (Schmiedová et al. 2023).

The gut microbiome also shifts in composition during the migratory period. In general, many studies report an increase of Proteobacteria and decrease of Firmicutes (Li et al. 2023, Trevelline et al. 2023); however, these phylum-level trends might be species-specific as other studies have not reported these patterns (Risely et al. 2018) or even found the opposite trends comparing migratory and non-migratory sub-species (Turjeman et al. 2020). Additionally, these studies commonly report a decrease in gut microbiome diversity during migration compared to breeding periods (Risely et al. 2018, Grond et al. 2023, Skeen et al. 2023, Trevelline et al. 2023).

As well as reduced diversity, active migration has been associated with hyper-inflation of a small number of taxa (Table 1), although these are not necessarily the same across studies. For example, in *Catharus* thrushes, bacterial genera *Babeliales,* Nannocystaceae and *Ralstonia* were over abundant in both spring and autumn migrants compared to breeders (Skeen et al. 2023). Similarly, in *Calidris* shorebirds, the genus *Corynebacterium* was strongly associated with migrating individuals across different species and sites (Risely et al. 2018).

Despite changes to the abundance of a small number of taxa associated with migration being common in the literature (Table 1), there is little convergence across studies. This suggests the existence of either host species-specific associations between important gut microbial taxa and migration, or that important gut microbial functions during migration can be achieved by a plethora of gut bacterial species. Alternatively, remodelling of the gut microbiota may represent an uncontrolled disruption that may promote pathogen colonisation and infection, or have other negative physiological effects. Given studies generally apply different bioinformatics pipelines and present results at varying taxonomic levels, identifying taxonomic trends will require data to be analysed together under an evidence synthesis framework.

Drivers of gut microbiome remodelling during migration

A major outstanding question stemming from the observations reported above is whether gut microbiome remodelling during migration is largely controlled by the host (i.e. top-down), or simply represents microbial responses to changes in the gut environment, immigration of novel microbes, and/or changing resource availability (i.e. bottom-up; Fig. 1). Bottom-up processes may include microbial responses to a lack of feeding during prolonged migratory flights and the drastic reorganisation of the digestive track that occurs during migration (Piersma 1998), which could together create a hostile environment for most gut microbes. Additionally, changes in climate, weather, diet, and microbial exposure throughout migratory journeys (e.g. associated with different stop-over sites; Thie et al. 2022, Trevelline et al. 2023, Włodarczyk et al. 2024) could also rapidly alter available microbial resources within the gut, contributing to the observed patterns of gut microbiome composition during migration (Skeen et al. 2021, 2023). Switches in diet and nutrition are likely to be a major bottom-up mechanism shaping microbiome remodelling (Hicks et al. 2018, Baniel et al. 2021), given that migrants can switch from herbivores to insectivores over the migratory cycle (Bairlein 1996, Podlesak et al. 2005). Strong bottom-up effects, if present, could entail important costs for migrants, where the gut microbiome becomes maladapted to the physiological state of the host.

Alternatively, host-mediated (top-down) mechanisms include control of the gut microbiota through the immune or endocrine systems, for example through gut antibodies (Macpherson et al. 2012), or processes such as nutritional immunity whereby the host limits microbial access to critical nutrients required for microbial growth (Murdoch and Skaar 2022). The restructuring of gut microbiomes to resemble those of resident species in the breeding and non-breeding areas (Schmiedová et al. 2023) suggest that the majority of the gut microbiome is shaped by microbial responses to host diet and microbial landscape. However, a certain component of the microbiome may be controlled by the host. For instance, gulls implanted with glucocorticoids exhibited an altered gut microbiome composition (Noguera et al. 2018). Moreover, studies from mice and pigeons indicate that the gut microbiome undergoes seasonal changes in composition independently from diet and environment (Dietz et al. 2022, Matsumoto et al. 2023), suggestive of some level of top-down seasonal (possibly immune) control and provides the substrate for natural selection on gut microbiome composition in (seasonal) migratory birds.

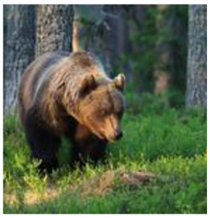
Functional links between gut microbiomes and migrant physiology

Despite clear signatures of migratory behaviour in the composition of the gut microbiome, it remains largely unknown whether such changes confer survival benefits to migrants via adaptive mediation of host physiology. The diversity of genes and metabolic pathways within gut microbial communities adds to the molecular toolkit available for hosts offering new physiological capacities (Alberdi et al. 2016). Migratory birds undergo large changes in metabolic and immune profiles before, during, and after migration (Landys et al. 2005, Hegemann et al. 2012), and many of these processes are known to involve the gut microbiota (Table 2). However, compared to studies assessing gut microbial composition, few studies have yet investigated the functional role of the gut microbiome on bird migration or their contribution to observed fluctuations in metabolic and immune profiles across life history stages.

Metabolism

From a metabolic perspective, long-distance migrants must gain fat at an exceptional rate in preparation for long distance flights, whilst avoiding the physiological complications of obesity, such as inflammation and liver damage.

Table 2. Potential links between physiological traits relevant to migration and the gut microbiome. Examples of physiological traits shown to be modulated by the gut microbiome and that could be of relevance for the study of bird migration. Photos accessed on Flickr. Creative Commons Licenses. Photo credits from top to bottom: Frank Vassen, Spencer Wrigth, Dhruvaraj S, Franco Folini, Glenn Berry, Laetita C, Bettina Arrigoni. Studies presented for metabolic and immune traits by alphabetical order of the study species name.

Host physiological process	Organism		Description
Fat deposition and circadian synchronisation	*Ailuropoda melanoleuca*		Gut microbiome promotes fat deposition in giant pandas during the shoot-eating season. Gut microbiome-derived butyrate (a short-chain fatty acid) synchronises host metabolism via regulating the expression of host peripheral circadian genes (Huang et al. 2022)
Maintenance of muscle mass and protein balance	*Ictidomys tridecemlineatus*		In hibernating ground squirrels, the gut microbiota recycles nitrogen from urea which is reabsorbed by the host to maintain muscle mass during hibernation (Regan et al. 2022)
Fat deposition, prevention of liver injury from obesity	*Marmota himalayana*		Specific gut commensals promotes fat deposition and also prevents obesity-related liver damage during hibernation (Bao et al. 2023)
Heat tolerance	*Sceloporus occidentalis*		Changes to the gut microbiota in response to experimental shifts in temperature linked to thermal tolerance (Moeller et al. 2020)
Fat deposition	*Ursus arctos*		Brown bears experience seasonal shifts in their gut microbiota during hibernation, with reduced microbial diversity and changes in lipid metabolism. These microbiota changes promote fat deposition, as shown by the transfer of seasonal metabolic traits to germ-free mice (Sommer et al. 2016)
Pathogen defence	*Chlorodrepanis virens*		Resistance to *Plasmodium* associated with microbiome composition (Navine et al. 2023)
Immunity	*Gryllus veletis*		Concurrent with overwintering changes in the gut microbiome, immune function shifted temporarily, returning to summer levels of activity in the spring (Ferguson et al. 2018)

Active migration is fuelled by a continuous supply of glucose that is created largely through lipid metabolism, and to a lesser extent though protein and carbohydrate metabolism (Butler 2016). These metabolic processes can be ramped up, dampened, or switched by the gut microbiota through various mechanisms (Table 2). For instance, the gut microbiota can alter the absorption of lipids and other nutrients (Zhang et al. 2020b) and generate metabolites that can be used directly in metabolic processes or act as signalling molecules that trigger changes in host metabolism (Wikoff et al. 2009, Krautkramer et al. 2021). These regulatory properties are exploited by hibernating species to ramp up fat deposition prior to hibernation (Sommer et al. 2016, Bao et al. 2023), prevent obesity related liver damage (Bao et al. 2023) and to maintain protein balance through nitrogen recycling (Regan et al. 2022).

Multiple metabolites of potential microbial origin have been suggested to play an important role in host health and performance (extensively covered by Krautkramer et al. 2021); see also Table 2 for microbially-mediated metabolic processes potentially involved in bird migration). Amongst these, fatty acids have a crucial role in migration (Landys et al. 2005, Guglielmo 2010) and, interestingly, are also a prime product of gut bacterial metabolism (Krautkramer et al. 2021). Blood levels of butyrate, a four-carbon short-chain fatty acid (SCFA), are strongly increased during migration suggesting a metabolic role of this component during active migration (Landys et al. 2005). While a large proportion of this component is likely to be synthesised by birds in the liver (as a secondary metabolic product from triglycerides, whose circulating levels in blood are also increased during migration [Landys et al. 2005]), butyrate production by gut microbiota also occurs, and it has been shown to have biological relevance in adaptation to seasonal changes in diet (Huang et al. 2022). Levels of other metabolites produced by the gut microbiome, such as lactic acid and L-valine, spike in the blood during migratory periods even in captivity, potentially through changes in the gut microbiome (Gupta et al. 2023).

There is some recent evidence of the link between the gut microbiome and metabolic capacity in migrating birds. The gut microbiome of ruddy turnstones *Arenaria interpres* expresses genes for enzymes related with the metabolism of polyunsaturated fatty acids (PUFAs), and this was associated with weight gain in staging individuals (Grond et al. 2023). PUFAs can efficiently fuel migration (Price 2010) and, hence, an intriguing possibility is that re-structuring of the gut microbiome upon arrival at staging grounds facilitate PUFA accumulation in preparation for long migratory flights (Grond et al. 2023). It is, however, uncertain whether bacterial metabolism had a causal effect on the metabolism and migratory performance of host individuals (Grond et al. 2023). Assessing whether changes in the gut microbiome associated with migration occur before birds depart, in an anticipatory manner, could provide evidence for their adaptive role.

Similarly, sampling the gut metagenome of blackpoll warblers *Setophaga striata* across life history stages revealed that several bacterial metabolic routes were enriched in staging compared to breeding individuals (e.g. vitamin, amino acid and fatty acid biosynthesis, and fermentation of carbohydrates to lactate; Trevelline et al. 2023). Some of these bacterial pathways were associated with the standardised mass index and subcutaneous fat deposits of staging blackpoll warblers, suggesting a link between the functional profile of the gut microbiome and fitness-related host traits. It is, however, still unknown whether such associations are indeed causal and whether hypothetically positive effects of gut microbiomes are driven by host adaptations rather than gut microbiome effects.

Immunity

Microbiome remodelling during migration may also impact host immunity and pathogen resistance. Migratory birds are exposed to a higher diversity of novel microbes and pathogens (Figuerola and Green 2000, Leung and Koprivnikar 2016, Gutiérrez et al. 2019), yet often downregulate most components of their immune system during migration (Nebel et al. 2012, Eikenaar and Hegemann 2016), presumably to funnel energy resources into flight in the presence of a trade-off between immunity and flight (Buehler et al. 2009, Hegemann et al. 2022). This could lead to migratory culling of infected individuals (Majewska et al. 2022, Gangoso et al. 2024). Surprisingly, migratory species also seem to have lost some immunogenetic diversity compared to residents (O'Connor et al. 2018), despite exposure to a higher diversity of pathogens. This opens the question as to whether the microbiome plays a role in pathogen resistance during migratory journeys, a period of heightened infection risk.

Gut microbiome remodelling during migration may increase vulnerability to pathogen invasion and infection. However, the major adaptive advantage of having a gut microbiome is proposed to be protection against pathogens and parasites (McLaren and Callahan 2020), suggesting that microbiome remodelling could alternatively have a protective effect against infection, at least for some parasites and pathogens. The gut is a permeable interface between the environment and the host body and, therefore, highly vulnerable to invasion and a major route of infection. The commensal microbiome protects hosts from pathogens in three ways: firstly, it provides a benign microbial layer along the epithelium that acts to block colonisation and infection by pathogens (Abt and Pamer 2014). Secondly, immunomodulatory molecules such as lipopolysaccharide, flagellin, peptidoglycan and microbial DNA produced by the gut microbiota stimulate the production and circulation of antibodies that have cross-reactivity to a wide range of gut and blood pathogens and parasites, including malaria and influenza viruses (Villarino et al. 2016, Schluter et al. 2020).

There are numerous potential pathways by which the gut microbiome could modulate the immunity of migrating individuals. One possibility is that either via top-down or bottom-up processes the gut microbiota of migrants become a low diversity ecosystem. Whilst high diversity communities are often assumed to be more robust to invasion, this is not always the case. For instance, the vaginal microbiome is a low diversity community dominated by *Lactobacillus*, which produces lactic acid, thereby reducing the pH of the vaginal tract and limiting colonisation of pathogens (Edwards et al. 2019). The low diversity microbiomes observed during migration could represent a similar mechanism that acts temporarily during migratory flights. Shifts in diet during stopover and staging may also trigger adaptive shifts in the gut microbiome that enhance pathogen defence. For example, experimental diet manipulation in humans alters the gut microbiota with consequences for immune responses (Wastyk et al. 2021). Together, these studies raise the possibility of adaptive immune-microbiota crosstalk, potentially mediated by switches in diet across the migratory period.

Whilst adaptive remodelling of the gut microbiome during migration could potentially confer protection against a wide variety of infective agents, it is reasonable to propose that such responses may be targeted towards the parasites and pathogens that exert the strongest selective forces in birds. Avian malaria and avian influenza are likely two of the most important groups of infective agents faced by migrants, with large impacts on survival (Causey and Edwards 2008, Samuel et al. 2015). Resistance to both groups of pathogens has been linked to gut microbiome composition (Villarino et al. 2016, Yitbarek et al. 2018, Navine et al. 2023). For instance, there is evidence that *E. coli* is important for protection against avian malaria (Aželytė et al. 2022), and has additionally been linked to protective effects against malaria in Hawaiian honeycreepers (Navine et al. 2023). *Escherichia coli* is used as a vaccine against avian malaria, with mosquitoes fed on the blood of inoculated birds having reduced *Plasmodium* loads (Aželytė et al. 2022). This protection is hypothesised to be mediated by *E. coli*-specific antibodies produced by the host, which potentially provide cross-protection against malaria. In contrast, high levels of *Bacteroides* in humans has been associated with increased malaria susceptibility (Mandal et al. 2023). Gram negative bacteria, such as those represented by the phylum Pseudomonadota, may play a particularly important role in the protection against major bird pathogens by stimulating the production of cross-reactive antibodies. As such, the proliferation of putatively pathogenic taxa sometimes observed in migratory birds (Włodarczyk et al. 2024) may play an important role in protection against more virulent parasites and pathogens.

Outstanding questions

Previous papers have reviewed the (general) importance of variation in gut microbiomes for avian ecology and evolution (Bodawatta et al. 2022), and the methodological tools that can be applied to investigate variation in wild gut microbiomes (Worsley et al. 2024). Here, we highlight some unsolved questions, generally framed, whose answer is, in our opinion, crucial to further our understanding of the role of gut microbiomes in bird migration and propose methods to tackle some of those questions.

Isolating the effect of migratory state on changes in gut microbiomes

During migration, many external factors change concurrently with the physiology and behaviour of birds. For example, diet commonly changes between breeding, stopover and wintering grounds. Disentangling whether changes in the gut microbiome during migration are caused by environmental variation (e.g. diet) or have an endogenous origin (e.g. they are caused by physiological changes associated with migration) will be an important step towards stablishing the causal role and implications of variation in gut microbiomes for migration. Eliciting migratory behaviour in laboratory conditions is possible, has been used to understand migratory restlessness and this methodology can also be used to understand how the onset of migration impact variation in gut microbiomes while environmental conditions are controlled (Gupta et al. 2023 for a recent example). Investigating whether changes in the gut microbiome associated with active migration already occur before birds depart could also be informative of whether migration-associated changes in gut microbiomes are endogenous or promoted by the external environment (e.g. sampling migratory individuals at departure, during migration and on arrival within a narrow time frame).

What is the relative importance of top-down versus bottom-up processes for shaping the gut microbiome during migration?

As discussed above, it is still not clear whether top-down or bottom-up processes drive variation in gut microbiome composition and function during bird migration; or, if both apply at the same time, their relative importance. Background information on the extent to which gut microbiome variation is driven by endogenous physiological changes triggered by migratory behaviour (Outstanding question i) will be an important first step to provide a reference level against which the influence of top-down processes can be assessed. In a wild set up, gut microbiome comparisons of individuals of the same species at the same sites but with varying migratory phenotypes would provide an ideal study set up (Grond et al. 2014, Risely et al. 2018, Włodarczyk et al. 2024).

Is there an effect of migration strategy on gut microbiome composition and function

The diversity of migratory strategies displayed by birds provides the unique opportunity to assess how inter-species variation in migratory behaviour impacts gut microbiomes. A phylogenetically-controlled comparative study investigating the gut microbiomes of long-distance and short-distance migrants using different migratory flyways and wintering grounds could be used. In this context, it could be particularly informative to collect samples from species with different migratory strategies from the same locations to control for variation associated with sampling location. The analysis of gut microbiomes of resident species along the flyway and non-breeding grounds would provide additional information on environmental effects on the gut microbiomes of migratory species (Schmiedová et al. 2023). As data accumulates across migratory flyways and species, meta-analyses looking at the effect of migratory strategy on gut microbiomes could be a powerful tool for evidence synthesis.

Does the remodelling of the gut microbiome during migration impact pathogen susceptibility and resistance?

Given the potential for substantial spatial and temporal co-correlation between immunity, gut microbiome composition, and pathogen exposure, this question can only be truly answered experimentally, for example, through infection experiments that incorporate gut microbiome manipulation or transfer. Wide-spread pathogens, such as avian malaria, may be particularly good model organisms with which to test this question. However, observational study designs that correlate immunity, pathogen infection, and the gut microbiome may shed initial light on important connections. Moreover, metagenomic sequencing across the migratory period could identify changes in diversity or abundance of pathogenic strains and/or virulence genes.

How much variation in circulating metabolites and immune cells does gut microbiome composition explain across the migratory period?

A major question to decipher the functional role of the gut microbiome in bird migration will be to evaluate to what extent circulating metabolites and immune cells in migrating birds arise from host–gut microbiome interactions. Assessment of blood metabolites / immunity following gut microbiome manipulations (above) combined with new analytical tools to identify metabolites of microbial origin (Shaffer et al. 2019) provide promising avenues to detect microbial-derived metabolites of relevance for migration. The identification of such metabolites and immune components would open possibilities to targeted experimental approaches where the abundance of specific microbial taxa of hypothesised importance is experimentally manipulated.

Does the gut microbiome have a causal effect on migratory behaviour?

Given the link between the gut microbiome and behaviour in other systems (reviewed by Cryan and Dinan 2012, Davidson et al. 2020), it is possible that the gut microbiome also influences migration-related behavioural traits. Experiments treating migratory birds with antibiotics provide suggestive evidence for a gut microbiome effect on bird orientation (Werber et al. 2022); though it is still not clear whether such effect is mediated by the gut microbiome. Another largely unexplored hypothesis is that effects of neurotoxic insecticides that are known to impact bird migratory behaviour (Eng et al. 2019) are (fully or partly) mediated via effects on gut microbiomes, which are known to be negatively impacted by neurotoxic insecticides (Favaro et al. 2023). While experimental manipulation of the gut microbiome in wild migratory birds is challenging, it is certainly possible and has been successfully achieved in other wild systems (reviewed in Davidson et al. 2020; see also Somers et al. 2024). Probiotics or antibiotics can be used to modify gut microbiome composition while migratory behaviour can be assessed simultaneously using a tracking system (e.g. MOTUS, GPS devices or geolocators) to assess whether changes in gut microbiomes impact migratory behaviour. Links between variation in gut microbiomes and migratory behaviour are still largely speculative but initial evidence and findings from other systems indicate this might be a fruitful avenue for future research (e.g. navigation, food choice along migratory route, etc).

The effects of global change on the interaction between gut microbiomes and migratory species

Global change due to climate change and land-use changes are impacting migratory birds worldwide (Wilcove and Wikelski 2008). Temporal (i.e. time of arrival at breeding grounds) and spatial (i.e. variation in migratory routes) changes to migratory behaviour caused by global change could have important consequences for host–microbiome interactions in migratory systems. For example, reduction in migratory distance could dramatically impact the diversity of microbial species that migratory birds are exposed to, with yet unknown consequences for gut microbiome function. As migrating birds effectively shuttle gut microbial species across the planet, global change effects on migration will likely impact the distribution of microbial species with potential consequences for host birds but also human public health (Cohen 2023).

Conclusions

Due to its extreme physiological requirements and novel exposure to pathogens along the migratory journey, bird migration represents an ideal biological phenomenon in which to investigate host–gut microbiome interactions and their consequences for host fitness. Studies to date indicate clear signatures of migratory behaviour on the gut microbiome migratory bird species. Changes in gut microbiomes associated with migration are not consistent taxonomically, suggesting species-specific patterns or, possibly, that important functions of the gut microbiome are conserved across diverse microbial species. Experimental manipulations in combination with ‘omics approaches are now needed to elucidate the functional relevance of the gut microbiome in migratory species, and to test whether such effects are adaptive or, indeed, maladaptive. Ultimately, understanding the role of the gut microbiome on migration eco-physiology would allow us to better predict the effects of global change on both, migratory species and the global dynamics of gut microbial species.

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Data availability statement

The content of this manuscript does not build on an original dataset.

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