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#### ABSTRACT

Avian species are commonly infected by multiple parasites, however few studies have investigated the environmental determinants of the prevalence of co-infection over a large scale. Here we believe that we report the first, detailed ecological study of the prevalence, diversity and co-infections of four avian blood-borne parasite genera: *Plasmodium* spp., *Haemoproteus* spp., *Leucocytozoon* spp. and *Trypanosoma* spp. We collected blood samples from 47 resident and migratory bird species across a latitudinal gradient in Alaska. From the patterns observed at collection sites, random forest models were used to provide evidence of associations between bioclimatic conditions and the prevalence of parasite co-infection distribution. Molecular screening revealed a higher prevalence of haematozoa (53%) in Alaska than previously reported. *Leucoytozoons* had the highest diversity, prevalence and prevalence (11%), negatively correlated with *Trypanosoma* prevalence (11%), negatively correlated with *Haemoproteus* prevalence (7%). We found temperature, precipitation and tree cover to be the primary environmental drivers that show a relationship with the prevalence of co-infection. The results provide insight into the impacts of bioclimatic drivers on parasite ecology and intra-host interactions, and have implications for the study of infectious diseases in rapidly changing environments.

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#### 1. Introduction

Wildlife populations can be infected with a diverse set of parasites; individual hosts may be infected with multiple parasite species and/or multiple lineages/strains of the same species concurrently (collectively hereafter referred to as "co-infections") (Read and Taylor, 2001; Mideo, 2009; Juliano et al., 2010; Palinauskas et al., 2011). For instance, numerous studies show that in areas where malaria is endemic malaria infections commonly include multiple strains (Babiker et al., 1999; Bruce et al., 2000a,b; Engelbrecht et al., 2000; Juliano et al., 2010). It has been suggested that the observed diversity in pathogen species may be due to both within-host pathogen competition (de Roode et al., 2005; Bell et al., 2006) and the host immune response against

\* *Note:* Nucleotide sequence data reported in this paper are available in GenBank under accession numbers KF314757–KF314799.

\* Corresponding author. Tel.: +1 41 4531 0076; fax: +1 41 5338 2295. E-mail address: ksouvong@gmail.com (K.S. Oakgrove). pathogen antigens (Bruce et al., 2000a). Interactions between genetically distinct parasite lineages can affect host fitness, determine pathogen transmission competence and influence disease epidemiology; these co-infections can provide insight into hostparasite co-evolution, which may be important for shaping parasite virulence and drug resistance (Deviche et al., 2001; Read and Taylor, 2001; de Roode et al., 2005; Bell et al., 2006; Marzal et al., 2008; Telfer et al., 2010). While many studies of co-infections have examined their effects on host fitness (i.e. pathogenicity) (de Roode et al., 2005; Bell et al., 2006; Marzal et al., 2008; Palinauskas et al., 2011; van Rooyen et al., 2013b), research on the interactions between multiple parasite lineages and the environmental variables that contribute to the prevalence of co-infections remains less studied.

It is important to understand the ecological determinants that affect multiple infections because these interactions can contribute heavily to disease outcome. In theory, the most successful parasite competitor would most effectively invade and utilise host resources at the lowest host fitness cost and thereby successfully

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evade the host immune response (de Roode et al., 2005). However, within-host parasite competition may select for higher virulence, as the parasite that most effectively exploits limited host resources may outcompete other strains (Bell et al., 2006). Co-infections may cause parasites to either: (i) compete for host resources and overlapping ecological niches (exploitation competition) to continue replication (reproduction) and future survival (transmission), or (ii) compete for parasite abundance to gain advantage in evading host immune capture (immune-mediated apparent competition) (Read and Taylor, 2001; Bell et al., 2006; McQueen and McKenzie, 2006; Mideo, 2009; Pollitt et al., 2011a). Primary infections can compromise the host immune system, changing intra-host resources, and this can lead to an increase in host susceptibility to secondary infections (de Roode et al., 2005; Bell et al., 2006; McQueen and McKenzie, 2006; Cornet and Sorci, 2010: Telfer et al., 2010). Thus, co-infections can arise when primary infections provide opportunities for secondary infections. Knowledge about multiple infections may help in monitoring health outcomes and inform how environmental perturbations can affect parasite prevalence (Knowles et al., 2013).

Environmental changes are evident in Arctic habitats. With sea ice coverage at a record low, considerable melting of permafrost and landscape changes (Comiso et al., 2008; Bintanja et al., 2013; Parkinson and Comiso, 2013; Tingley and Huybers, 2013), the northern latitude host-pathogen relationships will ostensibly change (Patz et al., 1996, 2002; Kutz et al., 2009). Studies suggest that with a warmer habitat, vector distribution and parasite prevalence may increase due to favourable thermal conditions (Paaijmans et al., 2009, 2010; LaPointe et al., 2010; Garamszegi, 2011; Sternberg and Thomas, 2014). A recent report provides the first evidence of Plasmodium (the causative agent of malaria) transmission in Alaskan bird populations (Loiseau et al., 2012a). Numerous additional studies provide evidence to suggest that avian malaria and other blood parasites may increase in prevalence and northerly distributions with global warming (Patz et al., 1996; Githeko et al., 2000; Garamszegi, 2011; LaPointe et al., 2012: Zamora-Vilchis et al., 2012: Loiseau et al., 2013).

Arctic regions, predicted to undergo extensive environmental transformation (Comiso et al., 2008), make an excellent model system to study the impact of bioclimatic correlates on patterns of disease distribution and co-infections (Kutz et al., 2009). While a large number of disease studies of both human and avian populations have been performed in temperate and tropical regions (Reiter, 1998; Sattenspiel, 2000; Beadell et al., 2004; Szymanski and Lovette, 2005; Hellgren et al., 2007; Chasar et al., 2009), few have investigated Arctic regions. Motivations for conducting studies in Arctic regions include: (i) these regions harbour relatively low biological diversity, (ii) naïve host populations may be vulnerable to invasion, and (iii) direct anthropogenic changes are not as pronounced (Jetz et al., 2007; Alessa and Chapin, 2008; Kutz et al., 2009; Lafferty, 2009). Combined, these factors suggest that Arctic regions will have a rapid and quantifiable response to environmental disturbance (Kutz et al., 2009), and further compel the development of models that focus on bioclimatic perturbations.

Here, we studied the co-infection status of four genera of avian blood parasites: *Plasmodium* spp., *Haemoproteus* spp., *Leucocytozoon* spp., and *Trypanosoma* spp. (Valkiūnas, 2005; Pollitt et al., 2011b). These ubiquitous haematozoan (protozoan) parasites can cause mortality and morbidity in naïve songbird communities (van Riper et al., 1986; Atkinson et al., 1995; Knowles et al., 2010; Olias et al., 2011; Pollitt et al., 2011b; LaPointe et al., 2012), and are transmitted by numerous vectors: *Plasmodium* spp. by mosquitoes (*Culicidae*), *Haemoproteus* spp. by biting midges (*Ceratopogonidae*), *Leucocytozoon* spp. by blackflies (*Simuliidae*) and *Trypanosoma* spp. by a variety of arthropods (*Simuliidae*, *Culicidae*, *Ceratopogonidae*, *Hippoboscidae* and *Dermanyssidae*) (Baker, 1976; Molyneux, 1977; Miltgen and Landau, 1982; Votýpka and Svobodová, 2004; Valkiūnas, 2005; Valkiūnas et al., 2011). As avian haematozoa are widespread (Valkiūnas, 2005; van Rooyen et al., 2013b) and host populations may be exposed to different parasites across a variety of ecological habitats, investigating haematozoan communities may shed light on host–parasite interactions (Bensch et al., 2007; van Rooyen et al., 2013a).

Currently, the effects of co-infections by multiple haematozoans are poorly understood and reported results remain inconclusive. For instance, Deviche et al. (2010) found a positive relationship between Trypanosoma and Haemoproteus, and no association between Haemoproteus and Leucocytozoon in White-winged Crossbills, while van Rooyen et al. (2013a) found no relationship between Plasmodium parasitemia and the presence of Leucocytozoon parasites or host fitness cost, although co-infections with either Plasmodium or Haemoproteus and Leucocvtozoon were common. Other studies have examined effects of co-infections on reproductive success and body conditions (Sanz et al., 2001; Marzal et al., 2008). Palinauskas et al. (2011), investigating two Plasmodium spp., found synergetic effects of co-infections dependent on host species and discovered that co-infections were more virulent than single infections. Avian haematozoan parasites of the Arctic offer a relatively simple platform that may help to clarify the complexity of within-host parasite relationships.

Through molecular and computational approaches, we believe that we provide the first comprehensive study of blood-borne parasites in Alaskan bird populations. The aims were to determine over a latitudinal gradient: (i) the prevalence variation of Plasmodium, Haemoproteus, Leucocytozoon and Trypanosoma parasites within a diverse group of songbirds and; (ii) the environmental correlates associated with higher prevalence of each of these parasites and their co-infection trends. The prediction was that specific bioclimatic drivers correlate with the prevalence of co-infections and the likelihood of contracting certain haematozoan parasites. In addition, based on several reports suggesting that environmental factors, and temperature in particular, impact blood-borne parasite development and distribution, presumably temperature variables would be key predictors of parasite prevalence and geographical distribution (Garamszegi, 2011; LaPointe et al., 2012; Ramey et al., 2012; Loiseau et al., 2013). Moreover, as Leucocytozoon is able to persist at higher elevations and in colder regions (Haas et al., 2012; van Rooyen et al., 2013a), high prevalence of infection and co-infection of Leucocytozoon in northern Arctic regions are to be expected. In contrast, due to thermal and vector constraints (van Riper et al., 1986; LaPointe et al., 2010), a low prevalence of *Plasmodium* infection was predicted, compared with other haematozoans, in the Arctic.

#### 2. Materials and methods

#### 2.1. Study area and sampling methods

Samples were collected in 2011 and 2012 at 13 sites over a latitudinal gradient in Alaska: one site at Anvik and Yellow River Junction (63°N, 161°W), four sites in the vicinity of Anchorage (61°N, 150°W), one site in Fairbanks (65°N, 148°W), two sites on the Denali Highway (63°N, 147°W) and five sites at Coldfoot (67°N, 150°W) (for detailed GPS coordinates see Supplementary Table S1). In total, 913 individuals were captured representing 47 bird species, 13 of which were resident species (n = 164) and 34 migratory species (n = 749 total, which included hatch year birds (n = 197)). Birds were caught using mist nets and banded. Birds were aged (after hatch year (AHY) versus hatch year (HY); adults and juvenile birds, respectively) by examination for the presence or absence of a cloacal protuberance/brood patch or by skull Download English Version:

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