

Flying into the future: avian haemosporidians and the advancement of understanding host–parasite systems

Editorial

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There is a long history of avian haemosporidian parasites being used to address ecological and evolutionary questions (e.g. Hamilton and Zuk, 1982; Norris *et al.*, 1994; McCurdy *et al.*, 1998). Since the development of PCR techniques allowing molecular identification of haemosporidians from avian blood samples in the early 2000s (Bensch *et al.*, 2000), however, there has been an explosion in our understanding of the species- and genus-level diversity within these parasites (Clark *et al.*, 2014). Recent papers continue to add new lineages to the avian haemosporidian phylogeny but the focus is less on uncovering diversity and increasingly on understanding how this diversity has come about (e.g. Fecchio *et al.*, 2018). Not surprisingly though, the system continually reminds researchers just how complex it is, and at times, seems unwilling to share its secrets.

This collection of eight papers published in *Parasitology* in 2017 and 2018 encompasses and highlights the range and importance of ecological parasitology in understanding the factors that drive diversity among avian haemosporidians. Specifically, these papers highlight the diversity of avian malaria parasites, and the range of ecological questions this system can be used to address. We have broadly classified these papers into two collections: (1) basic biology of host/parasite systems and (2) ecological and evolutionary diversity.

One of the take-home messages from this body of work is that, collectively, these papers show the variety of questions that can be addressed using avian haemosporidians as a system, but simultaneously, they show what questions remain unanswered. Many of these studies have uncovered previously unknown lineages (possibly species) of haemosporidians and most have tried to answer questions about mechanisms to explain how this diversity has arisen. Strikingly however, each study that has explicitly addressed factors to explain haemosporidian diversification has concluded that a multitude of other factors needs to be considered, leaving the field with more follow-up questions. This has led to a dramatic increase in known haemosporidian diversity but also to incremental advances in our understanding of the factors that drive the generation of this diversity. We hope that as we synthesize the many contributions of authors to the advancement of this field, we can spur more collaborative investigations of the ‘why and how’.

Basic biology of host/parasite systems

Using samples collected across four years, Schultz *et al.* (2018) examined possible predictors of haemosporidian parasite prevalence and intensity (i.e. parasitaemia) in the red crossbill *Loxia curvirostra*, an ecologically specialized host that breeds opportunistically to coincide with erratic food abundance. The authors conclude that a combination of physiological factors, such as white-blood-cell count, and environmental factors, such as food availability across years, correlate with parasite prevalence and infection intensity. These results show that both parasite prevalence and parasitaemia are associated with a number of factors including host physiology *via* the immune response and by vector dynamics *via* variation in dipteran abundance. Crucially, this paper highlights the potential importance of dipteran vectors – the definitive hosts of avian haemosporidians that remain poorly studied in relation to the avian intermediate hosts – in determining the patterns of parasite distribution we see among bird species.

Dunn *et al.* (2017) addressed the question of when avian hatchlings become infected with haemosporidians by investigating parasite prevalence in nestling doves and pigeons that differ in their nest location strategy. They found a high prevalence of infection across species but prevalence was markedly higher in open-nesting *vs* closed-nesting species, and in older *vs* younger nestlings. Moreover, their results suggest a high prevalence of coinfection by haemosporidians at the nestling stage, further showing the vulnerability of nestlings to dipterans and any pathogens that these insects carry. Because birds are infected at such a young age, this research suggests that future work should focus on the impacts of infection at this vulnerable life stage, on both individual birds and populations. An important question that remains is what proportion of initial infections introduced through the bite of a vector and potentially detected in the bloodstream as sporozoites successfully become patent (as opposed to resulting in abortive infections).

Most of the studies considered here examine haemosporidians from the host’s point of view. Instead, Valkiūnas *et al.* (2017) focus specifically on the parasite and describe a common

and abundant haemosporidian species, *Plasmodium matutinum*, using both morphological and molecular tools. Even though the species had been previously evaluated using microscopy, this paper provides the first molecular characterization of *P. matutinum*, and provides markers that can be used to identify this parasite in other hosts even in the absence of expertise in microscopy. The description of the species includes both a phylogenetic analysis using markers from the haemosporidians' three genomes, and a detailed species description from morphological characteristics from host blood smears. An important point from this study is the very frequent lack of overlap between molecular and morphological studies, a lacking that can confound interpretations of the biological relevance of a host carrying a particular parasite.

Ecological and evolutionary diversity

Ayadi *et al.* (2018) are the first to evaluate haemosporidians within desert oases with the aim of extrapolating hypotheses of island biogeography to these often-overlooked habitats. The authors investigated parasite prevalence and diversity in two abundant sedentary bird species between island-like oases that varied in their habitats and distance from the Tunisian coast. The study identified new lineages of haemosporidians from both hosts. Denser vegetation was linked with higher *Plasmodium* and lower *Haemoproteus* prevalence, but distance from the coast also impacted parasite prevalence albeit to a much lesser extent. This study, being the first of its kind, outlines that to address its unanswered questions, the sampling of birds would need to increase across species and locations.

In an effort to summarize haemosporidian diversity across the African continent, Outlaw *et al.* (2017) compiled known sub-Saharan African parasite lineages and compared patterns of diversity between major avian faunal regions. The primary conclusion is that sampling has driven our current understanding of parasite diversity and remedying these gaps – whether in Africa or any other continent – is key if we want to understand the factors that govern diversity and turnover. The authors highlight sampling gaps (geographic and host taxonomic) that make the characterization of parasite diversity challenging. The relative proportions of *Haemoproteus*, *Plasmodium* and *Leucocytozoon* vary in part due to vector habitat preferences and also due to sampling bias. However, there is no apparent phylogenetic structuring across regions. The authors argue that broad sampling across regions and hosts essential in order to understand parasite diversity in Africa.

Also in Africa, Jones *et al.* (2018) investigated the roles of host heterogeneity and host–parasite interactions in host community assemblages, and evaluated the explanatory power of four hypotheses: the host-neutral hypothesis, the super-spreader hypothesis, the host specialist hypothesis and the heterogeneity hypothesis. The host-neutral and host-specialist hypotheses received the most support in explaining parasite prevalence by lineage. The host-neutral hypothesis stipulates that net host abundance drives overall levels of parasite prevalence, and the host-specialist hypothesis purports that it is strong relationships among single host/parasite associations that drive levels of prevalence. More specifically, parasite prevalence was associated with increases or decreases of variation in host and/or parasitic taxonomic levels. *Leucocytozoon* seemed to have the most impact and its abundance influenced prevalence at various taxonomic levels within heterogeneous host communities. *Plasmodium*, in contrast, had the least impact.

In a large study focusing on a single but diverse family of birds (manakins), Fecchio *et al.* (2017a) investigated factors that shape diversity and host and geographic distribution of parasite lineages

within 30 host species throughout the Neotropics. Despite evaluating the potential impact of factors that are thought to be critical to host/parasite dynamics, the authors found no clear drivers of lineage turnover, suggesting instead that host switching in manakins is not constrained at the broad scale. The authors conclude by suggesting that research about vector specificity and transmission would determine whether parasite lineage diversity is driven by the diversity of definitive or intermediate hosts. In a follow-up study focusing on mosquitoes, Fecchio *et al.* (2017b) found that the prevalence of *Plasmodium* was only tied to mosquito abundance and not tied to host and environmental factors.

A common thread among many of the studies included here is that anthropogenic changes to landscapes have a marked effect on diversity and community composition. Turcotte *et al.* (2017) addressed this explicitly by examining the environmental predictors of parasite prevalence across human-modified habitats in a population of tree swallows that is in documented decline. The authors examined the potential for environmental stressors, using three habitats that varied in their level of anthropogenic influence, to amplify effects of parasitism. The study confirms that infection occurs in the breeding season because the authors found that both adults and nestlings were infected, and found that there are associations between landscape composition and parasite prevalence. The results suggest that anthropogenic changes to the landscape can directly influence parasite prevalence, likely *via* effects on vector abundance and distribution.

Conclusions

Three key themes emerge from this diverse collection of papers. The first is that the known diversity of haemosporidian lineages is ever-increasing, but that broad and thorough sampling of hosts is required in order to begin to fully understand these complex systems. The second is that the drivers of diversity in these systems are likely to be interacting and complex, and may differ geographically, between communities and possibly between host families. The third is that vectors are likely to play a key role in the diversity and distribution of parasites that we see in avian hosts. We know remarkably little about the role of vectors in driving haemosporidian distribution (Žięgtytė and Valkiūnas, 2014), and are only beginning to address questions such as which vector species can act as competent hosts for these parasites; whether these relationships are lineage-specific; and whether vector host choice may drive infection patterns. From our review of the included papers, it is clear that ecological parasitologists will continue to investigate and contribute to this ever-expanding field, and that avian haemosporidian research will be vital in advancing our understanding of host–parasite systems.

Indeed, over the last year, several papers have reintroduced the theme that avian haemosporidian parasites can be used once again as a model for understanding the dynamics of host/parasite systems more broadly. This is due partly to their diversity and partly to their facility in laboratory settings. In a broad review, Rivero and Gandon (2018) trace the history of the importance of avian haemosporidians to our understanding of human malaria parasites, which waned with the establishment of rodent malaria systems, but has risen to prominence once again because the diversity of avian haemosporidians provides countless ways in which to assess adaptation and evolution. Further, genomic resources are rapidly increasing for avian haemosporidians (see Barrow *et al.*, 2019), and these types of tools are shedding light on how avian malaria parasites, like human malaria parasites, have been so evolutionarily successful (Böhme *et al.*, 2018).

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