

# Impacts of coprophagic foraging behaviour on the avian gut microbiome

Alice Dunbar<sup>1</sup>, Barbara Drigo<sup>1,2,\*</sup> , Steven P. Djordjevic<sup>3,4</sup>, Erica Donner<sup>1,5</sup> and Bethany J. Hoye<sup>6</sup>

<sup>1</sup>*Future Industries Institute (FII), University of South Australia, Mawson Lakes Campus, GPO Box 2471 5095, Adelaide, South Australia, Australia*

<sup>2</sup>*UniSA STEM, University of South Australia, GPO Box 2471, Adelaide, South Australia 5001, Australia*

<sup>3</sup>*Australian Institute for Microbiology and Infection, University of Technology Sydney, PO Box 123, Ultimo, New South Wales 2007, Australia*

<sup>4</sup>*Australian Centre for Genomic Epidemiological Microbiology, University of Technology Sydney, PO Box 123, Ultimo, New South Wales 2007, Australia*

<sup>5</sup>*Cooperative Research Centre for Solving Antimicrobial Resistance in Agribusiness, Food, and Environments (CRC SAAFE), University of South Australia, GPO Box 2471 5095, Adelaide, South Australia, Australia*

<sup>6</sup>*School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia*

## ABSTRACT

Avian gut microbial communities are complex and play a fundamental role in regulating biological functions within an individual. Although it is well established that diet can influence the structure and composition of the gut microbiota, foraging behaviour may also play a critical, yet unexplored role in shaping the composition, dynamics, and adaptive potential of avian gut microbiota. In this review, we examine the potential influence of coprophagic foraging behaviour on the establishment and adaptability of wild avian gut microbiomes. Coprophagy involves the ingestion of faeces, sourced from either self (autocoprophagy), conspecific animals (allocoprophagy), or heterospecific animals. Much like faecal transplant therapy, coprophagy may (i) support the establishment of the gut microbiota of young precocial species, (ii) directly and indirectly provide nutritional and energetic requirements, and (iii) represent a mechanism by which birds can rapidly adapt the microbiota to changing environments and diets. However, in certain contexts, coprophagy may also pose risks to wild birds, and their microbiomes, through increased exposure to chemical pollutants, pathogenic microbes, and antibiotic-resistant microbes, with deleterious effects on host health and performance. Given the potentially far-reaching consequences of coprophagy for avian microbiomes, and the dearth of literature directly investigating these links, we have developed a predictive framework for directing future research to understand better when and why wild birds engage in distinct types of coprophagy, and the consequences of this foraging behaviour. There is a need for comprehensive investigation into the influence of coprophagy on avian gut microbiotas and its effects on host health and performance throughout ontogeny and across a range of environmental perturbations. Future behavioural studies combined with metagenomic approaches are needed to provide insights into the function of this poorly understood behaviour.

*Key words:* coprophagy, foraging behaviour, diet, herbivory, nutrition, microbiome development, excreta, antimicrobial resistance.

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\* Author for correspondence (Tel.: +61 8 8302 5639; E-mail: [barbara.drigo@unisa.edu.au](mailto:barbara.drigo@unisa.edu.au)).

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## I. INTRODUCTION

The microbiota of an individual's gastrointestinal tract, comprising microbes, their genes, and their functional traits, is fundamental to host digestion (McWhorter, Caviedes-Vidal & Karasov, 2009), detoxification (Kohl *et al.*, 2016), development (Parfrey, Moreau & Russell, 2018), immune function (Broom & Kogut, 2018), protection from pathogenic bacteria (Roggenbuck *et al.*, 2014; Mendoza *et al.*, 2017), and cognitive performance (Davidson, Raulo & Knowles, 2020a). Gastrointestinal microbiota are thus critical to the maintenance of organismal health and have been suggested to play a significant role in host adaptation to novel and changing environments (Alberdi *et al.*, 2016; Shapira, 2016). Given the importance of the gut microbiome to host health and performance, it is important to understand what shapes the composition and dynamics of these communities, including their establishment, development, maintenance, and any punctuated changes throughout the life of an organism.

Dynamics of an individual's gut microbiota include fluctuations in microbial species composition and abundance, with ensuing changes to gut function and signalling (Waite & Taylor, 2014; Teyssier *et al.*, 2018). These changes may play out over a wide range of timescales, from predictable daily fluctuations reflecting feeding–fasting rhythms (Risely *et al.*, 2021) to cyclical seasonal fluctuations (Wienemann *et al.*, 2011; Bodawatta *et al.*, 2021b), ontogenic changes (van Dongen *et al.*, 2013; Teyssier *et al.*, 2018; Maraci *et al.*, 2022a), and even shifts during senescence (Bosco & Noti, 2021). Animals may also experience unpredictable punctuated fluctuations in microbiota composition associated with shifts in resource availability as a result of habitat destruction, land-use change and urbanization (Furst *et al.*, 2018; Murray *et al.*, 2020; San Juan *et al.*, 2020; Maraci *et al.*, 2022b), and exposure to environmental pollutants, including antimicrobials (Ward *et al.*, 2019; Ruuskanen *et al.*, 2020). Similarly, animals entering captivity (Lamberski *et al.*, 2003; Oliveira *et al.*, 2020; Sun *et al.*, 2022; West *et al.*, 2022) or being released after rehabilitation or captive rearing also experience changes in their microbiota (Diaz & Reese, 2021). While predictable changes in microbiota are thought to support host adaptation to altered intrinsic (within-host) or extrinsic (external) environments (Alberdi *et al.*, 2016; Mendoza *et al.*, 2017; Troha & Ayres, 2020),

unanticipated disruptions to the microbiota have the potential to alter host development (Kohl *et al.*, 2018), health, and performance (Davidson *et al.*, 2020b). Given the critical role gut microbiomes can play in modulating host ontogeny, behaviour, and health, it is important to understand the mechanisms that allow animals to form and reshape their microbiota in the face of intrinsic and extrinsic change.

Wild birds are among the most mobile of all animals. This mobility, together with extreme morphological diversity, has enabled this taxon to occupy every habitat on every continent (Cooney, Seddon & Tobias, 2016; Navalón *et al.*, 2019; Pigot *et al.*, 2020). However, the mobility afforded by flight also presents an energetic and nutritional trade-off (Scanes, 2020), potentially necessitating mechanisms for enhancing the adaptability of their microbiomes (Grond *et al.*, 2018; Bodawatta *et al.*, 2021b). Adaptation to flight has also resulted in birds having intestines with smaller surface area and volume compared to similar-sized mammals (Caviedes-Vidal *et al.*, 2007; McWhorter *et al.*, 2009). Microbiota may therefore be especially important for such taxa to access adequate nutrition and energy.

An expanding body of research into avian microbiomes has demonstrated profound differences in the gut microbiota associated with different host species (Kohl, 2012; Capunitan *et al.*, 2020), host habitats (Gillingham *et al.*, 2019; Berlow, Phillips & Derryberry, 2021), and host diet (Furst *et al.*, 2018; Loo *et al.*, 2019; Bodawatta *et al.*, 2021a; Góngora, Elliott & Whyte, 2021). Influential aspects of host diet include feeding guild (Wang *et al.*, 2019; Bodawatta *et al.*, 2021c; Ingala, *et al.*, 2021), dietary breadth (Drovetski *et al.*, 2019; Schmiedová *et al.*, 2022) and macronutrient composition (Coogan *et al.*, 2017). However, drivers of microbiota dynamics in wild birds have been less explored than those of wild mammals and domestic birds (Grond *et al.*, 2018; Matheen, Gillings & Dudaniec, 2022). Several recent reviews have therefore called for further research to gain a more comprehensive understanding of the impact of environmental drivers on avian gut microbiota and how it influences avian behaviour, ecology, pathogen transmission, and conservation (Grond *et al.*, 2019; Davidson *et al.*, 2020b).

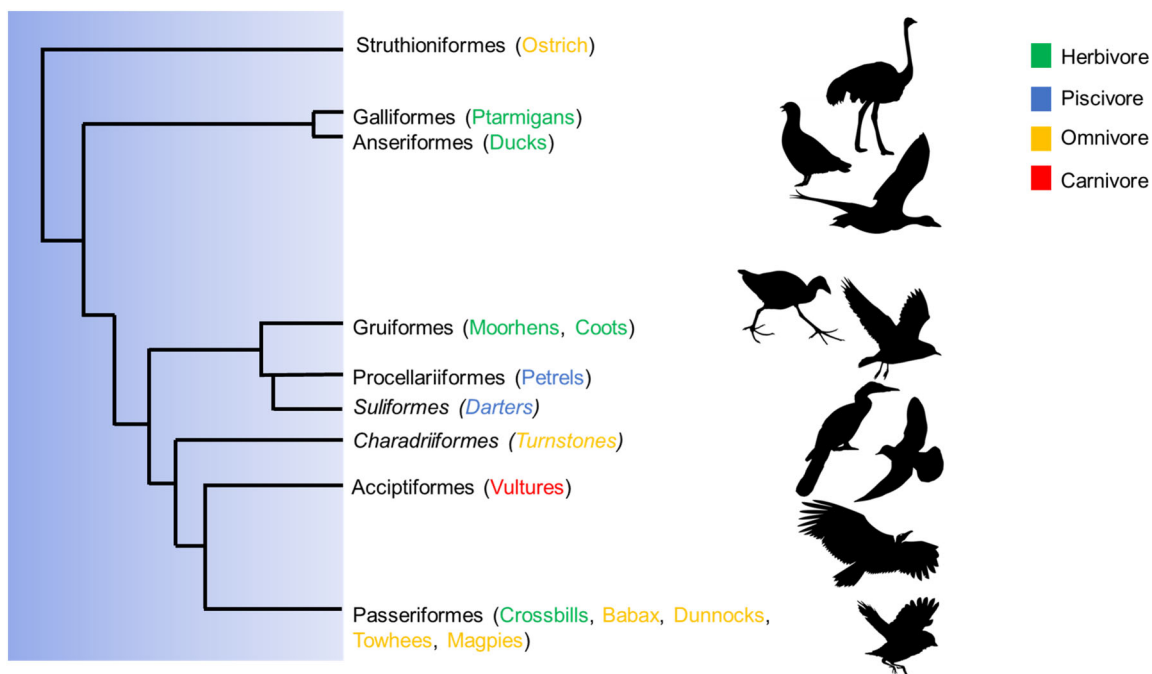
Foraging behaviour (including all activities involved in searching for, procuring or capturing, and processing or handling of diet items prior to ingestion, as well as the choice of food items for consumption), presents a range of potential mechanisms that support dynamic changes in avian

microbiota (Vispo & Karasov, 1997; Pigot *et al.*, 2020). However, in contrast to the well-established role of diet composition on vertebrate gut microbiota, the role of foraging behaviour has received less attention. One particular foraging behaviour that could have a profound influence on gut microbiota composition and dynamics is coprophagy. Coprophagy is defined as the ingestion of faeces, whether they are an animal's own (*autocoprophagy*), from a different individual of the same species (*allocoprophagy*), or from a distinct species (*heterospecific coprophagy*) (Hirakawa, 2001). This behaviour is considered a natural physiological phenomenon in many wild and domestic species (Soave & Brand, 1991; Flachowsky, 1997). Coprophagy has been particularly well-documented in mammals where it is considered a means by which animals gain energetic or nutritional supplementation, especially in herbivores (Hörnigke & Björnhag, 1980; Soave & Brand, 1991; Hirakawa, 2001; Waggershauser *et al.*, 2022). Although coprophagic behaviour is considered commonplace in poultry (Line, Hiatt & Colan, 2008), our understanding of the importance of coprophagic behaviour in wild birds is in its infancy. In contrast to insects and mammals, avian species reported to practice coprophagy are not limited to herbivores; this behaviour is also seen in avian omnivores, piscivores, and carnivores (Fig. 1). Moreover, although most studies on avian coprophagy have inferred energetic and nutritional benefits of these readily available 'resources' (Fig. 2), there is growing evidence to suggest that coprophagy may be a mechanism by which birds augment and dynamically modify their gut microbiome (Kobayashi *et al.*, 2019; Gao, *et al.*, 2020).




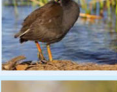
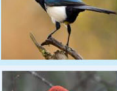
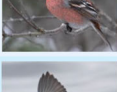






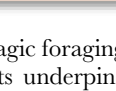
Coprophagy may therefore be beneficial to birds during development as well as during times of seasonal fluctuation, facilitating the adaptation of an individual's gut microbiota to its surrounding environment (Fig. 3). Here, we review the potential for coprophagy to influence the establishment and adaptability of wild avian gut microbiomes. We draw particular attention to what may drive the propensity for birds to engage in this behaviour, which may play a unique, yet unassessed role in microbiome dynamics. We go on to demonstrate that these behaviours may be beneficial to the overall health of an individual, by promoting adaptation of an individual's microbiota to available food resources or other environmental conditions but may also entail detrimental effects.

## II. INFLUENCE OF EARLY COPROPHAGY ON GUT MICROBIOME ESTABLISHMENT

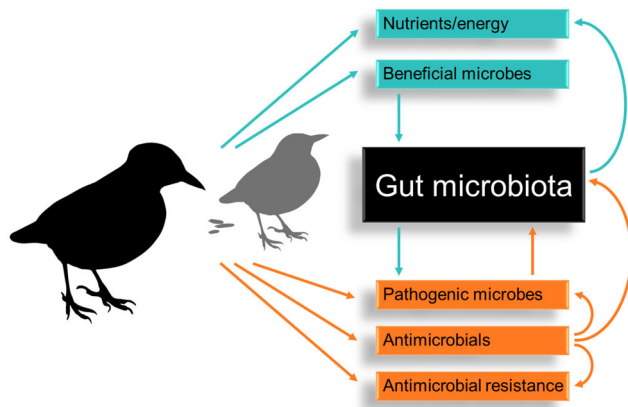
Like mammals, where colonization of the gut microbiome begins during and after birth by maternally acquired bacteria (de Goffau *et al.*, 2019; Kuperman *et al.*, 2020), initial acquisition of microbiota in birds occurs after hatching, as the egg generally remains sterile (Grond *et al.*, 2017; Zhou *et al.*, 2020a). Although bacteria from the oviduct and/or cloaca of the female parent may penetrate the egg and inoculate the growing foetus (Ballou *et al.*, 2016; Ilina *et al.*, 2016; Ding *et al.*, 2017; Broom & Kogut, 2018; Dietz *et al.*, 2019; Lee *et al.*, 2019b; Těšický *et al.*, 2023) this may only



**Fig. 1.** Coprophagic foraging behaviour has been reported across a wide range of phylogenetically distant avian taxa, with substantial variation in their predominant feeding guild. Italicized taxon names represent species recently reported as engaging in coprophagy (2020–present). The other branches of the tree have been removed in order to highlight the connections between the listed species. Phylogeny based on Petkov & Jarvis (2012), images sourced from Pixabay and Shutterstock under a standard license.

		AVIAN SPECIES	COPROPHAGIC BEHAVIOUR
NUTRIENT &/OR ENERGY	Heterospecific coprophagy	Giant petrel ( <i>Macronectes giganteus</i> )	 Visit Weddell seal haul-out sites during incubation and during chick-rearing. Potentially feed on seal faeces to recover rapidly from fasting bout and fuel foraging trip (Corá <i>et al.</i> , 2020)
		Dabbling ducks ( <i>Anas platyrhynchos</i> , <i>A. crecca</i> , <i>A. formosa</i> )	 Feed on whooper swan faeces, presumably accessing undigested vegetation, when regular food resources are inaccessible due to ice cover (Shimada, 2012)
		Eurasian coot ( <i>Fulica atra</i> )	 Feed on faeces of black-headed gulls and waterfowl likely when regular food resources are unavailable (Boot, 1987.; Vogrin, 1997.; Wall, 1983)
		Dusky moorhen ( <i>Gallinula tenebrosa</i> )	 Exclusively searched for gull faeces and consumed them presumably to satisfy a nutritional requirement (Starks & Peter, 1991)
		Magpie ( <i>Pica pica</i> )	 Feed on domestic dog faeces, possibly consuming undigested food (Summers-Smith, 1983)
		White-winged crossbill ( <i>Loxia leucoptera</i> )	 Feed on river otter faeces, potentially supplementing diet with calcium from undigested fish bones (Gallant, 2004)
		Wilson's storm petrel ( <i>Oceanites oceanicus</i> )	 Feed on faeces from North Atlantic right whale, likely an opportunistic source of protein and nutrients (Kraus & Stone, 1995)
		Turkey vulture ( <i>Cathartes aura</i> )	 Consume puma faeces putatively to satisfy a nutritional requirement (González-Jáuregui <i>et al.</i> , 2021)
		Egyptian vulture ( <i>Neophron percnopterus</i> )	 Captive individual consumed cow faeces as a reliable and readily available source of carotenoids for facial ornamentation (Negro <i>et al.</i> , 2002)
MICROBIAL	Allocoprophagy	Spotted towhee ( <i>Pipilo maculatus</i> )	 Parents consume nestling faecal sacs potentially to replenish energy and nutrients used in reproductive efforts (McKay <i>et al.</i> , 2009)
		Dunnoch ( <i>Prunella modularis</i> )	 Parents theoretically consume nestling faeces to recycle nutrients and/or reduce time away from the nest (Lamb <i>et al.</i> , 2017)
		Ostrich ( <i>Struthio camelus</i> )	 Faecal-supplemented chicks showed increase in gut microbial diversity, higher growth rate, and reduced gut disease compared to control chicks (Videvall <i>et al.</i> , 2023)
		Giant babax ( <i>Babax waddelli</i> )	 Parents consume nestling faecal sacs to sanitise the nest. Potentially also a method by which adults acquire <i>Firmicutes</i> , an important taxon in the avian gut microbiome (Gao <i>et al.</i> , 2020)
		Japanese rock ptarmigan ( <i>Lagopus muta japonica</i> )	 Chicks consume cecal faeces from parents, possibly to establish gut microbiome (Kobayashi <i>et al.</i> , 2019)

**Fig. 2.** The majority of studies investigating coprophagic foraging behaviour in wild birds have assessed heterospecific coprophagy, speculating that nutritional and/or energetic benefits underpin this behaviour. Only recently have studies noted the potential microbial benefits of coprophagy. Papers were found by a direct review of existing literature including a *Google Scholar* and *Web of Science* search, using the term ‘avian coprophagy’ and ‘bird coprophagy’ and consulting references cited in each paper collected. Images have been sourced from Shutterstock and Pixabay under a standard license. Giant babax reference has image of a Chinese babax (*Pterorhinus lanceolatus*).



**Fig. 3.** Potential benefits and hazards of coprophagic foraging. Coprophagy may enable birds to benefit (blue) from increased access to nutrients and energy, and directly and indirectly from beneficial microbes. However, this behaviour may also have deleterious effects (orange) on the gut microbiota and hence host health and performance, including increased exposure to pathogenic microbes, antimicrobial compounds and antimicrobial resistance genes, either directly or as a result of selection pressures imposed by ingested antimicrobials.

occur when the bacteria are pathogenic, rather than commensal (Iliina *et al.*, 2016). The vast majority of colonization and recruitment therefore involves post-hatch exposure to microbes acquired through the environment (Grond *et al.*, 2019) and foraging (Grond *et al.*, 2017; Kobayashi *et al.*, 2019). Foraging strategy and developmental trajectory therefore play a profound role in shaping the establishment of avian gut microbiomes.

Prior to fledging, developmental trajectories of avian young range from altricial to precocial. Altricial chicks are underdeveloped at hatching and therefore completely dependent on their parents for food and protection for an extended period, ranging from 30 days to 4 months (Schekkerman, Visser & Blem, 2001; Perrig *et al.*, 2017; Martin *et al.*, 2018; Matsubayashi *et al.*, 2021). Precocial chicks, on the other hand, are more developed at hatching and able to leave the nest and forage directly from their environment (Naef-Daenzer & Grüebler, 2016; Grond *et al.*, 2018), with parents providing some protection and guidance to suitable resources (Naef-Daenzer & Grüebler, 2016). Parents of altricial chicks can provide food at a much higher rate than precocial chicks are able to self-source, and as a result, altricial young show a faster growth rate (Naef-Daenzer & Grüebler, 2016). Parents of altricial young are also likely to provision them with microbes by salivary transfer during feeding (Grond *et al.*, 2018; Chen *et al.*, 2020). In addition, extended occupation of the nest increases opportunities for microbial seeding from the nest environment, particularly parental faecal matter (Somers *et al.*, 2023; Grond *et al.*, 2018; Dietz *et al.*, 2019; Diez-Méndez *et al.*, 2022; Maraci *et al.*, 2022a). By contrast, precocial chicks establish their microbiota from the environment, within as little as 2 days after hatching (Ballou *et al.*, 2016; Grond *et al.*, 2017).



The stark difference in microbial sources between these developmental trajectories plays a fundamental role in the composition and dynamics of the gut microbial communities of birds. Altricial species have been shown to undergo profound changes in the abundance of different bacterial phyla early in their development, with a progressive increase in the abundance of Firmicutes up to 21 days post hatching, and a concomitant decrease in Proteobacteria (Grond *et al.*, 2017; Zhou *et al.*, 2020a; Xu *et al.*, 2022). These compositional shifts were accompanied by shifts in metabolic function, which have been found to facilitate the digestion efficiency, rapid body mass gain and development typically seen in altricial species (Caviedes-Vidal *et al.*, 2007; Evans *et al.*, 2017; Teyssier *et al.*, 2018).

By contrast, precocial chicks are highly mobile and forage independently on various food items in addition to any microbiota seeding from their parents. As a result, their gut microbiome is expected to be more dynamic during ontogeny, fluctuating in response to changes in their diet and surrounding environment (Grond *et al.*, 2019). For example, in dunlin (*Calidris alpina*) and semipalmated sandpiper (*Calidris pusilla*) chicks, bacterial diversity and abundance was highest at 3 days of age with Clostridia and Gammaproteobacteria being the most abundant, however from 3 to 10 days of age bacterial abundance and diversity stabilized with Clostridia and Bacilli becoming the most dominant classes (Grond *et al.*, 2017). In coprophagic Japanese rock ptarmigans (*Lagopus muta japonica*) Coriobacteriia and Clostridia were consistently the most abundant class at all growth stages and there was a considerable variability in microbiota colonization during development (Kobayashi *et al.*, 2019). Coprophagy may therefore allow precocial chicks to seed their microbiota with microbes suited to efficient digestion of the available food items (Kobayashi *et al.*, 2019) and may also benefit from a microbial structure that reduces susceptibility to disease (Videvall *et al.*, 2023). Indeed, captive precocial species like ostrich (*Struthio camelus*) show a high frequency of the behaviour in their early life stages (Fericean *et al.*, 2021). Indeed, recent experimental research assessing faecal-supplemented ostrich chicks has shown that coprophagy is associated with distinct gut microbial composition, phylogenetic structure, and taxonomic abundance compared to control chicks, with microbiomes that progressed more rapidly to that of adult ostriches (Videvall *et al.*, 2023). Coprophagy-treatment chicks also had higher growth rates, with lower rates of gut disease (Videvall *et al.*, 2023), suggesting coprophagy is not only important for establishing the gut microbiota of the chicks, but that this foraging behaviour plays a foundational role in chick growth, development, and health. This may, in part, relate to the herbivorous diet of adult ostriches. In early life, young ostriches supplement their diet with insects after hatching, before progressing to the herbivorous diet of adulthood. Vispo & Karasov (1997) suggest this may be because chicks lack the microbiota needed to assist with utilization of a plant-based diet in their infancy. Although this has not been definitively established, the experimental study of

Videvall *et al.* (2023) provides an insight into this possibility. Given the paucity of species and environmental contexts in which these observations have been made (Fig. 1), the limited number of studies of allocoprophagy (Fig. 2), and the lack of mechanistic investigations into the causes and benefits of this behaviour (Fig. 2), further studies into the importance of coprophagy in seeding the gut microbiota of avian young are sorely needed. Experimental manipulations controlling energy and nutrient intake would improve our understanding of the importance of coprophagy to microbiota ontogeny. Detailed data on avian microbial communities throughout development, and their functional profiles, would be especially valuable in quantifying how coprophagy can assist with dietary changes during ontogeny (Fig. 4).

### III. ROLE OF COPROPHAGY ON ADULT GUT MICROBIOME STABILIZATION

Once a bird's microbiota is established, rapid changes in gut microbiota may still be necessary to adapt dynamically to different diets, exposure to toxins (Kohl *et al.*, 2016) and pathogenic bacteria (Roggenbuck *et al.*, 2014; Mendoza *et al.*, 2017), and for the ongoing maintenance of immune function (Broom & Kogut, 2018). Dynamic shifts in microbiota could be particularly important in birds with temporally varying diet composition. Research has shown that changes in diet can alter gut microbiota composition within

	Life stage	Ecological context
	Establishment of gut microbiota	Precocial species Diets with hard-to-digest components
	Seasonal diet switches	Species with diet items that show strong seasonal variation Diets with hard-to-digest components
	Migratory refuelling	Long-distance migratory species
	Moult	Complete, pre-basic moult Species with temporally constrained moult periods
	Extreme weather events	Dietary specialists
	Novel diets through anthropogenic disturbance	Dietary specialists Anthropogenically dominated landscapes

**Fig. 4.** Life stages and ecological contexts in which wild birds are predicted to be more likely to undertake, and benefit from, coprophagy when considering the potential impact of this foraging behaviour on the gut microbiota and its function. These represent key stages and contexts for future investigations into the importance of coprophagy to the dynamics of avian gut microbiota.

24 h (Wu *et al.*, 2011) and that the relative abundance of microbial taxa varies according to diet. Vegetative cell walls are less digestible than nectar or invertebrate and vertebrate prey (McWhorter *et al.*, 2009), and microbially derived enzymes thus play a key role underpinning digestion and nutrient uptake in herbivorous species. In many herbivorous mammals, foregut fermentation is a digestive method which allows the detoxification of secondary plant compounds and the breakdown of cellulose using fermentation in pregastric chambers (Grajal, 1995a,b; Lopez-Calleja & Bozinovic, 2000). However, the only bird species known to use this digestive system is the hoatzin (*Opisthocomus hoazin*) (Grajal, 1995b). In other herbivorous avian species, the microbiota involved in digestion occur primarily in the caecum (Soave & Brand, 1991; McWhorter *et al.*, 2009; Hunt *et al.*, 2019). In these species, some nutrients and short-chain fatty acids may be absorbed by the caecum (McWhorter *et al.*, 2009), but primary absorption by the small intestine is missed. In such cases, coprophagy has been suggested to be a critical foraging behaviour that facilitates the uptake of lost or missing nutrients (Soave & Brand, 1991; Starks & Peter, 1991; Gallant, 2004; McWhorter *et al.*, 2009). In some mammalian species, thiamine, K and B vitamins, and proteins are primarily excreted in faeces without absorption, but uptake can be increased *via* faeces reingestion (Soave & Brand, 1991). This level of detail is currently lacking from avian studies (González-Jáuregui, Esparza-Carlos & Mir, 2021) (Fig. 2), however, birds have been shown to be less efficient in metabolizing plant-based diets compared to mammals (Buchsbaum, Wilson & Valiela, 1986), suggesting coprophagy may play a significant role in nutrient uptake in birds, particularly those with an herbivorous diet. Interestingly, however, coprophagy has been described across a wide range of distantly related avian species from several different dietary niches (Fig. 1). For example, aquatic herbivores such as coot (Gruiformes: Rallidae) and ducks (Anseriformes: Anatidae), marine piscivores such as giant petrel (*Macronectes giganteus*) (Procellariiformes: Procellariidae) and Wilson's storm petrel (*Oceanites oceanicus*) (Procellariiformes: Oceanitidae), carrion-feeding Old World (Accipitriformes: Accipitridae) and New World vultures (Accipitriformes: Cathartidae), and insectivorous dunnock (*Prunella modularis*) (Passeriformes: Prunellidae), babax (Passeriformes: Leiotrichidae), and towhee (Passeriformes: Passerellidae) have all been reported as displaying coprophagic behaviour (Fig. 1). Most studies have presumed this behaviour is undertaken to access undigested or microbially digested food resources (Summers-Smith, 1983; Kraus & Stone, 1995; Negro *et al.*, 2002; Gallant, 2004) (Fig. 2). Although some studies have suggested a role for coprophagy in seeding the microbiota of developing birds, to date there has been only one (Videvall *et al.*, 2023) directly investigating the role of coprophagy in renewing or augmenting the gut microbiota of adult birds (Fig. 2). Yet the evidence detailed throughout this review suggests that shifts in microbiota, aided by coprophagy, could be particularly important for dynamic adaptation in adult birds.

## (1) Dietary specialization

Specialization in diet leads to a dependence on specific, and often limited, resources, making specialists more vulnerable to environmental change (Morelli *et al.*, 2021). A specialist species which feeds exclusively on a specific food source may be predicted to have a gut microbiome low in bacterial diversity, as a narrow specialist food range is less variable in its digestion pathways. For example, hummingbirds feed entirely on nectar and have been reported to harbour bacteria only from five or six phyla including Proteobacteria, Firmicutes, and Actinobacteria (Lee *et al.*, 2019a; Herder *et al.*, 2021). Kakapo (*Strigops habroptilus*), which feed on a limited diet of roots, bulbs, and leaves, also harbour low bacterial diversity (Waite, Deines & Taylor, 2012). Their microbiome comprises two main phyla, Gammaproteobacteria and Firmicutes, with Fusobacteria present only when feeding on rimu tree (*Dacrydium cupressinum*) fruits (Houston *et al.*, 2007; Waite *et al.*, 2012). However, this is not always the case. Although hoatzin have a primarily folivorous diet, their microbiome comprises a highly diverse bacterial community covering 40 phyla, with ~1400 different taxa (Godoy-Vitorino *et al.*, 2010). In this species, Bacteroidetes are dominant in the crop whilst a higher proportion of Protobacteria and Firmicutes can be found in the caecum (Godoy-Vitorino *et al.*, 2010, 2012). These differences in bacterial diversity may be more strongly correlated with diet items and not with feeding guild, as the hoatzin predominantly eat young leaves which are high in plant secondary metabolites and their foregut may be used to detoxify these compounds (Dearing, Foley & McLean, 2005). Small variations in a specialized diet as a result of environmental change could have a high impact within the gut. Thus, it could be predicted that dietary specialists consuming novel items may benefit from coprophagy to seed their gut microbiota with microbes that are adaptive for these new diets. Whilst the research is lacking in birds, faecal transplant/inoculation in clinical patients has been shown to alter the gut microbiota and allow for dietary expansion (Blyton *et al.*, 2019) and has also influenced foraging behaviour and diet selection in mice (Trevelline & Kohl, 2022). Collectively, these findings suggest that coprophagy is likely to facilitate diet shifts, even for dietary specialists.

Assessing the role of coprophagy in facilitating diet switching, particularly in dietary specialist species, would aid in developing a mechanistic understanding of the potential for birds to adapt to novel diets which are increasingly common in the Anthropocene, and the risks this may entail. For instance, red knot (*Calidris canutus canutus*) offspring are becoming progressively smaller and shorter billed as a result of summers with early snowmelt, with these smaller individuals unable to consume highly nutritious bivalve prey and instead having to consume more seagrass rhizomes (van Gils, *et al.*, 2016). Currently, shorter-billed individuals have reduced survival rates because they cannot gain the nutrients they need from their new diet (van Gils *et al.*, 2016). Experimental studies in species that have undergone such massive

diet shifts could yield critical insights into the nutritional, microbial, and synergistic benefits of auto-, allo- or hetero-specific coprophagy, as well as potential risks in terms of exposure to novel pathogens (Fig. 4).

## (2) Seasonal variation

Species that show flexibility in foraging behaviour and diet are known as generalists and may be comparatively responsive and adaptive to environmental change (Morelli *et al.*, 2021). The microbiomes of generalists can be anticipated to be highly dynamic, particularly if feeding at different trophic levels at different times, as has been demonstrated for thick-billed murres (*Uria lomvia*) (Elliott, Gaston & Crump, 2010; Góngora *et al.*, 2021). The microbiomes of generalist species are likely to be most dynamic at times of opportunistic foraging or seasonal diet shifts and may involve transient bacterial strains (Waite *et al.*, 2012; Michel *et al.*, 2018). For example, vampire finches (*Geospiza septentrionalis*) supplement their diet with blood during the dry season and their gut microbiota show an associated shift towards Fusobacteria, Tenericutes, and Deferribacterota, taxa which are typically attributed to carnivores and assist with blood digestion (Michel *et al.*, 2018). Seasonal changes in gut microbiota have also been recorded for capercaillie (*Tetrao urogallus*), an omnivorous species that subsists on pine needles during winter when regular food sources are unavailable (Wienemann *et al.*, 2011).

Coprophagy may assist birds to adapt to seasonally variable food sources and could be particularly relevant when switching to diets with difficult-to-digest components whereby particular bacteria and enzymes may assist (Amato *et al.*, 2015). Although there are no studies to date on birds, evidence from mammals suggests this is an area in need of investigation. For instance, in primates, the practice of coprophagy varies seasonally, in line with the seasonal availability of hard-to-digest food items (Krief, Jamart & Hladik, 2004; Sakamaki, 2009; Masi & Breuer, 2018) and/or times of food scarcity (Wall, 1983; Vogrin, 1997; Krief *et al.*, 2004; Shimada, 2012; Masi & Breuer, 2018). Seasonal shifts in foraging behaviour involving coprophagy have been documented in birds, albeit in relation to changes in energy requirements rather than changes in the digestibility of available resources (Fig. 2). For instance, during the breeding season, giant petrels undertake extended incubation bouts necessitating periods of fasting of up to 15 days. At the end of their incubation bout, each parent starts their foraging trip by consuming seal faeces at haul-out sites (Corá, Finger & Kruger, 2020). This behaviour is thought to assist the birds, who are in a fasted state, to refuel quickly from an easily accessible and energetically rich food source before they undertake extended foraging trips across the Southern Ocean in search of more valuable prey (Casaux, Baroni & Carlini, 1997; Corá *et al.*, 2020). However, it is also plausible that fasting may eliminate microbiota essential to digestion from the gut, as has been shown in other species (Dewar *et al.*, 2014; Zarrinpar *et al.*, 2014; Lee *et al.*, 2019c), and that

fasting giant petrels may be engaging in coprophagy to re-inoculate their microbiota for a digestive state. Microbial re-seeding after fasting due to incubation has been surmised to occur in other species. During incubation and early chick rearing, adults of several species, including dunlocks (Lamb *et al.*, 2017), spotted towhees (*Pipilo maculatus*) (McKay *et al.*, 2009) and giant babax (*Babax waddelli*) (Gao *et al.*, 2020) (Fig. 2), have been observed consuming nestling faecal sacs. This behaviour is suggested to be a means of not only retaining nutrients (Lamb *et al.*, 2017) and microbes (Gao *et al.*, 2020) but also keeping the nest hygienic (Azcarate-García *et al.*, 2019), and removing cues for predators (Burrows, 2018). However, in the case of giant babax, nestling faecal sacs were found to have a high abundance of Firmicutes – a keystone taxon in the gut of many bird and mammalian species (Waite & Taylor, 2014; Grond *et al.*, 2018). Coprophagic behaviour has therefore been suggested as a means by which parents could easily obtain these bacterial taxa (Gao *et al.*, 2020). Indeed, the reduced feeding rate in parents and the increased physiological demands of raising young could both impact the gut microbiome, limiting some bacterial species, although further experimental studies are required to demonstrate this.

Coprophagy may also play a key role in the switch between fasting and fuelling metabolic states in long-distance migratory birds. For instance, shorebirds in an active migratory state have been found to have a gut microbiota that is similar across species yet distinct from the microbiota of those same species in the non-migratory phase of the annual cycle (Risely *et al.*, 2018). Similarly, the gut microbiota of ruddy turnstones (*Arenaria interpres*) from the North Atlantic flyway has been shown to undergo dramatic changes in taxonomic composition and function, particularly in polyunsaturated fatty acid biosynthesis, over the course of refuelling during migratory stopover (Grond, Louyakis & Hird, 2023). How these migrants, arriving in a fasted state, can shift the composition of their microbiome so rapidly is not known, however direct sourcing of microbes from their foraging environment is unlikely (Risely *et al.*, 2017). Recent observations in ruddy turnstones during stopover, albeit on the Central Asian flyway, have indicated that these birds consumed human faeces recently deposited on the beach, suggesting coprophagy may play a role in refuelling dynamics (Kasambe & Kasambe, 2020). Currently, our understanding of the underlying imperative for these behaviours, and the degree to which auto-, allo- and heterospecific coprophagy supplements metabolic, nutritional, and microbial needs following fasting remains speculative. Detailed investigations to tease apart the potential benefits of coprophagy in the context of different life stages, with varying resource demands and resource availability, are sorely needed (Fig. 4).

Profound changes in gut microbiome composition have also been observed over the course of the moult period (Dewar *et al.*, 2014; Lee *et al.*, 2019c), including changes in alpha diversity in some species, and reductions in Firmicutes (Lee *et al.*, 2019c), Proteobacteria and Bacteroidetes (Dewar *et al.*, 2014) and increases in Fusobacteria

(Dewar *et al.*, 2014) in others. However, microbial dynamics during moult in free-living birds have, to date, only been reported from penguin species (family Spheniscidae), who have an intense moult during which they are confined to land for weeks and therefore abstain from eating (Lee *et al.*, 2019c). Similarly, studies in poultry have been confounded with fasting, as moult has been experimentally induced through an extended period of food removal (Han *et al.*, 2019). As a result, moult represents a critical, yet poorly studied, phase for the gut microbiota of birds. Although moult is characterized by the replacement of plumage, the energetic and nutritional costs incurred during this period vastly exceed the calorific and nutritional content of the feathers themselves (Murphy, 1996; Hoyer & Buttemer, 2011), instead reflecting a period of systemic physiological rejuvenation (Murphy & Taruscio, 1995; Buttemer, Addison & Klasing, 2020). In birds, adults typically lose the ability to reconfigure the immune system and proceed to a state of immunosenescence (Janeway *et al.*, 2004). Although the adaptive immune response is, by definition, adapting to novel pathogen's throughout an animal's life, preferential use of immunological memory stemming from a previous infection to a subsequent, slightly different, version of that pathogen hampers the immune system by preventing it from mounting potentially more effective responses during subsequent infections (Focosi *et al.*, 2021). In birds, however, profound changes in immune function have been reported in adults during the moult period, including enlargements of key organs like the thymus (Brake, Morgan & Thaxton, 1981) and spleen (Silverin *et al.*, 1999), increased abundance of basophils and monocytes (Nava, Veiga & Puerta, 2001; Buehler *et al.*, 2008) and immunoglobulins (Pap *et al.*, 2010), and suppressed inflammatory responses (Alodan & Mashaly, 1999; Martin, 2005; Buehler *et al.*, 2008; Moreno-Rueda, 2010). Collectively, these findings indicate that peak moult is associated with decreased innate immune responses, paired with increased cell-mediated (T-cell) and antibody-mediated (B-cell) acquired immunity, long-lived macrophages and antigen-presenting cells important for initiating acquired immune responses (Alodan & Mashaly, 1999; Buehler *et al.*, 2008). Historically, these shifts in immune strategy have been viewed as systemic adaptations to reduce the risk of innate immune responses competing with the increased energetic and nutritional demands of feather production (Buehler *et al.*, 2008; Martin, Weil & Nelson, 2008). Yet, moult-related shifts in immune function have also been observed in near-featherless birds, such that these adjustments are indicative of a recalibration of entire immune repertoires and recognition systems, with adults during peak moult being immunologically comparable to a newly hatched chick (A. DeRogatis & K. Klasing, unpublished data) and potentially capable of undoing their 'original antigenic sin' (Focosi *et al.*, 2021). Given the tight association between gut microbiota and immune repertoires and recognition systems (Broom & Kogut, 2018), moult may be a critical period for re-configuring avian microbiomes. Although there are currently no data on temporal changes in use of coprophagy in



wild birds, poultry are known to increase coprophagy during moult. It is therefore plausible that coprophagy may interact with moult-associated recalibration of the immune system. Studies assessing the degree and type of coprophagy birds undertake before, during and after moult, both in captivity and in the wild, are needed to assess the plausibility of this process. Ideally, these studies would be paired with dynamic quantification of immune function and coincident microbiotas to understand the potential for coprophagy to shape immune function and microbiota–immune interactions.

### (3) Opportunistic coprophagy

Birds are also known to engage in coprophagy opportunistically, in line with local weather conditions rather than predictable seasonal cycles. For instance, Eurasian coots (*Fulica atra*) common moorhen (*Gallinula chloropus*), tufted ducks (*Aythya fuligula*), and mallard (*Anas platyrhynchos*) were observed eating black-headed gull (*Larus ridibundus*) faeces from boulders and ice (Wall, 1983; Boot, 1987). Ducks (*Anas platyrhynchos*, *A. crecca*, *A. formosa*) were also observed consuming whooper swan (*Cygnus cygnus*) faeces under similar conditions (Shimada, 2012). In both cases, coprophagy was considered an opportunistic adaptation to the bird's regular food source being inaccessible due to ice covering the lakes where they feed (Wall, 1983; Boot, 1987; Shimada, 2012) (Fig. 2). This behaviour is often considered indicative of resource limitation (Wall, 1983; Boot, 1987; Krief *et al.*, 2004; Shimada, 2012; Masi & Breuer, 2018), however coprophagy has been seen in dusky moorhens (*Gallinula tenebrosa*) at times of high resource availability (Starks & Peter, 1991). Importantly, the nutritional, energetic and microbial consequences of opportunistic coprophagy, particularly the consumption of faeces from other species, has yet to be examined (Fig. 2).

## IV. POTENTIAL RISKS ASSOCIATED WITH COPROPHAGY

Although coprophagy has extensive potential to improve host health through access to nutrients and beneficial microbiota, there are several potential risks posed by this foraging behaviour (Fig. 3). These include potential ingestion of pathogens or antibiotic-resistant microbes, and exposure to compounds that might affect the microbiome (e.g. antimicrobials). The avian gastrointestinal tract is host to an array of bacterial species, most of which are beneficial and commensal (Benskin *et al.*, 2009; Furst *et al.*, 2018). However, several opportunistic gastrointestinal pathogens that can cause severe disease in birds are transmitted *via* the faecal–oral route, including bacteria belonging to the genera *Enterococcus*, *Salmonella*, *Clostridium*, *Escherichia*, *Campylobacter* and *Staphylococcus* (Benskin *et al.*, 2009; Furst *et al.*, 2018). These potentially pathogenic taxa could be transmitted through coprophagy, which has been extensively speculated in domestic poultry (Montrose, Shane & Harrington, 1985;

Folz *et al.*, 1986; Line, 2006; Line *et al.*, 2008; Pan & Yu, 2014; Alpigliani *et al.*, 2017; Craft *et al.*, 2022). However, the role of coprophagy in the transmission of opportunistic pathogens has rarely been studied (von Waldburg-Zeil, van Staaveren & Harlander-Matauschek, 2019). To date, the only studies in birds have been in domestic species of poultry, particularly in mass-production environments (Hörnigke & Björnag, 1980). Moreover, the effects of coprophagy have been inferred from increased incidence of infection after feed withdrawal (Byrd *et al.*, 1998; Corrier *et al.*, 1999), rather than through direct assessment of the effect of coprophagy. These studies have also been conducted on birds living at high stocking density with direct contact, where they might ingest contaminated feed and water (Shanker, Lee & Sorrell, 1990; Line *et al.*, 2008).

In wild birds, the degree to which a species aggregates, particularly in mixed-species assemblages, may be particularly important for unintentional coprophagy (Kohl, 2012), and hence intra- and inter-species pathogen transmission (Kohl, 2012). Indeed, studies using animal social networks have shown similarities in gut microbiota between individuals of the same species groups (Downing, Griffin & Cornwallis, 2020) and mixed-species aggregations (Grond *et al.*, 2018). To investigate the risk of pathogen transmission presented by coprophagy, experimental studies altering ability to engage in allo- and heterospecific-coprophagy and using whole-genome sequencing of pathogenic bacterial strains to give insight into the phylogenetic relationships among strains and accessory genes, including resistance and virulence genes (Ingle, Howden & Duchene, 2021; Djordjevic *et al.*, 2023), are needed.

In addition to exposing birds to a wider range of pathogens, coprophagy could represent a mechanism by which these infections can be treated. Although some ingested bacterial strains are only transient and not retained in the gut, many are retained and can affect the resident bacterial community, both directly and indirectly (Derrien & van Hylckama Vlieg, 2015). In addition to becoming a member of the microbiome, ingested bacteria can stimulate the growth of resident bacteria (Derrien & van Hylckama Vlieg, 2015) or have a negative impact on them through competitive exclusion (Derrien & van Hylckama Vlieg, 2015). Recently, faecal transplants have been used to treat infections and metabolic disease and to re-establish a healthy microbiome after medical treatment of clinical patients (West *et al.*, 2019). Whilst there have been limited studies in birds, there is evidence to suggest that faecal transplant may improve gut microbiomes and could be particularly beneficial for (re)introduction of animals into the wild after periods in captivity and/or following medical treatment (Eason & Moorhouse, 2006; West *et al.*, 2019; Li *et al.*, 2022). For example, faecal transplant has been successfully used in critically endangered kakapo to establish normal gastrointestinal microbiota (Eason & Moorhouse, 2006). Investigation into self-medication through coprophagy is a promising line for future research, particularly in terms of the conservation of threatened species and management of synanthropic

species (Eason & Moorhouse, 2006; Waite, Deines & Taylor, 2013; Guo *et al.*, 2020).

### (1) Anthropogenic influences

Many generalist avian species are capable of exploiting human-dominated habitats, such as areas rich in refuse or agricultural remains (Smith & Carlile, 1993; Mennechez & Clergeau, 2006; Dolejska *et al.*, 2015; Thabethe & Downs, 2018), and some of these species are also intentionally fed (Feng & Liang, 2020). Association with humans has been linked to lower diversity gut microbiota in some species (Knutie, Chaves & Gotanda, 2019), and could be a result of birds feeding on refuse or being provisioned and becoming specialized on a very narrow range of food items such as bread (Murray *et al.*, 2018; Thabethe & Downs, 2018). Species such as gulls (family Laridae) and ibis (family Threskiornithidae) foraging at a variety of natural sites have greater microbial diversity compared to those foraging at sites of significant human impact (Merkeviciene *et al.*, 2017; Furst *et al.*, 2018; Murray *et al.*, 2020). Long-term shifts towards increased synanthropic foraging behaviours are therefore expected to have profound consequences for wildlife microbiome composition and function (Fig. 4).

Synanthropic birds, through their use of waste depots, sewage treatment plants, and human refuse, are exposed to chemicals and heavy metals that can profoundly alter their microbiota (Poole, 2017). Although some antimicrobial compounds occur naturally in the environment, the increased use of anthropogenically produced analogues in agriculture, veterinary medicine and human medicine combined with sub-optimal waste disposal and treatment has resulted in active antimicrobial compounds inadvertently being released into some environments through contaminated landfill leachate, wastewater, and effluents (Christou *et al.*, 2017). Many of these antimicrobials also persist in the environment in active forms, resulting in an increased number and diversity of these compounds in the environment, particularly in areas dominated by anthropogenic activities (Arnold, Williams & Bennett, 2016). Exposure to antimicrobial compounds can eliminate a considerable proportion of the microbiota, opening ecological niches within the gut for bacteria that carry antimicrobial resistance genes to survive the effects of antimicrobial compounds and confer the ability to invade and/or proliferate (Munita & Arias, 2016). Experimental administration of antibiotics in birds has been shown to alter their gut microbiota, impacting digestion, metabolic and immune functions (Kohl *et al.*, 2018; Zhou *et al.*, 2020b; Li *et al.*, 2022). Such profound changes in microbiota, together with reductions in host immune function by bacteria carrying antibiotic resistance genes (Jiang *et al.*, 2019), can lead to a state of dysbiosis (Schj rting & Krogfelt, 2011). As demonstrated in mammals, coprophagy may be a method for birds to overcome antimicrobial-induced dysbiosis (Soave & Brand, 1991). However, coprophagy may also increase exposure to antimicrobials, particularly those that have high

environmental persistence and/or bioaccumulate, including heavy metals (Fig. 3).

### (2) Antimicrobial resistance emergence and spread

Increased use of antimicrobial compounds has also altered the selective pressure on microbial populations (Martinez, 2009; Djordjevic, Stokes & Chowdhury, 2013; Smalla *et al.*, 2018; Ben *et al.*, 2019; Oniciuc *et al.*, 2019), increasing the prevalence of organisms resistant to antimicrobial compounds in the environment (Borges *et al.*, 2017). Synanthropic birds are increasingly found to have been exposed to microbial communities rich in antibiotic resistance genes (Borges *et al.*, 2017; Poole, 2017; Marcelino *et al.*, 2019; Wang *et al.*, 2019; Murray *et al.*, 2020; Wyrsh *et al.*, 2022). Coprophagy may further enhance the transmission of antibiotic resistance genes from humans to wildlife (through foraging on human faeces; Kasambe & Kasambe, 2020), and between wildlife, through several pathways. Firstly, the faeces from humans or animals (either domestic or wild after being treated in captivity) that have recently been treated with antimicrobials are expected to contain antimicrobials, which will directly select for resistant microbes in the gut of a bird engaging in coprophagy. Secondly, these faeces will also contain bacteria enriched in antimicrobial resistance genes (Baros Jorquera *et al.*, 2021). Birds engaging in heterospecific coprophagy, consuming faeces from medicated populations, may therefore be at greater risk of direct inoculation with bacterial strains carrying resistance genes to clinically important antimicrobials. Subsequent coprophagy between wild birds (either allo- or heterospecific) may then lead to widespread transmission through a population that would not otherwise occur in birds not utilizing this behaviour. Finally, resistance genes can be transmitted from bacteria ingested from food to gastrointestinal microbiota *via* horizontal gene transfer (Lester *et al.*, 2006; Feld *et al.*, 2008; Pinto *et al.*, 2015). High numbers of resistant strains in the gut, as may be the case when a bird consumes large quantities of faecal material from a bird carrying resistant bacteria, increases cell-to-cell contact and therefore further increases the opportunity of resistance gene transfer from ingested bacteria to bacteria in a bird's microbiota (Schj rting & Krogfelt, 2011).

In wild birds, whole-genome and metagenomic sequencing has demonstrated that antibiotic resistance genes are predominantly associated with phyla Bacteroidetes, Firmicutes and Proteobacteria (Wang *et al.*, 2019; Cao *et al.*, 2020; Feng *et al.*, 2021). Whilst many bacteria belonging to such phyla are harmless, some can colonize and become pathogenic, causing intestinal or extraintestinal disease, and may also be zoonotic (Woolhouse, Haydon & Antia, 2005; Santos *et al.*, 2020; Wyrsh *et al.*, 2022). Horizontal gene transfer may result in these bacteria acquiring and spreading antimicrobial resistance genes along with virulence genes, which would make infection exceedingly difficult to treat. Although there is evidence that antibiotic resistance genes are found in excreta, particularly in birds with synanthropic

associations (Silva *et al.*, 2009; Hernandez *et al.*, 2013; Mukerji, *et al.*, 2019; Wyrsh *et al.*, 2022), to date there have been no studies on the transmission of antibiotic-resistant bacteria or onward transmission of antibiotic resistance genes through coprophagy. Studies quantifying the connection between diet, coprophagy and resistance gene burden and transmission in different land-use contexts would shed valuable light on these risks. Whether there are traits that give some species a propensity for higher resistance-gene carriage should also be explored.

## V. FUTURE PERSPECTIVES

The ongoing development of next-generation sequencing has greatly accelerated the number of studies characterizing the avian microbiome (Waite & Taylor, 2014; Cao *et al.*, 2020; Aruwa *et al.*, 2021). Yet, the intrinsic and extrinsic factors driving dynamics in these microbial communities have yet to be explored in detail. In particular, the impact of the use of coprophagy on these dynamics, both in terms of benefits and risks to host health and nutrition warrants targeted investigation across a range of species and environmental contexts (Fig. 4). Given the fundamental role of gut microbiota for the maintenance of organismal health and performance, and the demonstrated potential for auto-, allo- and heterospecific coprophagy to impact gut microbiota, there is a pressing need to understand better when, where and why birds engage in coprophagy. In parallel, we need to understand the mechanistic impact of coprophagy on host health and performance, in order to understand the degree to which this foraging behaviour can assist wild birds in adapting to predictable and unpredictable change processes as well as the risks it might pose to host health and pathogen transmission. In this review, we have outlined several key life stages where there is considerable potential for coprophagy to modulate gut microbiota and have a profound influence on host health and fitness. Greater use of, and benefit from, coprophagy may be expected during ontogeny, moult, long-distance migration, and extreme weather events (Fig. 4). Coprophagy may also assist animals in adapting to longer-term changes, including adapting to novel environments as a result of anthropogenic land-use change. However, anthropogenic environments are predicted also to pose the highest risks as a result of coprophagy, particularly in terms of exposure to microbiota-altering antimicrobials as well as pathogenic and antimicrobial-resistant microbes.

Using coprophagy-prevention experiments and germ-free models to compare microbiota structure and dynamics during each of these periods, and assessing how this relates to physiology and health, would be highly beneficial. Coprophagy could be an underappreciated mechanism for obtaining limited or high-demand resources, and for augmenting a bird's gut microbiota to adapt to changing environmental conditions. In some species, for example ruddy turnstone

(Kasambe & Kasambe, 2020) and Australasian darter (*Anhinga novaehollandiae*) (Yong, 2018) coprophagy has only recently been documented and could therefore represent a novel adaptive behaviour. Whether coprophagy in birds is predominantly a mechanism for supplementation of a metabolic or microbial need could be assessed using metagenomics to characterize the gut microbial community, potential microbial target species or strains, and insights into microbial function (e.g. Grond *et al.*, 2023), from energy gains to pathogen exclusion and immune programming. Whole-genome sequencing approaches would provide complementary insights into the role of coprophagy in the transmission of pathogens and antimicrobial resistance genes (Ingle *et al.*, 2021). Finally, it is unknown if coprophagic behaviour is a learned behaviour, or a heritable trait that has evolved ancestrally, or convergently. As more studies on coprophagy in wild birds become available, meta-analysis could provide additional insights into the evolutionary origins of this behaviour.

## VI. CONCLUSIONS

- (1) The avian gut microbiome regulates a broad range of biological functions yet is dynamic across a range of time-scales. The gut microbiota may be fundamental in an individual's ability to adapt to new environments, due to its bacterial composition being dynamic both during development and after maturity.
- (2) Understanding the drivers of avian gut microbiota dynamics is critically important to determining the capacity of avian hosts to adapt to new and changing environments but has received little attention to date.
- (3) Although coprophagy in birds has been assumed to confer nutritional and energetic benefits, this foraging behaviour may present a unique and powerful mechanism for rapid seeding and augmenting the gut microbiota throughout a bird's life.
- (4) Conversely, this behaviour has the potential to expose birds to antimicrobial compounds and pathogenic microbes and may contribute to the emergence and spread of antimicrobial resistance in wildlife and the environments they inhabit.
- (5) Based on mechanistic predictions developed through this review, there is a pressing need for detailed investigation into the influence of auto-, allo-, and heterospecific coprophagy on avian gut microbiomes and their impact on host health and performance across several life stages and environmental contexts.

## VII. ACKNOWLEDGEMENTS

The authors declare that they have no competing interests. A. D. was supported by the University of South Australia's

Science, Technology, Engineering, and Mathematics (STEM) RTP scholarship, and B. J. H. was supported by a DECRA Fellowship from the Australian Research Council (DE200100884). The authors confirm that the funding bodies had no direct influence on the review design, data collection, analysis/interpretation, or writing. We express our gratitude to all individuals who assisted in facilitating this review, as well as the Editorial Office and reviewers for their valuable and constructive feedback. In memoriam of Judith Dawson 07/12/1956 to 25/10/2022.

## VIII. AUTHOR CONTRIBUTIONS

A. D.: conceptualization, data curation, writing of original draft, review & editing; B. D.: supervision, funding, conceptualization, data curation, writing of original draft, review & editing; S. P. D.: supervision, review & editing; E. D.: supervision, funding, conceptualization, review & editing; B. J. H.: supervision, conceptualization, data curation, writing of original draft, review & editing.

## IX. REFERENCES

- ALBERDI, A., AIZPURUA, O., BOHMANN, K., ZEPEDA-MENDOZA, M. L. & GILBERT, M. T. P. (2016). Do vertebrate gut metagenomes confer rapid ecological adaptation? *Trends in Ecology and Evolution* **31**(9), 689–699.
- ALODAN, M. A. & MASHALY, M. M. (1999). Effect of induced molting in laying hens on production and immune parameters. *Poultry Science* **78**(2), 171–177.
- ALPIGIANI, I., ABRAHANTES, J. C., MICHEL, V., HUNEAU-SALAÜN, A., CHEMALY, M., KEELING, L. J., GERVELMEYER, A., BACCI, C., BRINDANI, F., BONARDI, S. & BERTHE, F. (2017). Associations between animal welfare indicators and *Campylobacter* spp. in broiler chickens under commercial settings: a case study. *Preventive Veterinary Medicine* **147**, 186–193.
- AMATO, K. R., LEIGH, S. R., KENT, A., MACKIE, R. I., YEOMAN, C. J., STUMPF, R. M., WILSON, B. A., NELSON, K. E., WHITE, B. A. & GARBER, P. A. (2015). The gut microbiota appears to compensate for seasonal diet variation in the wild black howler monkey (*Alouatta pigra*). *Microbial Ecology* **69**(2), 434–443.
- ARNOLD, K., WILLIAMS, N. & BENNETT, M. (2016). Disperse abroad in the land: the role of wildlife in the dissemination of antimicrobial resistance. *Biology Letters* **12**(137), 20160137. <https://doi.org/10.1098/rsbl.2016.0137>.
- ARUWA, C. E., PILLAY, C., NYAGA, M. M. & SABIU, S. (2021). Poultry gut health – microbiome functions, environmental impacts, microbiome engineering and advancements in characterization technologies. *Journal of Animal Science and Biotechnology* **12**(1), 119. <https://doi.org/10.1186/s40104-021-00640-9>.
- AZCÁRATE-GARCÍA, M., RUIZ-RODRÍGUEZ, M., DÍAZ-LORA, S., RUIZ-CASTELLANO, C. & SOLER, J. J. (2019). Experimentally broken faecal sacs affect nest bacterial environment, development and survival of spotless starling nestlings. *Journal of Avian Biology* **50**(3), 1–10. <https://doi.org/10.7717/peerj.2837>.
- BALLOU, A. L., ALI, R. A., MENDOZA, M. A., ELLIS, J. C., HASSAN, H. M., CROOM, W. J. & KOCI, M. D. (2016). Development of the chick microbiome: how early exposure influences future microbial diversity. *Frontiers in Veterinary Science* **3**, Article 2, 1–12. <https://doi.org/10.3389/fvets.2016.00002>.
- BAROS JORQUERA, C., MORENO-SWITT, A. I., SALLABERRY-PINCHEIRA, N., MUNTA, J. M., FLORES NAVARRO, C., TARDONE, T., GONZÁLEZ-ROCHA, G., SINGER, R. S. & BUENO, I. (2021). Antimicrobial resistance in wildlife and in the built environment in a wildlife rehabilitation center. *One Health* **13**, 100298. <https://doi.org/10.1016/j.onehlt.2021.100298>.
- BEN, Y., FU, C., HU, M., LIU, L., WONG, M. H. & ZHENG, C. (2019). Human health risk assessment of antibiotic resistance associated with antibiotic residues in the environment: a review. *Environmental Research* **169**, 483–493.
- BENSKIN, C. M. H., WILSON, K., JONES, K. & HARTLEY, I. R. (2009). Bacterial pathogens in wild birds: a review of the frequency and effects of infection. *Biological Reviews* **84**(3), 349–373.
- BERLOW, M., PHILLIPS, J. N. & DERRYBERRY, E. P. (2021). Effects of urbanization and landscape on gut microbiomes in white-crowned sparrows. *Microbial Ecology* **81**(1), 253–266.
- BLYTON, M. D. J., SOO, R. M., WHISSON, D., MARSH, K. J., PASCOE, J., LE PLA, M., FOLEY, W., HUGENHOLTZ, P. & MOORE, B. D. (2019). Faecal inoculations alter the gastrointestinal microbiome and allow dietary expansion in a wild specialist herbivore, the koala. *Animal Microbiome* **1**(1), 6–24.
- BODAWATTA, K. H., FREIBERGA, I., PUZEJOVA, K., SAM, K., POULSEN, M. & JØNSSON, K. A. (2021a). Flexibility and resilience of great tit (*Parus major*) gut microbiomes to changing diets. *Animal Microbiome* **3**(1), 20–34.
- BODAWATTA, K. H., HIRD, S. M., GROND, K., POULSEN, M. & JØNSSON, K. A. (2021b). Avian gut microbiomes taking flight. *Trends in Microbiology* **30**(3), 268–280.
- BODAWATTA, K. H., KOANE, B., MAIAH, G., SAM, K., POULSEN, M. & JØNSSON, K. A. (2021c). Species-specific but not phyllosymbiotic gut microbiomes of New Guinean passerine birds are shaped by diet and flight-associated gut modifications. *Proceedings of the Royal Society B: Biological Sciences* **288**(1949), 20210446. <https://doi.org/10.1098/rspb.2021.0446>.
- BOOT, A. (1987). Coot feeding on black-headed gull droppings. *British Birds* **80**(11), 573.
- BORGES, C. A., BERALDO, L. G., MALUTA, R. P., CARDOZO, M. V., BARBOZA, K. B., GUASTALLI, E. A. L., KARIYAWASAM, S., DEBROY, C. & ÁVILA, F. A. (2017). Multidrug-resistant pathogenic *Escherichia coli* isolated from wild birds in a veterinary hospital. *Avian Pathology* **46**(1), 76–83.
- BOSCO, N. & NOTI, M. (2021). The aging gut microbiome and its impact on host immunity. *Genes & Immunity* **22**(5), 289–303.
- BRAKE, J., MORGAN, G. W. & THAXTON, P. (1981). Recrudescence of the thymus and repopulation of lymphocytes during an artificially induced molt in the domestic chicken: proposed model system. *Developmental and Comparative Immunology* **5**(1), 105–112.
- BROOM, L. J. & KOGUT, M. H. (2018). The role of the gut microbiome in shaping the immune system of chickens. *Veterinary Immunology and Immunopathology* **204**, 44–51.
- BUCHSBAUM, R., WILSON, J. & VALIELA, I. (1986). Digestibility of plant constituents by Canada geese and Atlantic Brant. *Ecology* **67**(2), 386–393.
- BUEHLER, D. M., PIERSMA, T., MATSON, K. & TIELEMAN, B. I. (2008). Seasonal redistribution of immune function in a migrant shorebird: annual-cycle effects override adjustments to thermal regime. *The American Naturalist* **172**(6), 783–796.
- BURROWS, A. M. (2018). *Faecal sac removal and parental coordination in relation to parental predation risk in the blue tit (Cyanistes caeruleus)*. PhD Thesis: Lancaster University (UK).
- BUTTEMER, W. A., ADDISON, B. A. & KLASING, K. C. (2020). The energy cost of feather replacement is not intrinsically inefficient. *Canadian Journal of Zoology* **98**(2), 142–148.
- BYRD, J. A., CORRIER, D. E., HUME, M. E., BAILEY, R. H., STANKER, L. H. & HARGIS, B. M. (1998). Effect of feed withdrawal on *Campylobacter* in the crops of market-age broiler chickens. *Avian Diseases* **42**(4), 802–806.
- CAO, J., HU, Y., LIU, F., WANG, Y., BI, Y., LV, N., LI, J., ZHU, B. & GAO, F. G. (2020). Metagenomic analysis reveals the microbiome and resistome in migratory birds. *Microbiome* **8**(1), 26–44.
- CAPUNITAN, D. C., JOHNSON, O., TERRILL, R. S. & HIRD, S. M. (2020). Evolutionary signal in the gut microbiomes of 74 bird species from Equatorial Guinea. *Molecular Ecology* **29**(4), 829–847.
- CASAU, R., BARONI, A. & CARLINI, A. (1997). The diet of the Weddell seal *Leptonychotes weddelli* at Harmony Point, South Shetland Islands. *Polar Biology* **18**(6), 371–375.
- CAVIEDES-VIDAL, E., MCWHORTER, T. J., LAVIN, S. R., CHEDIACK, J. G., TRACY, C. R. & KARASOV, W. H. (2007). The digestive adaptation of flying vertebrates: high intestinal paracellular absorption compensates for smaller guts. *Proceedings of the National Academy of Sciences* **104**(48), 19132–19137.
- CHEN, C. Y., CHEN, C. K., CHEN, Y. Y., FANG, A., SHAW, G. T. W., HUNG, C. M. & WANG, D. (2020). Maternal gut microbes shape the early-life assembly of gut microbiota in passerine chicks via nests. *Microbiome* **8**(1), 129–142.
- CHRISTOU, A., AGÜERA, A., BAYONA, J. M., CYTRYN, E., FOTOPoulos, V., LAMBROPOULOU, D., MANAIA, C. M., MICHAEL, M., REVITT, M., SCHRÖDER, P. & FATTA-KASSINOS, D. (2017). The potential implications of reclaimed wastewater reuse for irrigation on the agricultural environment: the knowns and unknowns of the fate of antibiotics and antibiotic resistant bacteria and resistance genes – a review. *Water Research* **123**, 448–467.
- COOGAN, S. C., MACHOVSKY-CAPUSKA, G. E., SENIOR, A. M., MARTIN, J. M., MAJOR, R. E. & RAUBENHEIMER, D. (2017). Macronutrient selection of free-ranging urban Australian white ibis (*Threskiornis moluccus*). *Behavioral Ecology* **28**(4), 1021–1029.
- COONEY, C., SEDDON, N. & TOBIAS, J. (2016). Widespread correlations between climatic niche evolution and species diversification in birds. *The Journal of Animal Ecology* **85**, 869–878.
- CORÁ, D. H., FINGER, J. V. G. & KRÜGER, L. (2020). Coprophagic behaviour of southern giant petrels (*Macronectes giganteus*) during breeding period. *Polar Biology* **43**(12), 2111–2116.

- CORRIER, D. E., BYRD, J. A., HARGIS, B. M., HUME, M. E., BAILEY, R. H. & STANKER, L. H. (1999). Presence of salmonella in the crop and ceca of broiler chickens before and after pre-slaughter feed withdrawal. *Poultry Science* **78**(1), 45–49.
- CRAFT, J., EDDINGTON, H., CHRISTMAN, N. D., PRYOR, W., CHASTON, J. M., ERICKSON, D. L. & WILSON, E. (2022). Increased microbial diversity and decreased prevalence of common pathogens in the gut microbiomes of wild turkeys compared to domestic turkeys. *Applied and Environmental Microbiology* **88**(5), e01423-21.
- DAVIDSON, G. L., RAULO, A. & KNOWLES, S. C. L. (2020a). Identifying microbiome-mediated behaviour in wild vertebrates. *Trends in Ecology & Evolution* **35**(11), 972–980.
- DAVIDSON, G. L., WILEY, N., COOKE, A. C., JOHNSON, C. N., FOUHY, F., REICHERT, M. S., DE LA HERA, I., CRANE, J. M. S., KULAHCI, I. G., ROSS, R. P., STANTON, C. & QUINN, J. L. (2020b). Diet induces parallel changes to the gut microbiota and problem solving performance in a wild bird. *Scientific Reports* **10**(1), 20783. <https://doi.org/10.1016/j.trec.2020.06.014>.
- DE GOFFAU, M. C., LAGER, S., SOVIO, U., GACCIOLI, F., COOK, E., PEACOCK, S. J., PARKHILL, J., CHARNOCK-JONES, D. S. & SMITH, G. C. S. (2019). Human placenta has no microbiome but can contain potential pathogens. *Nature* **572**(7769), 329–334.
- DEARING, M. D., FOLEY, W. & MCLEAN, S. (2005). The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annual Review of Ecology, Evolution, and Systematics* **36**(1), 169–189.
- DEBRIEN, M. & VAN HYLCKAMA VLEG, J. E. T. (2015). Fate, activity, and impact of ingested bacteria within the human gut microbiota. *Trends in Microbiology* **23**(6), 354–366.
- DEWAR, M. L., ARNOULD, J. P., KRAUSE, L., TRATHAN, P., DANN, P. & SMITH, S. C. (2014). Influence of fasting during moult on the faecal microbiota of penguins. *PLoS One* **9**(6), e99996. <https://doi.org/10.1371/journal.pone.0099996>.
- DIÁZ, J. & REESE, A. T. (2021). Possibilities and limits for using the gut microbiome to improve captive animal health. *Animal Microbiome* **3**(1), 89–103.
- DIETZ, M. W., SALLES, J. F., HSU, B. Y., DIJKSTRA, C., GROOTHUIS, T. G. G., VAN DER VELDE, M., VERKUIL, Y. I. & TIELEMAN, B. I. (2019). Prenatal transfer of gut bacteria in rock pigeon. *Microorganisms* **8**(1), 61–74.
- DIEZ-MÉNDEZ, D., BODAWATTA, K. H., FREIBERGA, I., KLEČKOVÁ, I., JÓNSSON, K. A., POULSEN, M. & SAM, K. (2022). Gut microbiome disturbances of altricial blue and great tit nestlings are countered by continuous microbial inoculations from parental microbiomes. *Molecular Ecology* 3657–3671. <https://doi.org/10.1111/2022.02.20.481211>.
- DING, J., DAI, R., YANG, L., HE, C., XU, K., LIU, S., ZHAO, W., XIAO, L., LUO, L., ZHANG, Y. & MENG, H. (2017). Inheritance and establishment of gut microbiota in chickens. *Frontiers in Microbiology* **8**, 1967–1978.
- DJORDJEVIC, S. P., JAROCKI, V. M., SEEMANN, T., CUMMINS, M. L., WATT, A. E., DRIGO, B., WYRSCH, E. R., REID, C. J., DONNER, E. & HOWDEN, B. P. (2023). Genomic surveillance for antimicrobial resistance — a One Health perspective. *Nature Reviews Genetics*. <https://doi.org/10.1038/s41576-023-00649-y>.
- DJORDJEVIC, S. P., STOKES, H. W. & ROY CHOWDHURY, P. (2013). Mobile elements, zoonotic pathogens and commensal bacteria: conduits for the delivery of resistance genes into humans, production animals and soil microbiota. *Frontiers in Microbiology* **4**, 86–98.
- DOLEJSKA, M., MASARIKOVA, M., DOBIASOVA, H., JAMBOROVA, I., KARPISKOVA, R., HAVLICEK, M., CARLILE, N., PRIDDEL, D., CIZEK, A. & LITERAK, I. (2015). High prevalence of *Salmonella* and IMP-4-producing *Enterobacteriaceae* in the silver gull on Five Islands, Australia. *Journal of Antimicrobial Chemotherapy* **71**(1), 63–70.
- DOWNING, P. A., GRIFFIN, A. S. & CORNWALLIS, C. K. (2020). Group formation and the evolutionary pathway to complex sociality in birds. *Nature Ecology & Evolution* **4**(3), 479–486.
- DROVETSKI, S. V., O'MAHONEY, M. J. V., MATTERSON, K. O., SCHMIDT, B. K. & GRAVES, G. R. (2019). Distinct microbiotas of anatomical gut regions display idiosyncratic seasonal variation in an avian folivore. *Animal Microbiome* **1**(1), 2–13.
- EASON, D. & MOORHOUSE, R. (2006). Hand-rearing kakapo (*Strigops habroptilus*), 1997–2005. *Notornis* **53**(1), 116–125.
- ELLIOTT, K. H., GASTON, A. J. & CRUMP, D. (2010). Sex-specific behavior by a monomorphic seabird represents risk partitioning. *Behavioral Ecology* **21**(5), 1024–1032.
- EVANS, J. K., BUCHANAN, K. L., GRIFFITH, S. C., KLASING, K. C. & ADDISON, B. (2017). Ecoimmunology and microbial ecology: contributions to avian behavior, physiology, and life history. *Hormones and Behavior* **88**, 112–121.
- FELD, L., SCHJØRRING, S., HAMMER, K., LICHT, T. R., DANIELSEN, M., KROGFELT, K. & WILCKES, A. (2008). Selective pressure affects transfer and establishment of a *Lactobacillus plantarum* resistance plasmid in the gastrointestinal environment. *Journal of Antimicrobial Chemotherapy* **61**(4), 845–852.
- FENG, C. & LIANG, W. (2020). Behavioral responses of black-headed gulls (*Chroicocephalus ridibundus*) to artificial provisioning in China. *Global Ecology and Conservation* **21**, e00873. <https://doi.org/10.1016/j.gecco.2019.e00873>.
- FENG, Y., WANG, Y., ZHU, B., GAO, G. F., GUO, Y. & HU, Y. (2021). Metagenome-assembled genomes and gene catalog from the chicken gut microbiome aid in deciphering antibiotic resistomes. *Communications Biology* **4**(1), 1305–1314.
- FERICAN, L., OSTAN, M., RADA, O., PRUNAR, S., IVAN, M., PRUNAR, F. & BANATEAN-DUNEA, I. (2021). Behaviour of captive ostrich chicks from 6 weeks to 1 year. *Research Journal of Agricultural Science* **53**(2), 126–132.
- FLACHOWSKY, G. (1997). Animal excreta as feedstuff for ruminants – a review. *Journal of Applied Animal Research* **12**(1), 1–40.
- FOCOSI, D., GENONI, A., LUCENTEFORTE, E., TILLATI, S., TAMBORINI, A., SPEZIA, P. G., AZZI, L., BAJ, A. & MAGGI, F. (2021). Previous humoral immunity to the endemic seasonal alphacoronaviruses NL63 and 229E is associated with worse clinical outcome in COVID-19 and suggests original antigenic sin. *Life (Basel)* **11**(4), 298. <https://doi.org/10.3390/life11040298>.
- FOLZ, S. D., RECTOR, D. L., CONDER, G. A. & LEE, B. L. (1986). Precluding coccidiosis with an anti-coprotophagia drug. *Veterinary Parasitology* **22**(3), 243–247.
- FURST, M., VEIT, R. R., HAHN, M., DHEILLY, N. & THORNE, L. H. (2018). Effects of urbanization on the foraging ecology and microbiota of the generalist seabird *Larus argentatus*. *PLoS One* **13**(12), e0209200.
- GALLANT, D. (2004). White-winged crossbills obtain forage from river otter feces. *Wilson Bulletin* **116**, 181–183.
- GAO, L. F., ZHANG, W., ZHANG, H. Y., ZHU, Z. Q., ZHANG, X. D., LI, J. C., FAN, L. Q. & DU, B. (2020). Fecal consumption by adults of altricial birds in relation to the temporal change in nestling gut microbiota. *Current Zoology* **66**(6), 689–691.
- GILLINGHAM, M. A. F., BÉCHET, A., CÉZILLY, F., WILHELM, K., RENDÓN-MARTOS, M., BORGHESI, F., NISSARDI, S., BACCETTI, N., AZAFZAF, H., MENKE, S., KAYSER, Y. & SOMMER, S. (2019). Offspring microbiomes differ across breeding sites in a parasitic species. *Frontiers in Microbiology* **10**(35), 1–12. <https://doi.org/10.3389/fmicb.2019.00035>.
- GODOY-VITORINO, F., GOLDFARB, K. C., BRODIE, E. L., GARCIA-AMADO, M. A., MICHELANGELI, F. & DOMÍNGUEZ-BELLO, M. G. (2010). Developmental microbial ecology of the crop of the folivorous hoatzin. *The ISME Journal* **4**(5), 611–620.
- GODOY-VITORINO, F., GOLDFARB, K. C., KARAOZ, U., LEAL, S., GARCIA-AMADO, M. A., HUGENHOLTZ, P., TRINGE, S. G., BRODIE, E. L. & DOMÍNGUEZ-BELLO, M. G. (2012). Comparative analyses of foregut and hindgut bacterial communities in hoatzins and cows. *The ISME Journal* **6**(3), 531–541.
- GÓNGORA, E., ELLIOTT, K. H. & WHYTE, L. (2021). Gut microbiome is affected by inter-sexual and inter-seasonal variation in diet for thick-billed murre (*Uria lomvia*). *Scientific Reports* **11**(1), 1200–1212.
- GONZÁLEZ-JÁUREGUI, M., ESPARZA-CARLOS, J. P. & MIR, M. F. B. (2021). Heterospecific coprophagy: Turkey vulture (*Cathartes aura*) feeding on cougar (*Puma concolor*) feces. *Western North American Naturalist* **81**(4), 626–629.
- GRAJAL, A. (1995a). Digestive efficiency of the hoatzin, *Opisthocomus hoazin*: a folivorous bird with foregut fermentation. *Ibis* **137**(3), 383–388.
- GRAJAL, A. (1995b). Structure and function of the digestive tract of the hoatzin (*Opisthocomus hoazin*): a folivorous bird with foregut fermentation. *The Auk* **112**(1), 20–28.
- GROND, K., LANCTOT, R. B., JUMPPONEN, A. & SANDERCOCK, B. K. (2017). Recruitment and establishment of the gut microbiome in arctic shorebirds. *FEMS Microbiology Ecology* **93**(12), 1–9.
- GROND, K., LOUYAKIS, A. S. & HIRD, S. M. (2023). Functional and compositional changes in the fecal microbiome of a shorebird during migratory stopover. *mSystems* **8**(2), e01128-22. <https://doi.org/10.1128/mSystems.01128-22>.
- GROND, K., SANDERCOCK, B. K., JUMPPONEN, A. & ZEGLIN, L. H. (2018). The avian gut microbiota: community, physiology and function in wild birds. *Journal of Avian Biology* **49**(11), e01788. <https://doi.org/10.1111/jav.01788>.
- GROND, K., SANTO DOMINGO, J. W., LANCTOT, R. B., JUMPPONEN, A., BENTZEN, R. L., BOLDENOW, M. L., BROWN, S. C., CASLER, B., CUNNINGHAM, J. A., DOLL, A. C., FREEMAN, S., HILL, B. L., KENDALL, S. J., KWON, E., LIEBEZEIT, J. R., ET AL. (2019). Composition and drivers of gut microbial communities in Arctic-breeding shorebirds. *Frontiers in Microbiology* **10**, 2258.
- GUO, W., REN, K., NING, R., LI, C., ZHANG, H., LI, D., XU, L., SUN, F. & DAI, M. (2020). Fecal microbiota transplantation provides new insight into wildlife conservation. *Global Ecology and Conservation* **24**, e01234. <https://doi.org/10.1016/j.gecco.2020.e01234>.
- HAN, G. P., LEE, K. C., KANG, H. K., OH, H. N., SUL, W. J. & KIL, D. Y. (2019). Analysis of excreta bacterial community after forced molting in aged laying hens. *Asian-Australasian Journal of Animal Science* **32**(11), 1715–1724.
- HERDER, E. A., SPENCE, A. R., TINGLEY, M. W. & HIRD, S. M. (2021). Elevation correlates with significant changes in relative abundance in hummingbird fecal microbiota, but composition changes little. *Frontiers in Ecology and Evolution* **8**(534), 597–609.
- HERNANDEZ, J., JOHANSSON, A., STEDT, J., BENTSSON, S., PORCZAK, A., GRANHOLM, S., GONZÁLEZ-ACUÑA, D., OLSEN, B., BONNEDAHL, J. & DROBNI, M. (2013). Characterization and comparison of extended-spectrum β-lactamase (ESBL) resistance genotypes and population structure of *Escherichia coli* isolated from Franklin's gulls (*Leucophaea pipixcan*) and humans in Chile. *PLoS One* **8**(9), e76150. <https://doi.org/10.1371/journal.pone.0076150>.

- HIRAKAWA, H. (2001). Coprophagy in leporids and other mammalian herbivores. *Mammal Review* **31**(1), 61–80.
- HÖRNICKE, H. & BJÖRNHAG, G. (1980). Coprophagy and related strategies for digesta utilization. In *Digestive Physiology and Metabolism in Ruminants: Proceedings of the 5th International Symposium on Ruminant Physiology, held at Clermont — Ferrand, on 3rd–7th September, 1979* (eds Y. RUCKEBUSCH and P. THIVEND), pp. 707–730. Springer Netherlands, Dordrecht.
- HOUSTON, D., MCINNES, K., ELLIOTT, G., EASON, D., MOORHOUSE, R. & COCKREM, J. (2007). The use of a nutritional supplement to improve egg production in the endangered kakapo. *Biological Conservation* **138**(1), 248–255.
- HOYE, B. J. & BUTTEMER, W. A. (2011). Inexplicable inefficiency of avian molt? Insights from an opportunistically breeding arid-zone species, *Lichenostomus xanthurus*. *PLoS One* **6**(2), e16230. <https://doi.org/10.1371/journal.pone.0016230>.
- HUNT, A., AL-NAKASH, L., LEE, A. H. & SMITH, H. F. (2019). Phylogeny and herbivory are related to avian cecal size. *Scientific Reports* **9**(1), 4243–4252.
- ILINA, L. A., YILDIRIM, E. A., NIKONOV, I. N., FILIPPOVA, V. A., LAPTEV, G. Y., NOVIKOVA, N. I., GROZINA, A. A., LENKOVA, T. N., MANUKYAN, V. A., EGOROV, I. A. & FISININ, V. I. (2016). Metagenomic bacterial community profiles of chicken embryo gastrointestinal tract by using T-RFLP analysis. *Doklady Biochemistry and Biophysics* **466**(1), 47–51.
- INGALA, M. R., SIMMONS, N. B., DUNBAR, M., WULTSCH, C., KRAMPIS, K. & PERKINS, S. L. (2021). You are more than what you eat: potentially adaptive enrichment of microbiome functions across bat dietary niches. *Animal Microbiome* **3**(1), 82–99.
- INGLE, D. J., HOWDEN, B. P. & DUCHENE, S. (2021). Development of phylogenetic methods for bacterial pathogens. *Trends in Microbiology* **29**(9), 788–797.
- JANEWAY, C. A., TRAVERS, P., WALPOT, M. & SHLOMCHIK, M. (2004). *Immunobiology: The Immune System in Health and Disease*. Garland, New York.
- JIANG, J.-H., BHUIYAN, M. S., HEN, H. H., CAMERON, D. R., RUPASINGHE, T. W. T., WU, C. M., LE BRUN, A. P., KOSTOULIAS, X., DOMENE, C., FULCHER, A. J., MCCONVILLE, M. J., HOWDEN, B. P., LIESCHKE, J. G. & PELEG, A. Y. (2019). Antibiotic resistance and host immune evasion in *Staphylococcus aureus* mediated by a metabolic adaptation. *Proceedings of the National Academy of Sciences* **116**(9), 3722–3727.
- KASAMBE, R. & KASAMBE, V. (2020). Coprophagy and coconut in the diet of migratory ruddy turnstones (*Arenaria interpres*). *Newsletter for Birdwatchers* **60**(5), 59.
- KNUTIE, S. A., CHAVES, J. A. & GOTANDA, K. M. (2019). Human activity can influence the gut microbiota of Darwin's finches in the Galapagos Islands. *Molecular Ecology* **28**(9), 2441–2450.
- KOBAYASHI, A., TSUCHIDA, S., UEDA, A., YAMADA, T., MURATA, K., NAKAMURA, H. & USHIDA, K. (2019). Role of coprophagy in the cecal microbiome development of an herbivorous bird Japanese rock ptarmigan. *The Journal of Veterinary Medical Science* **81**(9), 1389–1399.
- KOHL, K. D. (2012). Diversity and function of the avian gut microbiota. *Journal of Comparative Physiology B* **182**(5), 591–602.
- KOHL, K. D., BRUN, A., BORDENSTEIN, S. R., CAVIEDES-VIDAL, E. & KARASOV, W. H. (2018). Gut microbes limit growth in house sparrow nestlings (*Passer domesticus*) but not through limitations in digestive capacity. *Integrative Zoology* **13**(2), 139–151.
- KOHL, K. D., CONNELLY, J. W., DEARING, M. D. & FORBEY, J. S. (2016). Microbial detoxification in the gut of a specialist avian herbivore, the greater sage-grouse. *FEMS Microbiology Letters* **363**(14), 363–369.
- KRAUS, S. & STONE, G. (1995). Coprophagy by Wilson's-storm petrels, *Oceanites oceanicus*, on North Atlantic right whale, *Eubalaena glacialis*, faeces. *The Canadian Field-Naturalist* **109**(4), 443–444.
- KRIEF, S., JAMART, A. & HLADIK, C. M. (2004). On the possible adaptive value of coprophagy in free-ranging chimpanzees. *Primates* **45**(2), 141–145.
- KUPERMAN, A., ZIMMERMAN, A., HAMADIA, S., ZIV, O., GUREVICH, V., FICHTMAN, B., GAVERT, N., STRAUSSMAN, R., RECHNITZER, H., BARZILAY, M., SHVALB, S., BORNSTEIN, J., BEN-SHACHAR, I., YAGEL, S., HAVIV, I. & KOREN, O. (2020). Deep microbial analysis of multiple placentas shows no evidence for a placental microbiome. *British Journal of Obstetrics & Gynaecology* **127**(2), 159–169.
- LAMB, S. D., TAYLOR, H. R., HOLTSMAN, B., SANTOS, E. S. A., TAMAYO, J. H., JOHNSON, S. L., NAKAGAWA, S. & LARA, C. E. (2017). Coprophagy in dunlocks (*Prunella modularis*): a frequent behavior in females, infrequent in males, and very unusual in nestlings. *The Wilson Journal of Ornithology* **129**(3), 615–620.
- LAMBERSKI, N., HULL, A. C., FISH, M., BECKMEN, K. & MORISHITA, T. Y. (2003). A survey of the choanal and cloacal aerobic bacterial flora in free-living and captive red-tailed hawks (*Buteo jamaicensis*) and Cooper's hawks (*Accipiter cooperii*). *Journal of Avian Medicine and Surgery* **17**(3), 131–135.
- LEE, C., TELL, L. A., HILFER, T. & VANNETTE, R. L. (2019a). Microbial communities in hummingbird feeders are distinct from floral nectar and influenced by bird visitation. *Proceedings of the Royal Society B* **286**(1898), 20182295. <https://doi.org/10.1098/rspb.2018.2295>.
- LEE, S., LA, T. M., LEE, H. J., CHOI, I. S., SONG, C. S., PARK, S. Y., LEE, J. B. & LEE, S. W. (2019b). Characterization of microbial communities in the chicken oviduct and the origin of chicken embryo gut microbiota. *Scientific Reports* **9**(1), 6838–6849.
- LEE, W. Y., CHO, H., KIM, M., TRIPATHI, B. M., JUNG, J. W., CHUNG, H. & KIM, J. H. (2019c). Faecal microbiota changes associated with the moult fast in chinstrap and gentoo penguins. *PLoS One* **14**(5), e0216565. <https://doi.org/10.1371/journal.pone.0216565>.
- LESTER, C. H., FRIMODT-MØLLER, N., SØRENSEN, T. L., MONNET, D. L. & HAMMERUM, A. M. (2006). In vivo transfer of the *Enterococcus faecium* isolate of animal origin to an *E. Faecium* isolate of human origin in the intestines of human volunteers. *Antimicrobial Agents and Chemotherapy* **50**(2), 596–599.
- LI, P., GAO, M., SONG, B., LIU, Y., YAN, S., LEI, J., ZHAO, Y., LI, G., MAHMOOD, T., LV, Z., HU, Y. & GUO, Y. (2022). Fecal microbiota transplantation reshapes the physiological function of the intestine in antibiotic-treated specific pathogen-free birds. *Frontiers in Immunology* **13**, 884615–884628.
- LINE, J., HIETT, K. & CONLAN, A. (2008). Comparison of challenge models for determining the colonization dose of *Campylobacter jejuni* in broiler chicks. *Poultry Science* **87**(9), 1700–1706.
- LINE, J. E. (2006). Influence of relative humidity on transmission of *Campylobacter jejuni* in broiler chickens. *Poultry Science* **85**(7), 1145–1150.
- LOO, W. T., GARCÍA-LOOR, J., DUDANIEC, R. Y., KLEINDORFER, S. & CAVANAUGH, C. M. (2019). Host phylogeny, diet, and habitat differentiate the gut microbiomes of Darwin's finches on Santa Cruz Island. *Scientific Reports* **9**(1), 18781–18793.
- LOPEZ-CALLEJA, M. V. & BOZINOVIC, F. (2000). Energetics and nutritional ecology of small herbivorous birds. *Revista Chilena de Historia Natural* **73**, 411–420.
- MARACI, Ö., ANTONATOU-PAPAIANNOU, A., JÜNEMANN, S., ENGEL, K., CASTILLO-GUTIÉRREZ, O., BUSCHE, T., KALINOWSKI, J. & CASPERS, B. A. (2022a). Timing matters: age-dependent impacts of the social environment and host selection on the avian gut microbiota. *Microbiome* **10**(1), 202–222.
- MARACI, Ö., CORSINI, M., ANTONATOU-PAPAIANNOU, A., JÜNEMANN, S., SUDYKA, J., DI LECCE, I., CASPERS, B. A. & SZULKIN, M. (2022b). Changes to the gut microbiota of a wild juvenile passerine in a multidimensional urban mosaic. *Scientific Reports* **12**(1), 6872–6888.
- MARCELINO, V. R., WILLE, M., HURT, A. C., GONZÁLEZ-ACUÑA, D., KLAASSEN, M., SCHLUB, T. E., JOHN-SEBASTIAN, E., SHI, M., IREDELL, J. R., SORRELL, T. C. & HOLMES, E. C. (2019). Meta-transcriptomics reveals a diverse antibiotic resistance gene pool in avian microbiomes. *BMC Biology* **17**(31), 1–11. <https://doi.org/10.1186/s12915-019-0649-1>.
- MARTIN, L. (2005). Trade-offs between molt and immune activity in two populations of house sparrows (*Passer domesticus*). *Canadian Journal of Zoology* **83**(6), 780–787.
- MARTIN, L. B., WEIL, Z. M. & NELSON, R. J. (2008). Seasonal changes in vertebrate immune activity: mediation by physiological trade-offs. *Philosophical Transactions of the Royal Society of London B* **363**(1490), 321–339.
- MARTIN, T. E., TOBALSKE, B., RIORDAN, M. M., CASE, S. B. & DIAL, K. P. (2018). Age and performance at fledging are a cause and consequence of juvenile mortality between life stages. *Science Advances* **4**(6), eaar1988.
- MARTINEZ, J. L. (2009). Environmental pollution by antibiotics and by antibiotic resistance determinants. *Environmental Pollution* **157**(11), 2893–2902.
- MASI, S. & BREUER, T. (2018). Dialium seed coprophagy in wild western gorillas: multiple nutritional benefits and toxicity reduction hypotheses. *American Journal of Primatology* **80**(4), e22752.
- MATHEEN, M. I. A., GILLINGS, M. R. & DUDANIEC, R. Y. (2022). Dominant factors shaping the gut microbiota of wild birds. *Emu-Austral Ornithology* **122**(3–4), 255–268.
- MATSUBAYASHI, M., KOBAYASHI, A., KANEKO, M., KINOSHITA, M., TSUCHIDA, S., SHIBAHARA, T., HASEGAWA, M., NAKAMURA, H., SASAI, K. & USHIDA, K. (2021). Distribution of *Eimeria ueki* and *Eimeria yatchoi* in cage protection environments for the conservation of Japanese rock ptarmigan (*Lagopus muta japonica*) in the Japanese Alps. *International Journal for Parasitology: Parasites and Wildlife* **15**, 225–230.
- McKAY, J. E., MURPHY, M. T., SMITH, S. B. & RICHARDSON, J. K. (2009). Fecal-sac ingestion by spotted towhees. *The Condor* **111**(3), 503–510.
- McWHORTER, T. J., CAVIEDES-VIDAL, E. & KARASOV, W. H. (2009). The integration of digestion and osmoregulation in the avian gut. *Biological Reviews* **84**(4), 533–565.
- MENDOZA, M. L. Z., GRAVES, G. R., ROGGENBUCK, M., VARGAS, K. M., HANSEN, L. H., BRUNAK, S., GILBERT, M. T. P. & SICHERITZ-PONTÉN, T. (2017). Protective role of the vulture facial and gut microbiomes aid adaptation to scavenging. *Acta Veterinaria Scandinavica* **60**(61), 1–19. <https://doi.org/10.1186/s13028-018-0415-3>.
- MENNECHEZ, G. & CLERGEAU, P. (2006). Effect of urbanisation on habitat generalists: starlings not so flexible? *Acta Oecologica* **30**(2), 182–191.
- MERKELIACIENE, L., RUZAUSKAITE, N., KLIMIENE, I., STUGZINIENE, R., DAHLIDAVICIENE, J., VIRGAILIS, M., MOKELIUNAS, R. & RUZAUSKAS, M. (2017). Microbiome and antimicrobial resistance genes in microbiota of cloacal samples from European herring gulls (*Larus argentatus*). *Journal of Veterinary Research* **61**(1), 27–35.

- MICHEL, A. J., WARD, L. M., GOFFREDI, S. K., DAWSON, K. S., BALDASSARRE, D. T., BRENNER, A., GOTANDA, K. M., MCCORMACK, J. E., MULLIN, S. W., O'NEILL, A., TENDER, G. S., UY, J. A. C., YU, K., ORPHAN, V. J. & CHAVES, J. A. (2018). The gut of the finch: uniqueness of the gut microbiome of the Galápagos vampire finch. *Microbiome* **6**(1), 167–181.
- MONTROSE, M. S., SHANE, S. M. & HARRINGTON, K. S. (1985). Role of litter in the transmission of *Campylobacter jejuni*. *Avian Diseases* **29**(2), 392–399.
- MORELLI, F., BENEDETTI, Y., HANSON, J. O. & FULLER, R. A. (2021). Global distribution and conservation of avian diet specialization. *Conservation Letters* **14**(4), e12795. <https://doi.org/10.1111/conl.12795>.
- MORENO-RUEDA, G. (2010). Experimental test of a trade-off between moult and immune response in house sparrows *Passer domesticus*. *Journal of Evolutionary Biology* **23**(10), 2229–2237.
- MUKERJI, S., STEGGER, M., TRUSWELL, A., LAIRD, T., JORDAN, D., ABRAHAM, R., HARB, A., BARTON, M., O'DEA, M. & ABRAHAM, S. (2019). Resistance to critically important antimicrobials in Australian silver gulls (*Chroicocephalus novaeohollandiae*) and evidence of anthropogenic origins. *Journal of Antimicrobial Chemotherapy* **74**(9), 2566–2574.
- MUNITA, J. M. & ARIAS, C. A. (2016). Mechanisms of antibiotic resistance. *Microbiology Spectrum* **4**(2), 1128–1135.
- MURPHY, M. E. (1996). Energetics and nutrition of molt. In *Avian Energetics and Nutritional Ecology* (ed. C. CAREY), pp. 158–198. Springer US, Boston, MA.
- MURPHY, M. E. & TARUSCIO, T. G. (1995). Sparrows increase their rates of tissue and whole-body protein synthesis during the annual molt. *Comparative Biochemistry and Physiology Part A: Physiology* **111**(3), 385–396.
- MURRAY, M. H., KIDD, A. D., CURRY, S. E., HEPINSTALL-CYMERMAN, J., YABSLEY, M. J., ADAMS, H. C., ELLISON, T., WELCH, C. N. & HERNANDEZ, S. M. (2018). From wetland specialist to hand-fed generalist: shifts in diet and condition with provisioning for a recently urbanized wading bird. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **373**(1745), 20170100. <https://doi.org/10.1098/rstb.2017.0100>.
- MURRAY, M. H., LANKAU, E. W., KIDD, A. D., WELCH, C. N., ELLISON, T., ADAMS, H. C., LIPP, E. K. & HERNANDEZ, S. M. (2020). Gut microbiome shifts with urbanization and potentially facilitates a zoonotic pathogen in a wading bird. *PLoS One* **15**(3), e0220926. <https://doi.org/10.1371/journal.pone.0220926>.
- NAEF-DAENZER, B. & GRÜEBLER, M. U. (2016). Post-fledging survival of altricial birds: ecological determinants and adaptation. *Journal of Field Ornithology* **87**(3), 227–250.
- NAVA, M. P., VEIGA, J. P. & PUERTA, M. (2001). White blood cell counts in house sparrows (*Passer domesticus*) before and after moult and after testosterone treatment. *Canadian Journal of Zoology* **79**(1), 145–148.
- NAVALÓN, G., BRIGHT, J. A., MARUGÁN-LOBÓN, J. & RAYFIELD, E. J. (2019). The evolutionary relationship among beak shape, mechanical advantage, and feeding ecology in modern birds. *Evolution* **73**(3), 422–435.
- NEGRO, J. J., GRANDE, J. M., TELLA, M., GARRIDO, J., HORNERO, D., DONÁZAR, J. A., SANCHEZ-ZAPATA, J. A., BENÍTEZ, J. R. & BARCELL, M. (2002). An unusual source of essential carotenoids. *Nature* **416**(6883), 807–808.
- OLIVEIRA, B. C. M., MURRAY, M., TSENG, F. & WIDMER, F. (2020). The fecal microbiota of wild and captive raptors. *Animal Microbiome* **2**(1), 15–24.
- ONICIUC, E. A., LIKOTRAFITI, E., ALVAREZ-MOLINA, A., PRIETO, M., LÓPEZ, M. & ALVAREZ-ORDÓÑEZ, A. (2019). Food processing as a risk factor for antimicrobial resistance spread along the food chain. *Current Opinion in Food Science* **30**, 21–26.
- PAN, D. & YU, Z. (2014). Intestinal microbiome of poultry and its interaction with host and diet. *Gut Microbes* **5**(1), 108–119.
- PAP, P. L., VÁGÁSI, C. I., TÖRÖLYI, J., CZIRJÁK, G. Á. & BARTA, Z. (2010). Variation in haematological indices and immune function during the annual cycle in the great tit (*Parus major*). *Ardea* **98**(1), 105–112.
- PARFREY, L. W., MOREAU, C. S. & RUSSELL, J. A. (2018). Introduction: the host-associated microbiome: pattern, process and function. *Molecular Ecology* **27**(8), 1749–1765.
- PERRIG, M., GRÜEBLER, M. U., KEIL, H. & NAEF-DAENZER, B. (2017). Post-fledging survival of little owls *Athene noctua* in relation to nestling food supply. *Ibis* **159**(3), 532–540.
- PETKOV, C. & JARVIS, E. (2012). Birds, primates and spoken language origins: behavioral phenotypes and neurobiological substrates. *Frontiers in Evolutionary Neuroscience* **4**, 12–36.
- PIGOT, A. L., SHEARD, C., MILLER, E. T., BREGMAN, T. P., FREEMAN, B. G., ROLL, U., SEDDON, N., TRISOS, C. H., WEEKS, B. C. & TOBIAS, J. A. (2020). Macroevolutionary convergence connects morphological form to ecological function in birds. *Nature Ecology & Evolution* **4**(2), 230–239.
- PINTO, A., SIMÕES, R., OLIVEIRA, M., VAZ-PIRES, P., BRANDAO, R. & DA COSTA, P. M. (2015). Multidrug resistance in wild bird populations: importance of the food chain. *Journal of Zoo and Wildlife Medicine* **46**(4), 723–731.
- POOLE, K. (2017). At the nexus of antibiotics and metals: the impact of Cu and Zn on antibiotic activity and resistance. *Trends in Microbiology* **25**(10), 820–832.
- RISELY, A., WAITE, D., UJVARI, B., HOYE, B. & KLAASSEN, M. (2018). Active migration is associated with specific and consistent changes to gut microbiota in *Calidris* shorebirds. *Journal of Animal Ecology* **87**(2), 428–437.
- RISELY, A., WAITE, D., UJVARI, B., KLAASSEN, M. & HOYE, B. (2017). Gut microbiota of a long-distance migrant demonstrates resistance against environmental microbe incursions. *Molecular Ecology* **26**(20), 5842–5854.
- RISELY, A., WILHELM, K., CLUTTON-BROCK, T., MANSER, M. B. & SOMMER, S. (2021). Diurnal oscillations in gut bacterial load and composition eclipse seasonal and lifetime dynamics in wild meerkats. *Nature Communications* **12**(1), 6017–6029.
- ROGGENBUCK, M., BÆRHOLM SCHNELL, I., BLOM, N., BÆLUM, J., BERTENSEN, M. F., SICHERITZ-PONTÉN, T., SØRENSEN, S. J., GILBERT, M. T. P., GRAVES, G. R. & HANSEN, L. H. (2014). The microbiome of New World vultures. *Nature Communications* **5**(1), 5498–5506.
- RUUSKANEN, S., RAINIO, M. J., GÓMEZ-GALLEGO, C., SELENIUS, O., SALMINEN, S., COLLADO, M. C., SAIKKONEN, K., SALONIEMI, I. & HELANDER, M. (2020). Glyphosate-based herbicides influence antioxidants, reproductive hormones and gut microbiome but not reproduction: a long-term experiment in an avian model. *Environmental Pollution* **266**, 115108. <https://doi.org/10.1016/j.envpol.2020.115108>.
- SAKAMAKI, T. (2009). Coprophagy in wild bonobos (*Pan paniscus*) at Wamba in The Democratic Republic of the Congo: a possibly adaptive strategy? *Primates* **51**(1), 87–91.
- SAN JUAN, P. A., HENDERSHOT, J. N., DAILY, G. C. & FUKAMI, T. (2020). Land-use change has host-specific influences on avian gut microbiomes. *The ISME Journal* **14**(1), 318–321.
- SANTOS, A. C. D. M., SANTOS, F. F., SILVA, R. M. & GOMES, T. A. T. (2020). Diversity of hybrid- and hetero-pathogenic *Escherichia coli* and their potential implication in more severe diseases. *Frontiers in Cellular and Infection Microbiology* **10**, 339–350.
- SCANES, C. G. (2020). Avian physiology: are birds simply feathered mammals? *Frontiers in Physiology* **11**, 542466. <https://doi.org/10.3389/fphys.2020.542466>.
- SCHIEKERMANN, H., VISSER, G. H. & BLEM, C. (2001). Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development. *The Auk* **118**(4), 944–957.
- SCHJØRRING, S. & KROGFELT, K. A. (2011). Assessment of bacterial antibiotic resistance transfer in the gut. *International Journal of Microbiology* **2011**, 312956. <https://doi.org/10.1155/2011/312956>.
- SCHMIEDOVÁ, L., TOMÁŠEK, O., PINKASOVÁ, H., ALBRECHT, T. & KREISINGER, J. (2022). Variation in diet composition and its relation to gut microbiota in a passerine bird. *Scientific Reports* **12**(1), 3787–3800.
- SHANKER, S., LEE, A. & SORRELL, T. C. (1990). Horizontal transmission of *Campylobacter jejuni* amongst broiler chicks: experimental studies. *Epidemiology & Infection* **104**(1), 101–110.
- SHAPIRA, M. (2016). Gut microbiotas and host evolution: scaling up symbiosis. *Trends in Ecology and Evolution* **31**(7), 539–549.
- SHIMADA, T. (2012). Ducks foraging on swan faeces. *Wildfowl* **62**, 224–227.
- SILVA, V. L., NICOLI, J. R., NASCIMENTO, T. C. & DINIZ, C. G. (2009). Diarrheagenic *Escherichia coli* strains recovered from urban pigeons (*Columba livia*) in Brazil and their antimicrobial susceptibility patterns. *Current Microbiology* **59**(3), 302–308.
- SILVERIN, B., FÄNGE, R., VIEBKE, P. A. & WESTIN, J. (1999). Seasonal changes in mass and histology of the spleen in willow tits *Parus montanus*. *Journal of Avian Biology* **30**, 255–262.
- SMALLA, K., COOK, K., DJORDJEVIC, S., KLÜMPER, U. & GILLINGS, M. (2018). Environmental dimensions of antibiotic resistance: assessment of basic science gaps. *FEMS Microbiology and Ecology* **94**(12), fiy195. <https://doi.org/10.1093/femsec/fiy195>.
- SMITH, G. C. & CARLILE, N. (1993). Food and feeding ecology of breeding silver gulls (*Larus novaehollandiae*) in urban Australia. *Colonial Waterbirds* **16**(1), 9–16.
- SOAVE, O. & BRAND, C. D. (1991). Coprophagy in animals: a review. *The Cornell Veterinarian* **81**(4), 357–364.
- SOMERS, S. E., DAVIDSON, G. L., JOHNSON, C. N., REICHERT, M. S., CRANE, J. M. S., ROSS, R. P., STANTON, C. & QUINN, J. L. (2023). Individual variation in the avian gut microbiota: the influence of host state and environmental heterogeneity. *Molecular Ecology* **38**(12), 3322–3339. <https://doi.org/10.1111/mec.16919>.
- STARKS, J. & PETER, J. (1991). Dusky moorhens “*Gallinula tenebrosa*” eating gull faeces. *Australian Bird Watcher* **14**, 69.
- SUMMERS-SMITH, D. (1983). Magpies eating dog faeces. *British Birds* **76**(9), 411.
- SUN, F., CHEN, J., LIU, K., TANG, M. & YANG, Y. (2022). The avian gut microbiota: Diversity, influencing factors, and future directions. *Frontiers in Microbiology* **13**, 934272. <https://doi.org/10.3389/fmicb.2022.934272>.
- TEŠICKÝ, M., SCHMIEDOVÁ, L., KRAJZINGROVÁ, T., GOMEZ SAMBLAS, M., BAUEROVÁ, P., KREISINGER, J. & VINKLER, M. (2023). Nearly (?) sterile avian egg in a passerine bird. *bioRxiv*. <https://doi.org/10.1101/2023.02.14.528324>.
- TEYSSIER, A., LENS, L., MATTHYSEN, L. & WHITE, J. (2018). Dynamics of gut microbiota diversity during the early development of an avian host: evidence from a cross-foster experiment. *Frontiers in Microbiology* **9**, 1524.

- THABETHE, V. & DOWNS, C. T. (2018). Citizen science reveals widespread supplementary feeding of African woolly-necked storks in suburban areas of KwaZulu-Natal, South Africa. *Urban Ecosystems* **21**(5), 965–973.
- TREVELLINE, B. K. & KOHL, K. D. (2022). The gut microbiome influences host diet selection behavior. *Proceedings of the National Academy of Sciences* **119**(17), e2117537119. <https://doi.org/10.1073/pnas.2117537119>.
- TROHA, K. & AYRES, J. S. (2020). Metabolic adaptations to infections at the organismal level. *Trends in Immunology* **41**(2), 113–125.
- VAN DONGEN, W. F. D., WHITE, J., BRANDL, H. B., MOODLEY, Y., MERKLING, T., LECLAIRE, S., BLANCHARD, P., DANGHIN, É., HATCH, S. A. & WAGNER, R. H. (2013). Age-related differences in the cloacal microbiota of a wild bird species. *BMC Ecology* **13**(1), 1–12. <https://doi.org/10.1186/1472-6785-13-11>.
- VAN GILS, J. A., LISOVSKI, S., LOK, T., MEISSNER, W., OŻAROWSKA, A., DE FOUW, J., RAKHIMBERDIEV, E., SOLOVIEV, M. Y., PIERSMA, T. & KLAASSEN, M. (2016). Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. *Science* **352**(6287), 819–821.
- VIDEALL, E., BENSCH, H. M., ENGELBRECHT, A., CLOETE, S. & CORNWALLIS, C. K. (2023). Coprophagy rapidly matures juvenile gut microbiota in a precocial bird. *Evolution Letters* **7**(4), 240–251.
- VISPO, C. & KARASOV, W. H. (1997). The interaction of avian gut microbes and their host: an elusive symbiosis. In *Gastrointestinal Microbiology: Volume 1 Gastrointestinal Ecosystems and Fermentations* (eds R. I. MACKIE and B. A. WHITE), pp. 116–155. Springer US, Boston, MA.
- VOGRIN, M. (1997). A Coot (*Fulica atra*) eating waterfowl droppings. *Butlletí del Grup Català d'Anellament* **14**, 63–64.
- VON WALDBURG-ZEIL, C. G., VAN STAAVEREN, N. & HARLANDER-MATAUSCHEK, A. (2019). Do laying hens eat and forage in excreta from other hens? *Animal* **13**(2), 367–373.
- WAGGERSHAUSER, C. N., TABERLET, P., COISSAC, E., KORTLAND, K., HAMBLY, C. & LAMBIN, X. (2022). Interspecific coprophagia by wild red foxes: DNA metabarcoding reveals a potentially widespread form of commensalism among animals. *Ecology and Evolution* **12**(7), e9029. <https://doi.org/10.1002/ecc3.9029>.
- WAITE, D. W., DEINES, P. & TAYLOR, M. W. (2012). Gut microbiome of the critically endangered New Zealand parrot, the kakapo (*Strigops habroptilus*). *PLoS One* **7**(4), e35803. <https://doi.org/10.1371/journal.pone.0035803>.
- WAITE, D. W., DEINES, P. & TAYLOR, M. W. (2013). Quantifying the impact of storage procedures for faecal bacteriotherapy in the critically endangered New Zealand parrot, the kakapo (*Strigops habroptilus*). *Zoo Biology* **32**(6), 620–625.
- WAITE, D. W. & TAYLOR, M. W. (2014). Characterizing the avian gut microbiota: membership, driving influences, and potential function. *Frontiers in Microbiology* **5**, 223.
- WALL, T. (1983). Coots and other birds eating goose droppings and gull droppings. *British Birds* **76**(9), 410–411.
- WANG, W., ZHENG, S., LI, L., YANG, Y., LIU, Y., WANG, A., SHARSHOV, K. & LI, Y. (2019). Comparative metagenomics of the gut microbiota in wild Greylag geese (*Anser anser*) and ruddy shelducks (*Tadorna ferruginea*). *MicrobiologyOpen* **8**(5), e00725. [doi.org/10.1002/mb03.725](https://doi.org/10.1002/mb03.725).
- WARD, T. L., WEBER, B. P., MENDOZA, K. M., DANZEISEN, J. L., LLOP, K., LANG, K., CLAYTON, J. B., GRACE, E., BRANNON, J., RADOVIC, I., BEAUCLAIRE, M., HEISEL, T. J., KNIGHTS, D., CARDONA, C., KOGUT, M., ET AL. (2019). Antibiotics and host-tailored probiotics similarly modulate effects on the developing avian microbiome, mycobiome, and host gene expression. *mBio* **10**(5), 10–128. <https://doi.org/10.1128/mBio.02171-19>.
- WEST, A. G., DELAUNAY, A., MARSH, P., PERRY, E. K., JOLLY, M., GARTRELL, B. D., PAS, A., DIGBY, A. & TAYLOR, M. W. (2022). Gut microbiota of the threatened takahē: biogeographic patterns and conservation implications. *Animal Microbiome* **4**(1), 1–15. <https://doi.org/10.1186/s42523-021-00158-5>.
- WEST, A. G., WAITE, D. W., DEINES, P., BOURNE, D. G., DIGBY, A., MCKENZIE, V. J. & TAYLOR, M. W. (2019). The microbiome in threatened species conservation. *Biological Conservation* **229**, 85–98.
- WIENEMANN, T., SCHMITT-WAGNER, D., MEUSER, K., SEGELBACHER, G., SCHINK, B., BRUNE, A. & BERTHOLD, P. (2011). The bacterial microbiota in the ceca of capercaillie (*Tetrao urogallus*) differs between wild and captive birds. *Systematic and Applied Microbiology* **34**(7), 542–551.
- WOOLHOUSE, M. E. J., HAYDON, D. T. & ANTIA, R. (2005). Emerging pathogens: the epidemiology and evolution of species jumps. *Trends in Ecology & Evolution* **20**(5), 238–244.
- WU, G. D., CHEN, J., HOFFMANN, C., BITTINGER, K., CHEN, Y. Y., KEILBAUGH, S. A., BEWTRA, M., KNIGHTS, D., WALTERS, W. A., KNIGHT, R., SINHA, R., GILROY, E., GUPTA, K., BALDASSANO, R., NESSEL, L., ET AL. (2011). Linking long-term dietary patterns with gut microbial enterotypes. *Science* **334**(6052), 105–108.
- WYRSCH, E. R., NESPOROVA, K., TARABAI, H., JAMBOROVA, I., BITAR, I., LITERAK, I., DOLEJSKA, M. & DJORDJEVIC, S. P. (2022). Urban wildlife crisis: Australian silver gull is a bystander host to widespread clinical antibiotic resistance. *mSystems* **7**(3), e00158-22. <https://doi.org/10.1128/mSystems.00158-22>.
- XU, Q., ZHAO, W., LI, Y., ZOU, X. & DONG, X. (2022). Intestinal immune development is accompanied by temporal deviation in microbiota composition of newly hatched pigeon squabs. *Microbiology Spectrum* **10**(3), e0189221. <https://doi.org/10.1128/spectrum.01892-21>.
- YONG, R. (2018). An instance of coprophagy in the Australasian darter *Anhinga novaehollandiae*. *Australian Field Ornithology* **35**, 93–94.
- ZARRINPAR, A., CHAIX, A., YOUSEPH, S. & PANDA, S. (2014). Diet and feeding pattern affect the diurnal dynamics of the gut microbiome. *Cell Metabolism* **20**(6), 1006–1017.
- ZHOU, L., HUO, X., LIU, B., WU, H. & FENG, J. (2020a). Comparative analysis of the gut microbial communities of the Eurasian kestrel (*Falco tinnunculus*) at different developmental stages. *Frontiers in Microbiology* **11**, 592539. <https://doi.org/10.3389/fmicb.2020.592539>.
- ZHOU, Y., LI, Y., ZHANG, L., WU, Z., HUANG, Y., YAN, H., ZHONG, J., WANG, L. J., ABDULLAH, H. M. & WANG, H. H. (2020b). Antibiotic administration routes and oral exposure to antibiotic resistant bacteria as key drivers for gut microbiota disruption and resistance in poultry. *Frontiers in Microbiology* **11**, 1319. <https://doi.org/10.3389/fmicb.2020.01319>.

(Received 14 August 2023; revised 24 November 2023; accepted 27 November 2023; published online 8 December 2023)