



Contents lists available at ScienceDirect

International Journal for Parasitology: Parasites and Wildlife

journal homepage: www.elsevier.com/locate/ijppaw

Invited review

Manifold habitat effects on the prevalence and diversity of avian blood parasites

Ravinder N.M. Sehgal

Dept. of Biology, San Francisco State University, 1600 Holloway Ave., San Francisco, CA, 94132, USA

ARTICLE INFO

Article history:

Received 1 July 2015

Received in revised form

30 August 2015

Accepted 5 September 2015

Keywords:

Avian hematozoa

Haemosporidia

Plasmodium

Anthropogenic change

Deforestation

Habitat effects

ABSTRACT

Habitats are rapidly changing across the planet and the consequences will have major and long-lasting effects on wildlife and their parasites. Birds harbor many types of blood parasites, but because of their relatively high prevalence and ease of diagnosis, it is the haemosporidians – *Plasmodium*, *Haemoproteus*, and *Leucocytozoon* – that are the best studied in terms of ecology and evolution. For parasite transmission to occur, environmental conditions must be permissive, and given the many constraints on the competency of parasites, vectors and hosts, it is rather remarkable that these parasites are so prevalent and successful. Over the last decade, a rapidly growing body of literature has begun to clarify how environmental factors affect birds and the insects that vector their hematozoan parasites. Moreover, several studies have modeled how anthropogenic effects such as global climate change, deforestation and urbanization will impact the dynamics of parasite transmission. This review highlights recent research that impacts our understanding of how habitat and environmental changes can affect the distribution, diversity, prevalence and parasitemia of these avian blood parasites. Given the importance of environmental factors on transmission, it remains essential that researchers studying avian hematozoa document abiotic factors such as temperature, moisture and landscape elements. Ultimately, this continued research has the potential to inform conservation policies and help avert the loss of bird species and threatened habitats.

© 2015 The Author. Published by Elsevier Ltd on behalf of Australian Society for Parasitology. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Contents

1. Introduction	00
2. Habitat effects on avian hematozoa in the hosts	00
2.1. Habitat effects on avian hematozoa: birds	00
2.1.1. Habitat: prevalence and parasitemia	00
2.1.2. Habitat: distribution and diversity	00
2.1.3. Habitat: parasite evolution	00
2.2. Habitat effects on avian hematozoa: insect vectors	00
3. Migration, habitat and blood parasites	00
4. Habitat and host specificity	00
5. Anthropogenic changes and avian blood parasites	00
5.1. Global climate change	00
5.2. Deforestation	00
5.3. Urbanization	00
6. Conclusion	00
Conflict of interest	00
Acknowledgments	00
References	00

E-mail address: sehgal@sfsu.edu.<http://dx.doi.org/10.1016/j.ijppaw.2015.09.001>2213-2244/© 2015 The Author. Published by Elsevier Ltd on behalf of Australian Society for Parasitology. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Please cite this article in press as: Sehgal, R.N.M., Manifold habitat effects on the prevalence and diversity of avian blood parasites, International Journal for Parasitology: Parasites and Wildlife (2015), <http://dx.doi.org/10.1016/j.ijppaw.2015.09.001>

1. Introduction

The habitat of a living organism can broadly be defined as the ecological and environmental space that supports its existence. What constitutes a habitat depends on the species in question, but all the external biotic and abiotic factors that influence the life of the organism can be considered as components of habitat. Presently, climate change, deforestation, urbanization, desertification, invasive species and the expanding human population are leading to irrevocable effects on the habitats of wildlife and their pathogens. The field of wildlife disease ecology examines how these rapid changes will affect populations of animals worldwide. In particular, there has been much recent research centered on the effects of parasitic diseases on avian populations, in part because they harbor a tremendous diversity of parasites, and because they are relatively easy to study. However despite much progress, it is now becoming clear that the systems are exceedingly complex. This review sets out to highlight recent research that is making a major impact on our understanding of how birds, and the insect vectors that transmit their blood parasites are affected by the environments they inhabit.

Of the avian blood parasites, the haemosporidians are the most commonly studied in regards to ecology and evolution; this review will accordingly focus on this group. The highly diverse order Haemosporidia includes the genera *Plasmodium*, *Haemoproteus*, and *Leucocytozoon* (Atkinson et al., 2009). Another genus in the order, *Fallisia*, is much more rare, and in fact there are no recent published accounts of this parasite in birds (Valkiūnas, 2005). The genus *Plasmodium*, as in mammals, is the cause of the disease malaria in birds. *Plasmodium* is transmitted by many species of mosquitoes (Culicidae) (for a review of insect vectors that transmit haemosporidian parasites see Santiago-Alarcón et al., 2012). *Haemoproteus* differs in that it is transmitted by hippoboscids and ceratopogonid flies. *Leucocytozoon* is vectored by simuliid blackflies, or for the subgenus *Akiba*, ceratopogonids. Trypanosomes, unrelated to the haemosporidians, are also widely encountered in avian blood and can be transmitted by several insect species, most typically through the ingestion of the vector (Svobodová et al., 2015). Nematode microfilariae are also common in bird blood (Sehgal et al., 2001; Silveira et al., 2010). Other vector-borne blood parasites of birds include other sporozoan parasites of the genera *Hepatozoon*, *Babesia* and *Atoxoplasma* (Valkiūnas, 2005). Many of the parasites that infect birds have their counterparts in humans but since birds are not affected by socioeconomic factors, they provide an unbiased model system for how habitats can affect the transmission of parasitic diseases.

Since the turn of the 21st century, new methods have emerged to study how blood parasites are affected by their environment. First and foremost, the use of the polymerase chain reaction (PCR) and DNA sequencing has transformed how researchers detect, and classify these eukaryotic organisms. It is becoming clear that avian blood parasites, including the haemosporidians, trypanosomes and microfilariae are surprisingly diverse (Bensch et al., 2009; Svobodova et al., 2015; Sehgal et al., 2005b). Among the haemosporidian genera, the cytochrome *b* gene has most commonly been used as a “bar code” (Bensch et al., 2000). However recently, with the advent of high throughput DNA sequencing, it is apparent that the diversity of the avian haemosporidian order is even higher than previously thought. For example, presently it is known that the malaria genes *trap*, *msp-1*, *ama-1* and *chitinase* are more highly variable than cytochrome *b* when used for detecting haemosporidian diversity (Jarvi et al., 2008; Hellgren et al., 2013a; Lauron et al., 2014; García-Longoria et al., 2014). The publication of new hematozoan genomes and transcriptomes will eventually help clarify the confounding species concepts for these parasites

(Outlaw and Ricklefs, 2014; Perkins, 2014). Nevertheless, a synthesis of both microscopy and molecular approaches is the safest means to confirm infections of blood parasites from both avian and insect hosts. This is because PCR has been shown to selectively amplify certain lineages in mixed infections (Zehindjiev et al., 2012), and it cannot distinguish among the various life stages of the parasite (Valkiūnas et al., 2009). This can lead to misleading diagnoses because a positive PCR product from either avian blood or an insect does not necessarily mean that the parasite completes development in that particular host (Valkiūnas et al., 2009, 2014). On the other hand, it is also clear that some parasites can be cryptic and indistinguishable using solely microscopy (Sehgal et al., 2006; Valkiūnas et al., 2010; Palinauskas et al., 2015). In addition, there have been some efforts to use immunological methods for the detection of avian haemosporidians (Jarvi et al., 2002; Ito and Gotanda, 2005; Palmer et al., 2013), but the development of specific antibodies to avian blood parasite proteins would be a major asset for immunohistochemistry and cell sorting approaches.

Advances have also been made in how scientists measure and model environmental effects on disease transmission. With human infectious diseases, mathematical modeling has been useful for predicting and controlling epidemics (for a review see Heesterbeek et al., 2015). In addition, climate and habitats can be monitored at the microclimate scale with data loggers (da Cunha, 2015; Paaijmans et al., 2010), at the global scale with remote sensing and satellites (Hay et al., 2013), and more recently at the landscape level with drones (Fornace et al., 2014) and mobile phones (Wesolowski et al., 2012). As these methods and technologies develop, they will become increasingly useful to scientists studying the epizootiology of avian blood parasites. Some initial studies using these approaches with avian hematozoa are described below.

2. Habitat effects on avian hematozoa in the hosts

2.1. Habitat effects on avian hematozoa: birds

For parasite transmission to occur, the parasite must be in the correct life stage, the bird must be susceptible to the parasite, the vector must be present and competent, and the environment must be permissive (Fig. 1). Since birds are warm blooded, they serve as a constant and relatively safe environment for the blood parasites that have evolved to evade the host's immune system. On the other hand, during their life stages in their ectothermic insect vectors, parasites are subject to changes in temperature that can affect their development (Paaijmans et al., 2010, 2013). Thus when studying habitat effects on parasites, it is primarily the insect stages that will influence the prevalence and distribution. However, since scientists have traditionally focused on sampling birds, most of the data concerning the occurrence of avian blood parasites has been from wild-caught birds. This can lead to potential problems regarding the true patterns of distribution, since birds can fly long distances, and thus obscure the precise location of parasite transmission. In addition, methods and timing of bird capture can also greatly influence the observed prevalence and parasitemia of blood parasites (Valkiūnas, 1998; Holmstad et al., 2003; Valkiūnas, 2005). However, given these caveats, much has been learned from blood samples about how habitat can affect the prevalence, parasitemia, distribution, diversity and evolution of avian blood parasites.

2.1.1. Habitat: prevalence and parasitemia

Avian haemosporidians have been detected and studied on all the continents besides Antarctica, and prevalence can vary widely depending on the habitat and the bird species (Valkiūnas, 2005). Although numerous factors can affect the prevalence and parasitemia of blood parasites in birds, the habitat of the birds plays an

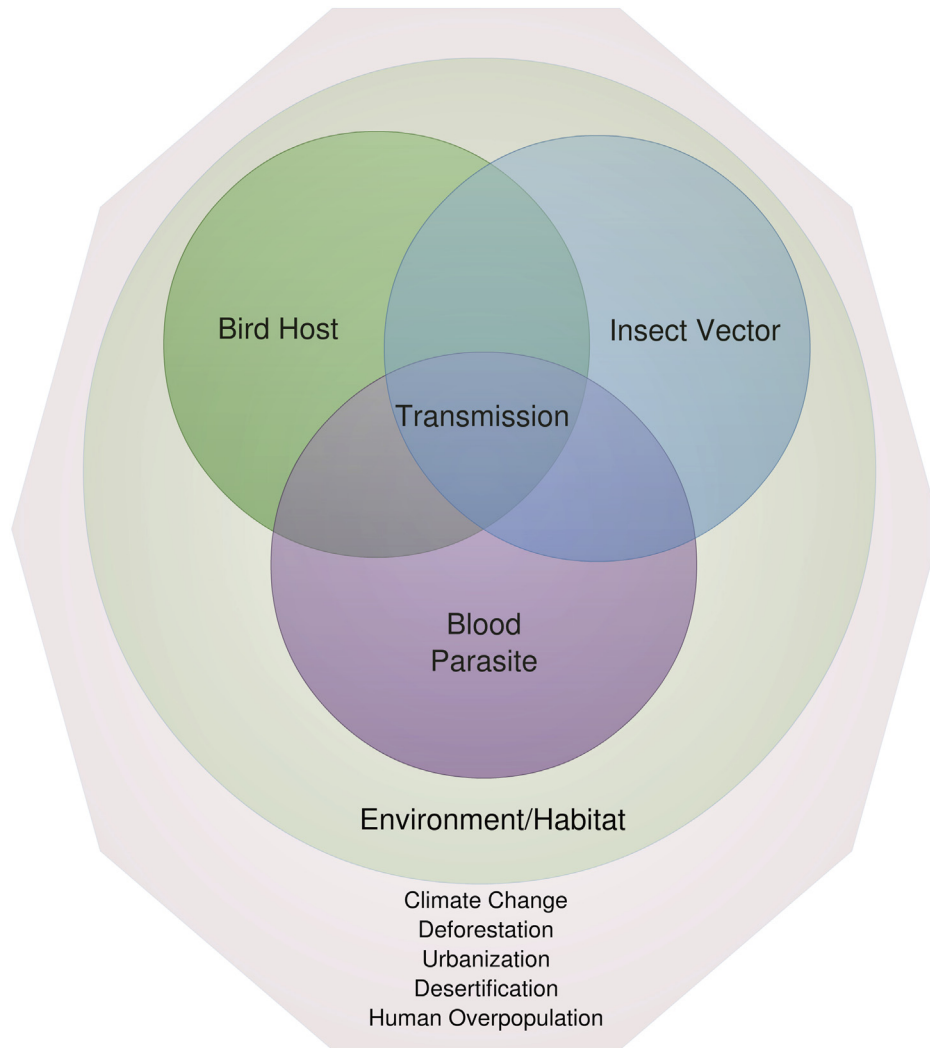


Fig. 1. Diagram illustrating how conditions of the vector, parasite, host and habitat must all be permissive for pathogen transmission to occur. The outer layer depicts some factors that are currently causing rapid environmental change, which will affect host–parasite dynamics.

important role. Several studies have observed patterns of prevalence at the local scale, shedding light on how widely parasite prevalence can vary, even within the space of a few kilometers. For example, Wood et al. (2007) described how parasite prevalence in blue tits varied between 10% and 60% in the 385 ha of Wytham Woods near Oxford, England. One habitat feature, distance from the river, served as a good positive predictor for combined *Plasmodium* prevalence (Wood et al., 2007). At the same site, parasitemia, as determined by quantitative PCR, could be correlated with the altitude, and distance from the woodland edge (Knowles et al., 2010). Proximity to water bodies was also a major predictor for avian malaria prevalence in studies from Costa Rica (Mendenhall et al., 2013) and Latvia (Krama et al., 2015). These works reveal that, as with malaria in humans (Paaijmans and Thomas, 2011), the infection status of birds can vary with the location of sampling and be influenced by landscape characters.

On the larger scale, across multiple habitats or landscapes, there have been numerous reports of the prevalence of haemosporidians in wild birds. Although some evidence suggest that the overall prevalence of parasites in a bird community is influenced more by the host composition than the geography (Scordato and Kardish, 2014), habitat characters can still be important in predicting the prevalence of blood parasites. In Africa, our work has shown that

remote sensing and modeling are useful in the development of predictive maps for avian blood parasites (Sehgal, 2011). From blood samples collected from 28 sites across Central and Western Africa, temperature proved to be the strongest positive predictor for *Plasmodium* prevalence in the olive sunbird (*Cyanomitra olivacea*), but for avian trypanosomes, surface moisture appeared to be more important (Sehgal, 2011). Similarly, in a recent study from Tenerife, Canary Islands, a temperature variable, minimum temperature of the coldest month, proved to be the best predictor for avian malaria prevalence in the Berthelot's pipit (*Anthus berthelotii*) (birds in locations with a higher minimum temperature were more likely to be infected) (González-Quevedo et al., 2014).

In the same vein, it is known that altitude can affect parasite prevalence, due to changes in temperature. The classic example is of the malaria parasite, *Plasmodium relictum* in threatened Hawaiian honeycreepers, where birds at low and mid-level elevations were lost due to the disease following the introduction of mosquitoes and subsequently the parasite to the islands (van Riper et al., 1986; La Pointe et al., 2012). There it was calculated that sporogonic development of *P. relictum* in the mosquito *Culex quinquefasciatus* does not occur below 13 °C (LaPointe et al., 2010) and thus prevalence in birds decreases along an altitudinal gradient (LaPointe et al., 2012). Models using a geographic information

system were used to predict how climate change would affect the transmission of avian malaria in Hawaii, and found that land use changes in combination with temperature changes would result in the likely extinction of several of the remaining honeycreeper species (Benning et al., 2002). Subsequent work has led to the description of conservation plans to mitigate the impacts of avian malaria on Hawaiian honeycreepers by modeling the management of mosquito breeding grounds and the translocation of disease-tolerant Amakihi birds (Hobbelen et al., 2012).

In a similar study in South America, monitoring haemosporidian parasites on an altitudinal gradient in the Peruvian Andes has shown that temperature and precipitation are the primary drivers of observed spatial patterns of prevalence (Jones et al., 2013). In the Andes of Ecuador, elevation and temperature proved to be the best predictors of avian haemosporidian prevalence, but *Plasmodium* was found at lower elevations than *Haemoproteus* and *Leucocytozoon* (Harrigan et al., 2014). Several other studies have also reported that *Leucocytozoon* parasites are common at higher altitudes (Haas et al., 2012; Imura et al., 2012; van Rooyen et al., 2013; Lotta et al., 2015), and latitudes (Oakgrove et al., 2014) than *Plasmodium* in birds. Murdock et al. (2013) developed a mathematical transmission model for blackfly-*Leucocytozoon* interactions at a high altitude site in the Colorado Rocky Mountains. That work surmised that *Leucocytozoon* prevalence is most affected by seasonal changes in environmental temperature that drive shifts in black fly emergence and gonotrophic cycles (Murdock et al., 2013). While these data reveal patterns of prevalence of parasites at different altitudes, more directed research will be needed to, for example, answer why *Leucocytozoon* prevalence varies in space and time. From the majority of these works, it is clear that temperature can be the major predictor for prevalence. Further experimental research is needed to determine the precise temperature constraints for the transmission of the various parasite genera, keeping in mind that each parasite species may have different requirements.

2.1.2. Habitat: distribution and diversity

The avian blood parasites, as characterized by their DNA bar codes, are exceedingly diverse. The MalAvi database for avian haemosporidian parasites currently catalogues nearly 2000 cytochrome *b* lineages from around the world (Bensch et al., 2009). From the numerous studies of haemosporidian diversity, we now know that some parasites have worldwide distributions, and others appear to be localized to specific regions and habitats. In general the genus *Plasmodium* appears to be more cosmopolitan than *Haemoproteus*, but with lower lineage diversity (Clark et al., 2014). The diversity of haemosporidian parasites seems to mirror that of their avian hosts, but sampling bias, with relatively more lineage information from Europe and North America than other continents, may distort overall results (Clark et al., 2014). Indeed, Svensson-Coelho et al. (2014) found that although there are nearly twice as many bird species in Ecuador as compared to North America, the difference in haemosporidian parasite diversity was just 1.2 times greater. More global comparisons of lineage diversity would be useful, and in particular, based on the lineages currently available in MalAvi, more sampling could be done from East and Northeast Asia, Western Australia, Central and North Africa and the Amazon basin.

It is assumed that the ecological determinants of parasite diversity should be the same as those that affect parasite prevalence. For example, temperature is important for predicting prevalence and a recent study has shown that it is also important in predicting distribution and diversity (Pérez-Rodríguez et al., 2013). However, in that study, other variables came into play: landscape features, rainfall and other geographical effects contributed to models predicting parasite diversity, and the models differed for each of the three haemosporidian genera (Pérez-Rodríguez et al., 2013). In

order to better understand environmental effects on parasite diversity, the next steps will be to develop models to generate maps of the individual species/lineages of the avian blood parasites, as has been done with *Plasmodium* species infecting humans (Dalrymple et al., 2015). In addition, the majority of studies linking habitat and parasite prevalence and/or diversity have largely been correlational, and the field would benefit from more experimental research.

2.1.3. Habitat: parasite evolution

How did all these haemosporidian parasites come to be, and why are there so many distinct lineages? A couple recent studies have examined the evolutionary processes of these parasites, and confirmed that host shifting plays a major role in speciation. Our work in Africa revealed that *Plasmodium* species infecting sunbirds likely originated in East Africa, and that vicariant events played a role in *Plasmodium* diversification (Lauron et al., 2015). The work suggests that *Plasmodium* parasites diversify by taxon pulses; episodes of vicariant events alternating with episodes of dispersal events (Lauron et al., 2015). Ricklefs et al. (2014) found similar results with North and Central American haemosporidian parasites: that speciation is principally allopatric and that host–parasite coevolution occurs following host range expansion. Secondary sympatry then results in the local shifting of parasite lineages across hosts. Both of these works exemplify that geography plays a major role in the diversification and distribution of avian haemosporidian parasites, although the underlying mechanisms of how speciation occurs following host shifting remain unclear. Clearly the insect vectors play a major role in the evolutionary process, given that they are the definitive hosts of haemosporidian parasites, yet relatively little is known about how the distribution of insects affects the diversity of these parasites.

2.2. Habitat effects on avian hematozoa: insect vectors

The potential for vector populations to transmit parasites is sensitive to the habitat and can be summarized as a basic reproductive number, R_0 , equal to the number of additional cases that arise from one case of the pathogen introduced into a susceptible host population. R_0 is defined by the following expression: $R_0 = ma^2bce^{-\mu\tau}/\mu\gamma$ (Macdonald, 1952; Smith et al., 2012), where m is the density of vectors in relation to hosts, a is the biting rate of vectors, b and c are coefficients of transmission to vertebrates and vectors, respectively, μ is the vector mortality rate, τ is the extrinsic incubation (EIP) of the infection in vectors and γ is the rate of recovery of the host from infection. Most of the components of R_0 are sensitive to temperature; especially biting, mortality, and parasite incubation rates. Thus the habitat of the vector is significant, and slight changes in temperature and other factors affecting vector competency can greatly affect parasite prevalence.

Some recent work has explored how landscape ecology affects the vectors of avian blood parasites. For example, a study of seven mosquito species from Spanish wetlands, including several known to transmit avian malaria, showed that remote sensing data was useful in monitoring mosquito abundance and distribution, and that environmental factors such as rainfall and NDVI (a general measure of greenness) are good predictors of mosquito abundance and distribution (Roiz et al., 2015). From wetlands of South Africa, it was observed that rainfall, mosquito prevalence, and season were the most influential vector-related factors on the prevalence of avian malaria in birds of the family Ploceidae (Okanga et al., 2013). In Panama, one mosquito species, *Aedeomyia squamipennis*, harbors *Plasmodium* infections year-round, while the population of another, *Culex ocosoa*, only expands during the rainy season, and is thus likely a less important vector (Loaiza and Miller, 2013). There are

many potential vectors of avian malaria (Santiago-Alarcón et al., 2012), and each mosquito species could potentially transmit several *Plasmodium* lineages (Gager et al., 2008; Njabo et al., 2011; Medeiros et al., 2013). Thus, it was generally believed that mosquitoes are catholic feeders and do not significantly contribute to the observed avian host specificity observed with some parasite lineages. However, a recent study from California suggests that not all *Culex* mosquito species are equally infective for *Plasmodium*, implying that mosquitoes can influence *Plasmodium* specificity, diversity and prevalence in certain locations (Carlson et al., 2015). In studies of insect vectors, trapping methods can also affect estimates of vector abundance and parasite prevalence (Carlson et al., 2015). It must be noted again that the molecular detection of a parasite in an insect does not necessarily indicate that the insect is capable of transmitting the parasite (Valkiūnas et al., 2013). Experimental infections are generally required to verify that sporozoites from mosquito salivary glands successfully infect birds. However this type of work is particularly challenging and much more research is needed to determine precisely how seasonality, rainfall, temperatures, and landscape features can affect the mosquito vectors and transmission of avian malaria.

Regarding biting midges (*Culicoides*) Santiago-Alarcón et al. (2013) showed that species assemblages are highly seasonal, with certain species dominating the community in certain months of the year. The majority of species of *Culicoides* were generalists, capable of feeding on birds and mammals including humans, and the abundance of vectors correlated with prevalence of *Haemoproteus* infections in blackcaps (Santiago-Alarcón et al., 2013). Similarly, with blackflies and *Leucocytozoon*, seasonality of the vectors can affect parasite transmission (Murdock et al., 2013), but since simuliids rely on fast flowing streams for their larval stages, infections of *Leucocytozoon* can only occur in favorable habitats (Valkiūnas, 2005; Sehgal et al., 2005a). Blackflies can also transmit trypanosomes and co-infections of trypanosomes and *Leucocytozoon* appear to be common: thus unrelated parasites that share the same vector can exhibit the same distribution patterns in their avian hosts (Oakgrove et al., 2014; Svobodová et al., 2015). In Alaska temperature, precipitation and tree cover were the best predictors for co-infections of *Trypanosoma* and *Leucocytozoon* (Oakgrove et al., 2014). But many questions remain open regarding how the distribution of vectors affects parasite diversity and prevalence. For example it is still unclear how vector abundance and community composition specifically affect the species diversity of avian blood parasites. It will be important to determine the current effects of vectors on the distribution of avian hematozoa so as to better understand how anthropogenic changes will affect bird pathogens in the future.

3. Migration, habitat and blood parasites

Since the prevalence of blood parasites can vary widely throughout the world, it is compelling to speculate that bird migration may have, in part, evolved as a means to escape infections (Møller and Szép, 2010; Altizer et al., 2011). There is some evidence to support this hypothesis with avian haemosporidians. For example, the garden warbler, *Sylvia borin*, appears to be infected by a higher diversity of avian malaria parasites at their wintering sites in Africa compared to breeding sites in Europe and during migration (Hellgren et al., 2013b). Also, migratory birds harbor more lineages of *Leucocytozoon* parasites than resident species (Jenkins et al., 2012). One recent study described the parasites of Eleonora's falcon, (*Falco eleonora*), a long-distance migratory raptor that breeds on small islands in the Mediterranean and overwinters in Madagascar (Gutiérrez-López et al., 2015). From the breeding sites in marine environments, no nestlings were infected

with blood parasites, but adults at the same sites were infected with the three common haemosporidian genera (Gutiérrez-López et al., 2015). Haemosporidian prevalence is generally found to be low in marine birds (Jovani et al., 2001) and the authors conjecture that the Eleonora's falcon might have chosen these particular breeding grounds since they lack the vectors responsible for transmitting parasites. Similar results have been shown with shorebirds, where when comparing prevalences of marine and freshwater habitats, both *Haemoproteus* and *Plasmodium* infections were more common in the freshwater environments (Mendes et al., 2005). Likewise, it appears that only one *Plasmodium* lineage is transmitted in Alaska, where many migratory birds breed, but the same birds are exposed to many *Plasmodium* lineages on their wintering grounds (Loiseau et al., 2012a; Oakgrove et al., 2014). Birds that fly to parasite poor habitats may have an advantage over non-migratory tropical birds that are continuously exposed to a high diversity of infectious diseases.

Bird migration is also relevant to this field because birds can introduce parasites to habitats where they were previously not found, and thus shape the world-wide distributions of parasites (Altizer et al., 2011). For example in both the Hawaiian and Galapagos archipelagos, it is believed that bird migration brought avian malaria to the islands following the introduction of competent mosquitoes (LaPointe et al., 2012; Levin et al., 2013).

Clearly insects cannot fly as far as birds, but the movement of insects can still impact the distribution avian blood parasites. For example, in addition to rising temperatures, avian malaria in Hawaii may also be affected by increasing movements of mosquitoes (Freed and Cann, 2013). One study at a Japanese zoological garden cleverly calculated the mosquito flying distances by monitoring their blood meals and avian malaria lineages from caged animals (Ejiri et al., 2011). Typical movements for blood fed females were about 40 m from their hosts, but could range up to 350 m (Ejiri et al., 2011). Although mosquitoes are known to travel short and sometimes, with wind, long distances (Service, 1997), more research is needed to determine how habitats can influence the movement of vectors, which can in turn influence the prevalence and diversity of bird pathogens.

4. Habitat and host specificity

Some pathogens affect only one species; others are generalists and can readily spread to naïve hosts through the process of host switching. These generalists thus represent an important pathway for emerging diseases. To help clarify how habitat can affect the host specificity of avian malaria, we tested measures of host specificity of *Plasmodium* parasites in three African habitats: the lowland forests of Cameroon, the highland forests of Tanzania, and the Fynbos habitat of South Africa (Loiseau et al., 2012b). The Cameroon samples were collected from pristine forests characterized by low levels of environmental change. In contrast, the sampling areas of the Tanzania highlands and the Fynbos experience greater fluctuations in seasonal temperature and rainfall. In total, from all sites and 25 bird species (1364 individuals), we found 34 *Plasmodium* lineages. To obtain a measure of both the diversity of host species and the taxonomic distance between these species, we used a modified version of the host specificity index S_{TD} (Poulin and Mouillot, 2003; Hellgren et al., 2009). These S_{TD} values can be associated with the phylogenetic relationships of the lineages (Loiseau et al., 2012b). A linear mixed effects model analysis indicated that the rainforests differed from the two other habitat types with respect to S_{TD} , even when controlling for lineage. Parasites tended to be more host-specific in the lowland rainforest habitats. In the Fynbos and highland forests, we found a higher prevalence of generalists. Thus habitat type appears to play a role in the

evolutionary strategy of parasites and can shape whether parasites are apt to be generalists or specialists.

A recent publication has reported that geographical barriers can affect the distribution of specialist vs. generalist parasites. Avian haemosporidians were sampled from Northwest Iberia and Northwest Africa, and it was found that the Mediterranean Sea, and likely the Strait of Gibraltar, seems to limit the movement of specialist parasites (Mata et al., 2015). The authors hypothesize that abundant haemosporidian parasites with large geographic ranges are more likely to cross biogeographic barriers and move between different bird populations than less common parasites with restricted geographic ranges, and that host specialists cannot colonize different areas unless their host species are abundant on both sides of the barrier (Drovetski et al., 2014; Mata et al., 2015). Using a similar approach in an island system, it was recently reported that in southern Melanesia *Plasmodium* parasites are largely generalists, and exhibited isolation-by-distance effects, with a significant amount of genetic variation distributed among islands, but insignificant amounts among host species and families (Olsson-Pons et al., 2015). These results together submit that geography and the abiotic environment can influence the distribution of specialist and generalist parasites. Further research will be needed to clarify the specific host–vector–parasite interactions that give rise to the observed patterns, but some work has begun to determine the molecular mechanisms that cause some parasites to be host specific in birds (Martinez et al., 2013; Lauron et al., 2014). With bioinformatics and the analysis of new parasite transcriptomes and genomes, this field will likely advance quickly.

5. Anthropogenic changes and avian blood parasites

Underlying the rapid changes taking place on the planet is the ever-expanding human population (Stephenson et al., 2010). With the human population expected to reach more than nine billion by 2050 (Bongaarts, 2009), we can expect more anthropogenic environmental changes, which will undoubtedly affect birds and their parasites. Primarily for the sake of conservation, ecologists, ornithologists and parasitologists are working to understand how these rapid changes will affect the prevalence and diversity of avian blood parasites. Since it was suggested that avian malaria had severely impacted bird populations of Hawaii (Warner, 1968; van Riper et al., 1986), research has been spawned worldwide to determine how these and other populations of birds may be affected in the future by avian parasites. Although the field is changing rapidly, presented below is some seminal research that describes how anthropogenic environmental changes are affecting avian blood parasites.

5.1. Global climate change

The increasing temperatures associated with climate change are expected to lead to altered distributions of arthropod vectors, which may undergo general range expansions or longer breeding seasons. Also, as mentioned earlier, vector-borne parasites may directly benefit from elevated temperatures, which can be conducive to parasite reproduction. Distributions of bird populations will also change and together, these changes will alter parasite transmission. Although somewhat controversial (Gething et al., 2010), climate change is expected to lead to altered distributions of malaria, both in humans and in birds. Avian malaria may expand to more northerly and southerly latitudes, higher elevations and, in general, become more prevalent. For example, an analysis by Garamszegi (2011) followed the literature of avian malaria infections over 70 years and found that *Plasmodium* prevalence has increased with increasing global temperatures. The last two decades showed the greatest acceleration in prevalence increases, and

the strongest effects were seen in Europe and Africa (Garamszegi, 2011). More recent literature has shown that the effects of climate change could vary with the parasite in question, so that in a given locality, parasite diversity could either increase or decrease, or potentially virulent parasites may substitute for the original taxa (Pérez-Rodríguez et al., 2014).

Our work has shown that avian malaria is transmitted in Alaska, and that temperature changes associated with climate change will extend the northern limit of malaria transmission (Loiseau et al., 2012a). Although sample size was limited, our models – based on the IPCC 4th Assessment A1 scenario – were among the first to show that temperature changes may lead to a latitudinal shift in avian malaria distributions. A subsequent study found very similar results; that climate change will also affect the transmission distributions of avian malaria in France (Loiseau et al., 2013).

The island of Hawaii is currently the best-studied location regarding how climate change will affect avian malaria along elevational gradients. Threatened native Hawaiian birds presently inhabit the higher altitude regions of the islands that lack avian malaria (LaPointe et al., 2012). Given that temperatures and rainfall patterns will change in the future, Liao et al. (2015) modeled future malaria risk and native bird populations. Implementing three different IPCC projection scenarios, they concluded that climate change will cause significant decreases in the abundance and diversity of the threatened bird communities. At all elevations, vector abundance will increase with temperatures and rainfall, thus increasing the likelihood of *Plasmodium* transmission (Liao et al., 2015). Zamora-Vilchis et al. (2012) reported similar results in Australia, which has greater parasite and vector diversity than Hawaii. These trends will largely be applicable to avian populations worldwide but climate change will certainly have non-linear effects on infectious diseases, with not all regions experiencing higher pathogen prevalence (Lafferty, 2009; Gallana et al., 2013).

5.2. Deforestation

Even more immediate than climate change is the impact that large-scale deforestation may have on disease emergence. The global rate of tropical deforestation is increasing rapidly (Hansen et al., 2013; Lewis et al., 2015) and rates of deforestation in parts of Africa are near 1% per year (Blaser, 2011). Deforestation is also increasing in temperate regions, due to logging in North America, Russia and Europe (FAO, 2012). Deforestation can transform whole ecosystems, and thus affect disease transmission (Taylor, 1997), yet the field of deforestation disease ecology is represented by few published scientific studies relative to such a globally pervasive threat (Sehgal, 2010).

There have been many examples of the direct effects of deforestation on human pathogens. First, it is clear that habitat alteration can affect the prevalence and incidence of human malaria (Stresman, 2010). The effects of deforestation on anopheline mosquitoes, the vectors of human malaria, are complex, and can be influenced by the nature of agricultural development and specific local ecological characteristics (Afrane et al., 2012). Increased levels of sunlight, as associated with open spaces, and increased plant-held water, have been correlated with increased anopheline mosquito densities (Yasuoka and Levins, 2007; Yanoviak et al., 2006). In addition, studies have shown that forest clearing increased the observed human feeding rate of *Anopheles darlingi*, the major vector of *Plasmodium falciparum* in Peru (Vittor et al., 2006, 2009). Moreover, deforestation in Cameroon caused the introduction of *Anopheles gambiae* into a habitat that was previously dominated by *An. moucheti*, which is less apt to feed on humans. Afrane et al. (2008) found that deforestation nearly doubled the vectorial capacity in western Kenyan highlands.

Less is known about how deforestation will affect avian parasitic diseases (Sehgal, 2010). In Ghana, we reported a decrease in prevalence and intensity of parasitemia of malaria in the Olive sunbird (*Cyanomitra olivacea*) associated with increased forest disturbance (Loiseau et al., 2010). When comparing pristine forests to deforested areas in Cameroon, results showed that the prevalence of the genus *Plasmodium* in birds was higher in the intact, forested areas (Bonneaud et al., 2009). Similar results were found with *Haemoproteus* in forest fragments in Australia (Laurance et al., 2013). With further work in Cameroon, we studied the diversity, prevalence and distribution of *Plasmodium* and *Haemoproteus* in two widespread species of African rainforest birds, the Yellow-whiskered greenbul (*Andropadus latirostris*, N = 411) and the Olive sunbird (N = 440) from nine paired sites (disturbed vs. undisturbed habitats). Our results revealed that different transmission patterns distinguished disturbed from undisturbed areas. In deforested areas, the prevalence of some parasite species increased, and others decreased, even among closely related strains of avian malaria (Chasar et al., 2009). Thus, although when grouped together the genera of haemosporidian parasites appeared to be more prevalent in intact rainforests, when studied separately, the different species of parasites responded differently to forest fragmentation.

In Costa Rica our work has begun to address how agriculture can affect the prevalence of avian malaria. There are two general strategies with regard to balancing conservation and agricultural land use: a “land sparing” approach involves large-scale nature reserves, and a “land sharing” approach promotes agriculture supporting wildlife through fine-scale conservation. Using a theoretical landscape simulation approach, we found that, of the two strategies, land sharing mitigates the prevalence of malaria more effectively (Mendenhall et al., 2013). In addition, with the lineage of *Plasmodium* found in the orange-billed nightingale-thrushes (*Catharus aurantiirostris*) of the system, field studies confirmed our models; that the highest prevalence was observed in the smallest forest patches and most deforested agricultural plots (Mendenhall et al., 2013).

Less is known about how the vectors of avian blood parasites are affected by deforestation. A recent study in New Zealand documented mosquito diversity and avian malaria prevalence at forest interior and forest edge sites. Although malaria prevalence in silvereyes (*Zosterops lateralis*) did not differ significantly among the sites, the authors found that introduced mosquitoes (*C. quinquefasciatus*) were not found in the forest interiors, but native mosquitoes were found in both habitats (Gudex-Cross et al., 2015). More work is needed in this system to ascertain the vector responsible for transmission, but the results are an important step in examining the distributions of disease vectors with regard to deforestation.

5.3. Urbanization

More than half of humans now live in cities, and future human population growth will happen primarily in urban environments (Eckert and Kohler, 2014). How will this trend affect birds and their infectious diseases? This topic is understudied, but one recent work has shown that trace metals associated with urban environments accumulate in birds and may affect their susceptibility to infections (Bichet et al., 2014). The authors of that study found that avian malaria in house sparrows was positively associated with lead concentrations found in the feathers. Pollution may in this case impair the bird's immune system, making them more prone to infections. On the other hand, urban and arid environments may hinder the development of competent vectors, and as a consequence reduce the prevalence of haemosporidian parasites. How urbanization, and also the process of desertification, will affect disease transmission will be an important area of future research.

6. Conclusion

The abiotic factors associated with habitats can greatly impact the host–vector–parasite interactions within the landscape. Even though an impressive amount of data is now available regarding the habitat effects on the ecology and evolution of avian blood parasite transmission, researchers are still far from understanding how the complex interactions will be affected by anthropogenic environmental changes. It is evident that avian blood parasites can threaten bird populations and may also impact the survival of their insect vectors (Žiegytė and Valkiūnas, 2015). However, developing generalizable principles about the important habitat effects on parasite transmission is hindered by the tremendous diversity of the parasites, birds, vectors and landscapes in which they are transmitted. More basic research using experimental systems will help to steer the course of the field and develop hypotheses that could be tested in natural environments. Coordinated sampling regimes worldwide, and a greater emphasis on collecting vector data would strengthen the conceptual framework for how infectious avian diseases respond to changes in habitat. Given that the environment can affect the prevalence and diversity of parasites, and different parasites may be affected differently by habitat conditions, scientists should be encouraged to clearly document as much environmental information as possible in their research studies. We are still in the early stages of understanding the complex interactions between avian hematozoa and their hosts in light of rapid environmental change, and a concerted effort to promote research in the field could lead to policy changes that may help avert the loss of more bird species and threatened habitats.

Conflict of interest

The author declared that there is no conflict of interest.

Acknowledgments

I thank the organizers of the 2015 “Impact of Environmental Changes on Infectious Diseases” meeting in Sitges, Spain, and the editors of *International Journal of Parasitology: Parasites of Wildlife* for inviting me to submit this manuscript. I also thank two anonymous reviewers for their suggestions in improving the manuscript. I am grateful to San Francisco State University for providing me with a sabbatical, which gave me the mindset to write this review.

References

- Afrane, Y.A., Githeko, A.K., Yan, G., 2012. The ecology of *Anopheles* mosquitoes under climate change: case studies from the effects of deforestation in East African highlands. *Ann. N. Y. Acad. Sci.* 1249, 204–210.
- Afrane, Y.A., Little, T.J., Lawson, B.W., Githeko, A.K., Yan, G., 2008. Deforestation and vectorial capacity of *Anopheles gambiae* Giles mosquitoes in malaria transmission, Kenya. *Emerg. Infect. Dis.* 14 (10), 1533.
- Altizer, S., Bartel, R., Han, B.A., 2011. Animal migration and infectious disease risk. *Science* 331, 296–302.
- Atkinson, C.T., Thomas, N.J., Hunter, D.B., 2009. *Parasitic Diseases of Wild Birds*. John Wiley & Sons.
- Benning, T.L., LaPointe, D., Atkinson, C.T., Vitousek, P.M., 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. *Proc. Natl. Acad. Sci. U. S. A.* 99, 14246–14249.
- Bensch, S., Stjernman, M., Hasselquist, D., Östman, Ö., Hansson, B., Westerdahl, H., Pinheiro, R.T., 2000. Host specificity in avian blood parasites: a study of *Plasmodium* and *Haemoproteus* mitochondrial DNA amplified from birds. *Proc. Biol. Sci.* 267, 1583–1589.
- Bensch, S., Høllgren, O., Pérez-Tris, J., 2009. MalAvi: a public database of malaria parasites and related haemosporidians in avian hosts based on mitochondrial cytochrome b lineages. *Mol. Ecol. Resour.* 9, 1353–1358.
- Bichet, C., Sorci, G., Robert, A., Julliard, R., Lendvai, A.Z., Chastel, O., Garnier, S., Loiseau, C., 2014. Epidemiology of *Plasmodium relictum* infection in the house

- sparrow. *J. Parasitol.* 100, 59–65.
- Blaser, J., 2011. Status of Tropical Forest Management 2011. International Tropical Timber Organization.
- Bongaarts, J., 2009. Human population growth and the demographic transition. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 364, 2985–2990.
- Bonneaud, C., Sepil, I., Milá, B., Buermann, W., Pollinger, J., Sehgal, R.N.M., Valkiūnas, G., Iezhova, T.A., Saatchi, S., Smith, T.B., 2009. The prevalence of avian *Plasmodium* is higher in undisturbed tropical forests of Cameroon. *J. Trop. Ecol.* 25, 439–447.
- Carlson, J.S., Walther, E., Fryxell, R.T., Staley, S., Tell, L.A., Sehgal, R.N.M., Barker, C.M., Cornel, A.J., 2015. Identifying avian malaria vectors: sampling methods influence outcomes. *Parasit. Vectors* 8, 365.
- Chasar, A., Loiseau, C., Valkiūnas, G., Iezhova, T., Smith, T.B., Sehgal, R.N., 2009. Prevalence and diversity patterns of avian blood parasites in degraded African rainforest habitats. *Mol. Ecol.* 18, 4121–4133.
- Clark, N.J., Clegg, S.M., Lima, M.R., 2014. A review of global diversity in avian haemosporidians (*Plasmodium* and *Haemoproteus*: Haemosporida): new insights from molecular data. *Int. J. Parasitol.* 44, 329–338.
- da Cunha, A.R., 2015. Evaluation of measurement errors of temperature and relative humidity from HOBO data logger under different conditions of exposure to solar radiation. *Environ. Monit. Assess.* 187, 236.
- Dalrymple, U., Mappin, B., Gething, P.W., 2015. Malaria mapping: understanding the global endemicity of falciparum and vivax malaria. *BMC Med.* 13, 140.
- Drovetski, S.V., Aghayan, S.A., Mata, V.A., Lopes, R.J., Mode, N.A., Harvey, J.A., Voelker, G., 2014. Does the niche breadth or trade-off hypothesis explain the abundance-occupancy relationship in avian Haemosporidia? *Mol. Ecol.* 23, 3322–3329.
- Eckert, S., Kohler, S., 2014. Urbanization and health in developing countries: a systematic review. *World Health Popul.* 15, 7–21.
- Ejiri, H., Sato, Y., Kim, K.-S., Hara, T., Tsuda, Y., Imura, T., Murata, K., Yukawa, M., 2011. Entomological study on transmission of avian malaria parasites in a zoological garden in Japan: bloodmeal identification and detection of avian malaria parasite DNA from blood-fed mosquitoes. *J. Med. Entomol.* 48, 600–607.
- FAO, J., 2012. Global Forest Land-use Change 1990–2005. FAO forestry paper 169.
- Fornace, K.M., Drakeley, C.J., William, T., Espino, F., Cox, J., 2014. Mapping infectious disease landscapes: unmanned aerial vehicles and epidemiology. *Trends Parasitol.* 30, 514–519.
- Freed, L.A., Cann, R.L., 2013. Vector movement underlies avian malaria at upper elevation in Hawaii: implications for transmission of human malaria. *Parasitol. Res.* 112, 3887–3895.
- Gager, A.B., Del Rosario Loaiza, J., Dearborn, D.C., Bermingham, E., 2008. Do mosquitoes filter the access of *Plasmodium* cytochrome b lineages to an avian host? *Mol. Ecol.* 17, 2552–2561.
- Gallana, M., Ryser-Degiorgis, M.-P., Wahli, T., Segner, H., 2013. Climate change and infectious diseases of wildlife: altered interactions between pathogens, vectors and hosts. *Curr. Zool.* 59, 427–437.
- Garamszegi, L.Z., 2011. Climate change increases the risk of malaria in birds. *Glob. Chang. Biol.* 17, 1751–1759.
- García-Longoria, L., Hellgren, O., Bensch, S., 2014. Molecular identification of the chitinase genes in *Plasmodium relictum*. *Malar. J.* 13, 239.
- Gething, P.W., Smith, D.L., Patil, A.P., Tatem, A.J., Snow, R.W., Hay, S.I., 2010. Climate change and the global malaria recession. *Nature* 465, 342–345.
- González-Quevedo, C., Davies, R.G., Richardson, D.S., 2014. Predictors of malaria infection in a wild bird population: landscape-level analyses reveal climatic and anthropogenic factors. *J. Anim. Ecol.* 83, 1091–1102.
- Gudex-Cross, D., Barraclough, R.K., Brunton, D.H., Derraik, J.G., 2015. Mosquito communities and avian malaria prevalence in silvereyes (*Zosterops lateralis*) within Forest edge and Interior habitats in a New Zealand Regional Park. *Ecohealth*. <http://dx.doi.org/10.1007/s10393-015-1039-y>.
- Gutiérrez-López, R., Gangoso, L., Martínez-de la Puente, J., Fric, J., López-López, P., Mailleux, M., Muñoz, J., Touati, L., Samraoui, B., Figuerola, J., 2015. Low prevalence of blood parasites in a long-distance migratory raptor: the importance of host habitat. *Parasit. Vectors* 8, 189.
- Haas, M., Lukán, M., Kisková, J., Hrehová, Z., 2012. Occurrence of blood parasites and intensity of infection in *Prunella modularis* in the montane and subalpine zone in the Slovak Carpathians. *Acta Parasitol.* 57, 221–227.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R., 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342, 850–853.
- Harrigan, R.J., Sedano, R., Chasar, A.C., Chaves, J.A., Nguyen, J.T., Whitaker, A., Smith, T.B., 2014. New host and lineage diversity of avian haemosporidia in the northern Andes. *Evol. Appl.* 7, 799–811.
- Hay, S.I., Battle, K.E., Pigott, D.M., Smith, D.L., Moyes, C.L., Bhatt, S., Brownstein, J.S., Collier, N., Myers, M.F., George, D.B., Gething, P.W., 2013. Global mapping of infectious disease. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 368, 20120250.
- Heesterbeek, H., Anderson, R.M., Andreasen, V., Bansal, S., De Angelis, D., Dye, C., Eames, K.T., Edmunds, W.J., Frost, S.D., Funk, S., Hollingsworth, T.D., House, T., Isham, V., Klepac, P., Lessler, J., Lloyd-Smith, J.O., Metcalf, C.J., Mollison, D., Pellis, L., Pulliam, J.R., Roberts, M.G., Viboud, C., Isaac Newton Institute, I.D.D.C., 2015. Modeling infectious disease dynamics in the complex landscape of global health. *Science* 347, aaa4339.
- Hellgren, O., Pérez-Tris, J., Bensch, S., 2009. A jack-of-all-trades and still a master of some: prevalence and host range in avian malaria and related blood parasites. *Ecology* 90, 2840–2849.
- Hellgren, O., Kutzer, M., Bensch, S., Valkiūnas, G., Palinauskas, V., 2013a. Identification and characterization of the merozoite surface protein 1 (*mSP1*) gene in a host-generalist avian malaria parasite, *Plasmodium relictum* (lineages SGS1 and GRW4) with the use of blood transcriptome. *Malar. J.* 12, 381.
- Hellgren, O., Wood, M.J., Waldenström, J., Hasselquist, D., Ottosson, U., Stervander, M., Bensch, S., 2013b. Circannual variation in blood parasitism in a sub-Saharan migrant passerine bird, the garden warbler. *J. Evol. Biol.* 26, 1047–1059.
- Hobbelen, P.H., Samuel, M.D., LaPointe, D.A., Atkinson, C.T., 2012. Modeling future conservation of Hawaiian honeycreepers by mosquito management and translocation of disease-tolerant Amakihi. *PLoS One* 7, e49594.
- Holmstad P.R., Anwar A., Iezhova T., and Skorpung A. Standard sampling techniques underestimate prevalence of avian haematozoa in willow ptarmigan (*Lagopus lagopus*). *J. Wildl. Dis.*, 39, 354–358
- Imura, T., Suzuki, Y., Ejiri, H., Sato, Y., Ishida, K., Sumiyama, D., Murata, K., Yukawa, M., 2012. Prevalence of avian haematozoa in wild birds in a high-altitude forest in Japan. *Vet. Parasitol.* 183, 244–248.
- Ito, A., Gotanda, T., 2005. A rapid assay for detecting antibody against leucocytozoonosis in chickens with a latex agglutination test using recombinant R7 antigen. *Avian. Pathol.* 34, 15–19.
- Jarvi, S.I., Schultz, J.J., Atkinson, C.T., 2002. PCR diagnostics underestimate the prevalence of avian malaria (*Plasmodium relictum*) in experimentally-infected passerines. *J. Parasitol.* 88, 153–158.
- Jarvi, S.I., Farias, M.E., Atkinson, C.T., 2008. Genetic characterization of Hawaiian isolates of *Plasmodium relictum* reveals mixed-genotype infections. *Biol. Direct* 3, 25.
- Jenkins, T., Thomas, G.H., Hellgren, O., Owens, I.P., 2012. Migratory behavior of birds affects their coevolutionary relationship with blood parasites. *Evolution* 66, 740–751.
- Jones, M.R., Cheviron, Z.A., Carling, M.D., 2013. Spatial patterns of avian malaria prevalence in *Zonotrichia capensis* on the western slope of the Peruvian Andes. *J. Parasitol.* 99, 903–905.
- Jovani, R., Tella, J.L., Forero, M.G., Bertelotti, M., Blanco, G., Ceballos, O., Donazar, J.A., 2001. Apparent absence of blood parasites in the Patagonian seabird community: is it related to the marine environment? *Waterbirds* 430–433.
- Knowles, S.C., Wood, M.J., Alves, R., Wilkin, T.A., Bensch, S., Sheldon, B.C., 2010. Molecular epidemiology of malaria prevalence and parasitaemia in a wild bird population. *Mol. Ecol.* 20, 1062–1076.
- Krama, T., Krams, R., Cirule, D., Moore, F.R., Rantala, M.J., Krams, I.A., 2015. Intensity of haemosporidian infection of pairs positively correlates with proximity to water bodies, but negatively with host survival. *J. Ornithol* 1–10.
- Lafferty, K.D., 2009. The ecology of climate change and infectious diseases. *Ecology* 90, 888–900.
- LaPointe, D.A., Goff, M.L., Atkinson, C.T., 2010. Thermal constraints to the sporogonic development and altitudinal distribution of avian malaria *Plasmodium relictum* in Hawai'i. *J. Parasitol.* 96, 318–324.
- LaPointe, D.A., Atkinson, C.T., Samuel, M.D., 2012. Ecology and conservation biology of avian malaria. *Ann. N. Y. Acad. Sci.* 1249, 211–226.
- Laurance, S.G., Jones, D., Westcott, D., McKeown, A., Harrington, G., Hilbert, D.W., 2013. Habitat fragmentation and ecological traits influence the prevalence of avian blood parasites in a tropical rainforest landscape. *PLoS One* 8, e76227.
- Lauron, E.J., Oakgrove, K.S., Tell, L.A., Biskar, K., Roy, S.W., Sehgal, R.N., 2014. Transcriptome sequencing and analysis of *Plasmodium gallinaceum* reveals polymorphisms and selection on the apical membrane antigen-1. *Malar. J.* 13, 282.
- Lauron, E.J., Loiseau, C., Bowie, R.C., Spicer, G.S., Smith, T.B., Melo, M., Sehgal, R.N., 2015. Coevolutionary patterns and diversification of avian malaria parasites in African sunbirds (Family Nectariniidae). *Parasitology* 142, 635–647.
- Levin, I.I., Zwiars, P., Deem, S.L., Geest, E.A., Higashiguchi, J.M., Iezhova, T.A., Jiménez-Uzcátegui, G., Kim, D.H., Morton, J.P., Perlut, N.G., Renfrew, R.B., Sari, E.H., Valkiūnas, G., Parker, P.G., 2013. Multiple lineages of Avian malaria parasites (*Plasmodium*) in the Galapagos Islands and evidence for arrival via migratory birds. *Conserv. Biol.* 27, 1366–1377.
- Lewis, S.L., Edwards, D.P., Galbraith, D., 2015. Increasing human dominance of tropical forests. *Science* 349, 827–832.
- Liao, W., Elison Timm, O., Zhang, C., Atkinson, C.T., LaPointe, D.A., Samuel, M.D., 2015. Will a warmer and wetter future cause extinction of native Hawaiian Forest birds? *Glob. Chang. Biol.* <http://dx.doi.org/10.1111/gcb.13005> (in press).
- Loaiza, J.R., Miller, M.J., 2013. Seasonal pattern of avian *Plasmodium*-infected mosquitoes and implications for parasite transmission in central Panama. *Parasitol. Res.* 112, 3743–3751.
- Loiseau, C., Iezhova, T., Valkiūnas, G., Chasar, A., Hutchinson, A., Buermann, W., Smith, T.B., Sehgal, R.N., 2010. Spatial variation of haemosporidian parasite infection in African rainforest bird species. *J. Parasitol.* 96, 137–143.
- Loiseau, C., Harrigan, R.J., Cornel, A.J., Guers, S.L., Dodge, M., Marzec, T., Carlson, J.S., Seppi, B., Sehgal, R.N., 2012a. First evidence and predictions of *Plasmodium* transmission in Alaskan bird populations. *PLoS One* 7, e44729.
- Loiseau, C., Harrigan, R.J., Robert, A., Bowie, R.C., Thomassen, H.A., Smith, T.B., Sehgal, R.N., 2012b. Host and habitat specialization of avian malaria in Africa. *Mol. Ecol.* 21, 431–441.
- Loiseau, C., Harrigan, R.J., Bichet, C., Julliard, R., Garnier, S., Lendvai, A.Z., Chastel, O., Sorci, G., 2013. Predictions of avian *Plasmodium* expansion under climate change. *Sci. Rep.* 3, 1126.
- Lotta, I.A., Gonzalez, A.D., Pacheco, M.A., Escalante, A.A., Valkiūnas, G., Moncada, L.I., Matta, N.E., 2015. *Leucocytozoon pterotenusis* sp. nov. (Haemosporida, Leucocytozoidae): description of the morphologically unique species from the

- Grallariidae birds, with remarks on the distribution of *Leucocytozoon* parasites in the neotropics. *Parasitol. Res.* 114, 1031–1044.
- Macdonald, G., 1952. The analysis of equilibrium in malaria. *Trop. Dis. Bull.* 49, 813–829.
- Martínez, C., Marzec, T., Smith, C.D., Tell, L.A., Sehgal, R.N., 2013. Identification and expression of *maeb1*, an erythrocyte-binding gene, in *Plasmodium gallinaceum*. *Parasitol. Res.* 112, 945–954.
- Mata, V.A., da Silva, L.P., Lopes, R.J., Drovetski, S.V., 2015. The strait of Gibraltar poses an effective barrier to host-specialised but not to host-generalised lineages of avian Haemosporidia. *Int. J. Parasitol.* 45 (11), 711–719.
- Medeiros, M.C., Hamer, G.L., Ricklefs, R.E., 2013. Host compatibility rather than vector-host-encounter rate determines the host range of avian *Plasmodium* parasites. *Proc. Biol. Sci.* 280, 20122947.
- Mendenhall, C.D., Archer, H.M., Brenes, F.O., Sekercioglu, C.H., Sehgal, R.N.M., 2013. Balancing biodiversity with agriculture: land sharing mitigates avian malaria prevalence. *Conserv. Lett.* 6, 125–131.
- Mendes, L., Piersma, T., Lecoq, M., Spaans, B., Ricklefs, R.E., 2005. Disease-limited distributions? Contrasts in the prevalence of avian malaria in shorebird species using marine and freshwater habitats. *Oikos* 109, 396–404.
- Møller, A.P., Szépl, T., 2010. The role of parasites in ecology and evolution of migration and migratory connectivity. *J. Ornithol.* 152, 141–150.
- Murdock, C.C., Foufopoulos, J., Simon, C.P., 2013. A transmission model for the ecology of an avian blood parasite in a temperate ecosystem. *PLoS One* 8, e76126.
- Njabo, K.Y., Cornel, A.J., Bonneaud, C., Toffelmier, E., Sehgal, R.N., Valkiūnas, G., Russell, A.F., Smith, T.B., 2011. Nonspecific patterns of vector, host and avian malaria parasite associations in a central African rainforest. *Mol. Ecol.* 20, 1049–1061.
- Oakgrove, K.S., Harrigan, R.J., Loiseau, C., Guers, S., Seppi, B., Sehgal, R.N., 2014. Distribution, diversity and drivers of blood-borne parasite co-infections in Alaskan bird populations. *Int. J. Parasitol.* 44, 717–727.
- Okanga, S., Cumming, G.S., Hockey, P.A., 2013. Avian malaria prevalence and mosquito abundance in the Western Cape, South Africa. *Malar. J.* 12, 1–14.
- Olsson-Pons, S., Clark, N.J., Ishtiaq, F., Clegg, S.M., 2015. Differences in host species relationships and biogeographic influences produce contrasting patterns of prevalence, community composition and genetic structure in two genera of avian malaria parasites in southern Melanesia. *J. Anim. Ecol.* 84, 985–998.
- Outlaw, D.C., Ricklefs, R.E., 2014. Species limits in avian malaria parasites (Haemosporida): how to move forward in the molecular era. *Parasitology* 141, 1223–1232.
- Paaijmans, K.P., Thomas, M.B., 2011. The influence of mosquito resting behaviour and associated microclimate for malaria risk. *Malar. J.* 10, 183.
- Paaijmans, K.P., Imbahale, S.S., Thomas, M.B., Takken, W., 2010. Relevant microclimate for determining the development rate of malaria mosquitoes and possible implications of climate change. *Malar. J.* 9, 196.
- Paaijmans, K.P., Heinig, R.L., Seliga, R.A., Blanford, J.I., Blanford, S., Murdock, C.C., Thomas, M.B., 2013. Temperature variation makes ectotherms more sensitive to climate change. *Glob. Chang. Biol.* 19, 2373–2380.
- Palinauskas, V., Žiegyte, R., Ilgūnas, M., Iezhova, T.A., Bernotiene, R., Bolshakov, C., Valkiūnas, G., 2015. Description of the first cryptic avian malaria parasite, *Plasmodium homocircumflexum* n. sp., with experimental data on its virulence and development in avian hosts and mosquitoes. *Int. J. Parasitol.* 45, 51–62.
- Palmer, J.L., McCutchan, T.F., Vargas, F.H., Deem, S.L., Cruz, M., Hartman, D.A., Parker, P.G., 2013. Seroprevalence of malarial antibodies in Galapagos penguins (*Spheniscus mendiculus*). *J. Parasitol.* 99, 770–776.
- Pérez-Rodríguez, A., Fernández-González, S., de la Hera, I., Pérez-Tris, J., 2013. Finding the appropriate variables to model the distribution of vector-borne parasites with different environmental preferences: climate is not enough. *Glob. Chang. Biol.* 19, 3245–3253.
- Pérez-Rodríguez, A., de la Hera, I., Fernández-González, S., Pérez-Tris, J., 2014. Global warming will reshuffle the areas of high prevalence and richness of three genera of avian blood parasites. *Glob. Chang. Biol.* 20, 2406–2416.
- Perkins, S.L., 2014. Malaria's many mates: past, present, and future of the systematics of the order Haemosporida. *J. Parasitol.* 100, 11–25.
- Poulin, R., Mouillot, D., 2003. Parasite specialization from a phylogenetic perspective: a new index of host specificity. *Parasitology* 126, 473–480.
- Ricklefs, R.E., Outlaw, D.C., Svensson-Coelho, M., Medeiros, M.C., Ellis, V.A., Latta, S., 2014. Species formation by host shifting in avian malaria parasites. *Proc. Natl. Acad. Sci. U. S. A.* 111, 14816–14821.
- Roiz, D., Ruiz, S., Soriguer, R., Figuerola, J., 2015. Landscape effects on the presence, abundance and diversity of mosquitoes in mediterranean wetlands. *PLoS One* 10, e0128112.
- Santiago-Alarcón, D., Palinauskas, V., Schaefer, H.M., 2012. Diptera vectors of avian Haemosporidian parasites: untangling parasite life cycles and their taxonomy. *Biol. Rev. Camb. Philos. Soc.* 87, 928–964.
- Santiago-Alarcón, D., Havelka, P., Pineda, E., Segelbacher, G., Schaefer, H.M., 2013. Urban forests as hubs for novel zoonosis: blood meal analysis, seasonal variation in Culicoides (Diptera: Ceratopogonidae) vectors, and avian haemosporidians. *Parasitology* 140, 1799–1810.
- Scordato, E.S., Kardish, M.R., 2014. Prevalence and beta diversity in avian malaria communities: host species is a better predictor than geography. *J. Anim. Ecol.* 83, 1387–1397.
- Sehgal, R.N., 2010. Deforestation and avian infectious diseases. *J. Exp. Biol.* 213, 955–960.
- Sehgal, R.N., Jones, H.I., Smith, T.B., 2001. Host specificity and incidence of *Trypanosoma* in some African rainforest birds: a molecular approach. *Mol. Ecol.* 10, 2319–2327.
- Sehgal, R.N., Jones, H.I., Smith, T.B., 2005a. Blood parasites of some West African rainforest birds. *J. Vet. Med. Sci.* 67, 295–301.
- Sehgal, R.N., Jones, H.I., Smith, T.B., 2005b. Molecular evidence for host specificity of parasitic nematode microfilariae in some African rainforest birds. *Mol. Ecol.* 14, 3977–3988.
- Sehgal, R.N., Hull, A.C., Anderson, N.L., Valkiūnas, G., Markovets, M.J., Kawamura, S., Tell, L.A., 2006. Evidence for cryptic speciation of *Leucocytozoon* spp. (Haemosporida, Leucocytozoidae) in diurnal raptors. *J. Parasitol.* 92, 375–379.
- Sehgal, R., Buermann, W., Harrigan, R., Bonneaud, C., Loiseau, C., Chasar, A., Sepil, I., Valkiūnas, G., Iezhova, T., Saatchi, S., 2011. Spatially explicit predictions of blood parasites in a widely distributed African rainforest bird. *Proc. R. Soc. Lond. B Biol. Sci.* 278, 1025–1033.
- Service, M., 1997. Mosquito (Diptera: Culicidae) dispersal—the long and short of it. *J. Med. Entomol.* 34, 579.
- Silveira, P., Belo, N.O., Rodello, D., Pinheiro, R.T., Braga, É.M., 2010. Microfilariae infection in wild birds from the Brazilian cerrado. *J. Wildl. Dis.* 46, 1305–1309.
- Smith, D.L., Battle, K.E., Hay, S.I., Barker, C.M., Scott, T.W., McKenzie, F.E., 2012. Ross, Macdonald, and a theory for the dynamics and control of mosquito-transmitted pathogens. *PLoS Pathog.* 8, e1002588.
- Stephenson, J., Newman, K., Mayhew, S., 2010. Population dynamics and climate change: what are the links? *J. Public Health* 32, 150–156.
- Stresman, G.H., 2010. Beyond temperature and precipitation: ecological risk factors that modify malaria transmission. *Acta Trop.* 116, 167–172.
- Svensson-Coelho, M., Ellis, V.A., Loiseau, B.A., Blake, J.G., Ricklefs, R.E., 2014. Reciprocal specialization in multihost malaria parasite communities of birds: a temperate-tropical comparison. *Am. Nat.* 184, 624–635.
- Svobodová, M., Weidinger, K., Peške, L., Volf, P., Votýpka, J., Vorišek, P., 2015. Trypanosomes and haemosporidia in the buzzard (*Buteo buteo*) and sparrowhawk (*Accipiter nisus*): factors affecting the prevalence of parasites. *Parasitol. Res.* 114, 551–560.
- Taylor, D., 1997. Seeing the forests for the more than the trees. *Environ. Health Perspect* 105, 1186–1191.
- Valkiūnas, G., 1998. Haematozoa of wild birds: peculiarities in their distribution and pathogenicity. *Bull. Scand. Soc. Parasitol.* 8, 39–46.
- Valkiūnas, G., 2005. Avian Malaria Parasites and Other Haemosporidia. CRC Press, Boca Raton.
- Valkiūnas, G., Iezhova, T.A., Loiseau, C., Sehgal, R.N., 2009. Nested cytochrome b polymerase chain reaction diagnostics detect sporozoites of haemosporidian parasites in peripheral blood of naturally infected birds. *J. Parasitol.* 95, 1512–1515.
- Valkiūnas, G., Sehgal, R.N., Iezhova, T.A., Hull, A.C., 2010. Identification of *Leucocytozoon toddi* group (Haemosporida: Leucocytozoidae), with remarks on the species taxonomy of leucocytozoids. *J. Parasitol.* 96, 170–177.
- Valkiūnas, G., Kazlauskienė, R., Bernotienė, R., Palinauskas, V., Iezhova, T.A., 2013. Abortive long-lasting sporogony of two Haemoproteus species (Haemosporida, Haemoproteidae) in the mosquito *Ochlerotatus cantans*, with perspectives on haemosporidian vector research. *Parasitol. Res.* 112, 2159–2169.
- Valkiūnas, G., Palinauskas, V., Ilgūnas, M., Bukauskaitė, D., Dimitrov, D., Bernotienė, R., Zehntindjiev, P., Ilieva, M., Iezhova, T.A., 2014. Molecular characterization of five widespread avian haemosporidian parasites (Haemosporida), with perspectives on the PCR-based detection of haemosporidians in wildlife. *Parasitol. Res.* 113, 2251–2263.
- van Riper III, C., van Riper, S.G., Goff, M.L., Laird, M., 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.* 56, 327–344.
- van Rooyen, J., Lalubin, F., Glaiot, O., Christie, P., 2013. Avian haemosporidian persistence and co-infection in great tits at the individual level. *Malar. J.* 12, 40.
- Vittor, A.Y., Gilman, R.H., Tielsch, J., Glass, G., Shields, T., Lozano, W.S., Pinedo-Cancino, V., Patz, J.A., 2006. The effect of deforestation on the human-biting rate of *Anopheles darlingi*, the primary vector of *Falciparum* malaria in the Peruvian Amazon. *Am. J. Trop. Med. Hyg.* 74, 3–11.
- Vittor, A.Y., Pan, W., Gilman, R.H., Tielsch, J., Glass, G., Shields, T., Sanchez-Lozano, W., Pinedo, V.V., Salas-Cobos, E., Flores, S., Patz, J.A., 2009. Linking deforestation to malaria in the Amazon: characterization of the breeding habitat of the principal malaria vector, *Anopheles darlingi*. *Am. J. Trop. Med. Hyg.* 81, 5–12.
- Warner, R.E., 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor* 101–120.
- Wesolowski, A., Eagle, N., Tatem, A.J., Smith, D.L., Noor, A.M., Snow, R.W., Buckee, C.O., 2012. Quantifying the impact of human mobility on malaria. *Science* 338, 267–270.
- Wood, M.J., Cosgrove, C.L., Wilkin, T.A., Knowles, S.C., Day, K.P., Sheldon, B.C., 2007. Within-population variation in prevalence and lineage distribution of avian malaria in blue tits, *Cyanistes caeruleus*. *Mol. Ecol.* 16, 3263–3273.
- Yanoviak, S.P., Paredes, J.R., Lounibos, L.P., Weaver, S.C., 2006. Deforestation alters phytotelm habitat availability and mosquito production in the Peruvian Amazon. *Ecol. Appl.* 16, 1854–1864.
- Yasuoka, J., Levins, R., 2007. Impact of deforestation and agricultural development on anopheline ecology and malaria epidemiology. *Am. J. Trop. Med. Hyg.* 76, 450–460.
- Zamora-Vilchis, I., Williams, S.E., Johnson, C.N., 2012. Environmental temperature affects prevalence of blood parasites of birds on an elevation gradient: implications for disease in a warming climate. *PLoS One* 7, e39208.

Zehtindjiev, P., Krizanauskienė, A., Bensch, S., Palinauskas, V., Asghar, M., Dimitrov, D., Scebba, S., Valkiūnas, G., 2012. A new morphologically distinct avian malaria parasite that fails detection by established polymerase chain reaction-based protocols for amplification of the cytochrome b gene. *J. Parasitol.*

98, 657–665.

Žiegytė, R., Valkiūnas, G., 2015. Recent advances in vector studies of avian haemosporidian parasites. *Ekologija* 60, 73–83.