

Effect of blood parasites on secondary sexual characteristics and morphology in mountain white-crowned sparrows

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Abstract

Blood parasites affect numerous species of birds across the world and can cause serious population declines. Haemosporidian blood parasites in Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) are known to affect certain behavioral and morphological characteristics of hosts, including dominance-related characters like song. Blood parasites cause a host of symptoms, including anemia, reduced aerobic capacity, and increased metabolic demand. This study investigates the presence of various blood parasites and their influence upon crown-stripe width in males, a secondary sexual characteristic. According to the Hamilton-Zuk hypothesis, secondary sexual characteristics should be reduced in parasitized males and their breeding success consequently lowered. Birds were captured and processed at the Rocky Mountain Biological Laboratory, and for each bird a blood smear was taken as well as body measurements like tarsus, tail, and wing length. The presence of blood parasites *Plasmodium*, *Haemoproteus*, and *Leucocytozoon* were tested in relation to crown-stripe width, crown-stripe proportion, and tail, wing, and tarsus length. There was no significant effect of infection on crown-stripe width or proportion or wing and tarsus length, but there was a significant effect of *Haemoproteus* infection on increasing male tail length in males, and on *Leucocytozoon* x *Plasmodium* cross-infection on female tail length. This study warrants further research on effects of blood infections on morphological and behavioral phenotypes in Mountain White-crown sparrows, as climate change impacts vector populations and infection could increase in high-elevation areas.

Introduction

Breeding birds are energy-limited and must balance the tradeoff between reproduction and survival (Martin 1987). Avian blood parasites are transmitted between parents and offspring and horizontally through insect vectors (Valkiunas 2005), which are increasing at high elevations as a result of climate change (Githeko 2000). Birds infected with blood parasites must allocate energy towards an immune response and are left with less energy for reproduction (Møller 1997). For example, avian blood infections are known to negatively impact male secondary sexual characteristics like showy plumage or song (Møller 1997). Blood parasites have been shown to induce negative effects on both male mating success (MacDougall Shackleton et al 2002) and nest success (Derryberry et al 2003) of their avian hosts.

Male secondary sexual characteristics often require additional energy to maintain (CITE). Parasites may cause energy normally allocated to reproductively important traits, like plumage and singing, to go to an increased immune response (Hamilton and Zuk 1982). The Hamilton-Zuk hypothesis (1982) states that male hosts infected with parasites will have reduced mate attraction as a consequence of less enhanced secondary sexual characters. Experimental evidence supports this hypothesis (Møller 1990), though Møller (1999) clarifies that it is host immune

function rather than parasite load that results in the most significant differences between infected and uninfected males. A secondary sexual characteristic of importance are status badges (Krebs and Dawkins 1978), which occur in a variety of avian species and can indicate social status (Rowher 1975). In male Mountain White-crown Sparrows, the crown stripe is a status badge. Since there is no inherent cost to status badge production regarding plumage coloration, cheating is prevented by receiver response (Lachmann et al 2001), which is costly when the sender is bluffing (Searcy and Nowicki 2005). Therefore stripe width should indicate energy not as a consequence of plumage coloration but as a consequence of conspecific interactions (Laubach 2012).

This study investigates the presence of blood parasite infections in a population of Mountain White-crown Sparrows. Mountain White-crown Sparrows have a secondary sexual characteristic, crown-stripe width, that is associated with dominance and mating success (Laubach 2012). Because crown-stripe width is known to mediate interactions between sexes in Mountain White-crown sparrows (Fugle et al. 1984; Watt 1986) and to be a reliable signal indicator of resource-holding potential (Laubach 2012), females should preferentially mate with males who have a greater crown-stripe width. In addition, Mountain White-crown Sparrows suffer from a number of hemosporidian blood parasites including the genera *Leucocytozoon*, *Plasmodium*, and *Haemoproteus*. Past findings indicate that the presence of *Leucocytozoon* and *Plasmodium* significantly altered male singing (Gilman et al 2006). This is likely due to the reduced aerobic capacity of males infected with *Plasmodium* and the accumulation of *Leucocytozoon* meronts in tissues of infected males (Valkiunas 2005). Avian malaria (*Plasmodium*) undergoes erythrocytic schizogony and can result in anemia of the host (Valkiunas 2005). It is unknown whether infection status affects crown-stripe width in males, though preliminary data (Foufopoulos, unpublished) suggests that *Plasmodium*-infected birds have a smaller crown-stripe width than uninfected birds. According to the Hamilton-Zuk hypothesis, crown-stripe width should be greater in uninfected males than in infected males.

Blood parasitism can affect both morphological and secondary sexual traits. A study on red-backed shrikes found that males parasitized with *Haemoproteus* had longer wing feathers than unparasitized males, and found a negative correlation between parasitism and secondary sexual tail plumage (Votypka 2003). *Haemoproteus* infection in yellowhammers (*Emberiza citrinella*) resulted in shorter wings (Dunn 2013), while another study shows that *Trypanosoma* infection in male pied flycatchers resulted in shorter tails (Ratti 1993). Ectoparasitism in European starlings (*Sturnus vulgaris*) did not affect tarsus length, determined during early development (Wolfs 2012). Though there is no published data on blood parasites and tarsus length, tarsus length is often used as a proxy for nestling body condition (Podmokla 2014, Tomás 2005) and is unlikely to be affected by blood parasites acquired after early development.

The objectives of this study are to understand energy tradeoffs in Mountain White-crowned sparrows and how they affect morphological features like crown-stripe width, and wing and tail feather length. These sparrows are high-altitude species that are extremely energy constrained, so they are an informative model with which to study the Hamilton-Zuk hypothesis. I hypothesize that *Plasmodium*-parasitized males should have a narrower crown-stripe width than un-parasitized males, that *Haemoproteus*-infected males could have longer or shorter wing feathers and shorter tail feathers than uninfected males, and that tarsus length should be unaffected by parasitism. Differences in morphological traits or crown-stripe width could elucidate potential consequences of increased parasitism among this population of Mountain White-crowned Sparrows.

Methods

Study Area

This study was conducted during summers of 2016-2017, north of the Rocky Mountain Biological Laboratory, in the Gunnison and White River National Forests of Gunnison County, Colorado. The GPS coordinates of the approximate mid-region of the site is at 38.99199, -107.01344. Study site locations included low elevation (East River Valley, 2924-2991 m) mid elevation (Schofield Park, 3167 m) and high elevation (North Pole Basin, 3480 m; Paradise Basin, 3550 m; Virginia Basin, 3465 m) (Figure 6). Plant composition in Mountain White-crown Sparrow breeding territories consisted primarily of willow (*Salix spp.*), corn lily (*Veratrum sp.*), cinquefoil (*Potentilla sp.*), mountain bluebell (*Mertensia spp.*) and larkspur (*Delphinium sp.*).

Bird trapping and processing

Birds were trapped using Potter's traps (Wingfield and Farner 1976), baited with baked wild bird seed (primarily, white proso millet) and locked open at least one day before trapping to habituate the birds to feeding in the traps. Up to eight traps were opened per trap session between 06:00 am and 12:00 pm, and were checked within less than one hour. Trapped birds were removed from traps and placed in a brown paper bag, kept in the shade, and immediately transported to a nearby banding station for processing. Birds were banded with a USGS-issued serial numbered band and a unique color band pattern to facilitate individual identification without recapture. Measurements taken on each bird included wing chord, tail, culmen, and tarsus length, cloacal protuberance (height and width), abdominal and furcular fat, brood patch, total crown and medial crown stripe width. Blood was taken from the brachial vein using a sterile 30 gauge lancet and micro-capillary tubes, which was then used to create blood slides for evaluating presence of blood parasites.

Blood Parasites

For each bird, a blood slide was created in the field and transported to the lab. Slides were fixed with alcohol and dyed using a Wright-Giemsa stain. To determine if blood parasites were present, each slide was analyzed using a compound microscope and the oil-immersion 100x lens. Blood parasites were identified using voucher images (J. Foufopoulos, unpublished data). A digital image was recorded for every parasite identified per slide. Slides were visually scanned for 10 minutes. Blood parasites that were detected include four genera and six species (*Leucocytozoon fringillinarum*, *L. majoris*, *Haemoproteus coatneyi*, *Plasmodium relictum*, *P. vaughni*, and *Trypanosoma avium*) (Figure 1).

Data Analysis

We used blood slides from the summers of 2016 and 2017, and referenced each blood slide with the corresponding banding and trapping data for each bird from those years. Our analysis only includes data from slides that were visually identifiable. In addition, if any inconsistencies arose between band number and color combination on the blood slide label and in the banding data, the data point was removed from the analysis (which was the case for eleven blood slides). In cases where birds were recaptured in the same year (eight cases), the parasites identified from each capture were compiled into one data point. In cases where birds were recaptured in different years, each capture was considered an independent data point because birds molt in overwintering grounds.

We conducted two-sample T-tests assuming equal variance to test for life-history differences between birds that were 1) infected by any parasite vs. uninfected by any parasite, 2) infected by *Plasmodium* vs. not, 3) infected by *Leucocytozoon* vs. not, 4) infected by *Haemoproteus* vs. not, 5) infected by both *Plasmodium* and *Leucocytozoon* vs. not, 6) infected by *Leucocytozoon* and *Haemoproteus* vs. not, 7) infected by *Plasmodium* and *Haemoproteus* vs. not, and 8) infected by all three vs. not.

Results

Of the 183 birds analyzed for parasites, 122 were infected with blood parasites. 98 (80%) were infected with *Leucocytozoon*, 39 (21%) with *Plasmodium*, 9 (5%) with *Haemoproteus*, and 0 (0%) with *Trypanosoma*. 29 birds were infected with two or more parasites (Table 1).

There was no significance in the relationship between infection status of the genera *Leucocytozoon*, *Plasmodium*, or *Haemoproteus* with crown-white proportion, crown stripe width, wing length, or tarsus length (Table 2, Table 3). Contrary to our hypothesis, there was no effect of *Plasmodium* on crown-stripe (Figure 1) or *Haemoproteus* on wing length. There was a significant effect of *Haemoproteus* infection on male tail length: infected males had longer tails than uninfected males ($p < 0.05$) (Figure 3). There was also a significant effect of *Leucocytozoon* and *Plasmodium* cross-infection on decreasing female tail length (Figure 4). In addition,

separating each genus into species (*L. majoris* and *L. fringinillarum*, and *P. vaughni* and *P. relictum*) did not significantly affect results.

Discussion

Infection with the studied blood parasites did not significantly affect crown-stripe or wing and tarsus length in male or female Mountain White-crown sparrows. Males infected with *Haemoproteus* had significantly longer tails, though females did not. In addition, females infected with both *Leucocytozoon* and *Plasmodium* had significantly shorter tails than uninfected females.

According to the Hamilton-Zuk hypothesis, parasitized males should display reduced secondary sexual characters (Hamilton and Zuk, 1982). The results of this study support the conclusion that the Hamilton-Zuk hypothesis does not apply to the crown-stripes of this population of Mountain White-crown sparrows. Crown-stripe width is a reliable indicator of dominance in males (Lachmann 2001), and because crown-stripe width was unaffected by parasites, this study indicates that blood parasites do not affect the resource-holding potential of male Mountain White-crown Sparrows.

The effects of blood parasites in birds are varied – while there is an effect on male singing ability (Gilman 2012), there is no effect of *Leucocytozoon* or *Haemoproteus* on body mass of passeriforms (Bennett 1988). A study on red-wing blackbirds (*Agelaius phoeniceus*) with *Plasmodium* infections found that anti-malarial treatment had no effect on body condition, but did reduce red blood cell production and increase hemoglobin and hematocrit (Schoenle 2017), suggesting that hemosporidian blood infections produce a cost of blood cell damage and repair. Because there is no effect on body condition, this cost could be mitigated by increased feeding of parasitized birds, or the cost could be negligible in affecting body condition. Wing feathers have been studied in correlation with blood parasites in a population of pied flycatchers, also migratory passerines, and found to decrease in length with the presence of *Trypanosoma* parasites, resulting in delayed arrival to the breeding ground. Longer wings in this species conferred a survival advantage (Rätti 1993). However, a study of *Haemoproteus* in the red-backed shrike found that infected males had significantly longer wings than uninfected males (Votýpka 2003).

In this study, males infected with *Haemoproteus* had significantly longer tails than uninfected males. This could be due to a confounding factor unaccounted for by the model, like age or elevation. *Haemoproteus* had the lowest incidence of infection, with only 5% of birds infected, so small sample could confound results. Additionally, this trend could be explained if older birds have longer tails and also have increased infection rates. Females with both *Leucocytozoon* and *Plasmodium* infections had shorter tails than females not cross-infected with

Leucocytozoon and *Plasmodium*, which could similarly be due to confounding factors like age or elevation, or a loss in fitness due to parasitism.

Total sample size was large (at 183 birds), but a more sophisticated model could enhance the accuracy of the study. This model did not take into account factors like age, elevation, or body condition, which could also affect crown-stripe width and morphological characters like tail and wing length. Additionally, this study was constrained by materials – though microscopy and blood smears are usually a good method for identifying parasites, a study showed that 25-35% of PCR-detected *Haemoproteus* parasites were undetected by microscopy (Fallon 2008). In addition, further studies could involve behavioral as well as morphological secondary sexual characteristics in males. A study on birds of paradise examined parasite effect on male reproduction, but considered behavioral phenotypes (i.e. rate of vocalization, court attendance, and rate of display) (Pruett-Jones 1990). A study on dark-eyed juncos *Junco hyemalis* compared female attraction to static vs. dynamic secondary sexual traits (for example, plumage vs. mating displays) and found that both static and dynamic SSTs were important in female choice (Hill 1999). Future studies on Mountain White-crown Sparrows could focus on dynamic secondary sexual traits, like aggression or mating attempts, rather than static traits like plumage phenotypes. Previous studies on morphology found an effect of *Haemoproteus* on wing and tail length (Ratti 1993, Votypka 2003), but the incidence of *Haemoproteus* infection in this study was low, at only 5%. The fact that tail length was the only trait affected by the presence of blood parasites could indicate that tail length is a sensitive indicator of the effects of parasitism on bird's body conditions.

Tables and Figures

Table 1 – Hemosporidian cross-infections between Mountain White-crowned sparrows. For example, 5 birds were infected with both *Haemoproteus* and *Leucocytozoon*.

	<i>Haemoproteus</i>	<i>Plasmodium</i>
<i>Leucocytozoon</i>	5	23
<i>Haemoproteus</i>		1

Table 2 – Table of T-statistic, p-value, and sample size for each effect (infection and cross-infection) on wing, tail, tarsus, crown stripe width, and crown stripe proportion of infected and uninfected female Mountain White-crown sparrows. *Haemoproteus* x *Plasmodium*, *Haemoproteus* *Leucocytozoon*, and *Leucocytozoon* x *Haemoproteus* x *Plasmodium* data is not shown because the samples of birds with those cross infections were too small to perform a statistical test. Values significant for $p < 0.05$ are bolded.

Effect	Dependent Variable	T-stat	p-value	Sample size
<i>Leucocytozoon</i>	Wing Length	1.271	0.2088	59
	Tail Length	1.0587	0.29405	61
	Tarsus Length	0.4434	0.6591	61
	Crown-stripe Width	0.09007	0.9285	67
	Crown-stripe Proportion	0.1341	0.8938	63
<i>Haemoproteus</i>	Wing Length	0.4574	0.3245	59
	Tail Length	0.2199	0.8267	60
	Tarsus Length	0.1717	0.8643	61
	Crown-stripe Width	0.59220	0.5558	67
	Crown-stripe Proportion	0.6108	0.5434	66
<i>Plasmodium</i>	Wing Length	0.06129	0.9513	61
	Tail Length	0.08552	0.9321	60
	Tarsus Length	0.7468	0.4581	61
	Crown-stripe Width	0.37790	0.7076	67
	Crown-stripe Proportion	0.8096	0.4212	66
<i>Leucocytozoon</i> x <i>Plasmodium</i>	Wing Length	1.865	0.07266	30
	Tail Length	2.971	0.0361	31
	Tarsus Length	1.571	0.1271	31
	Crown-stripe Width	0.02348	0.9813	67
	Crown-stripe Proportion	0.247	.8057	67

Table 3 – Table of T-statistic, p-value, and sample size for each effect (infection and cross-infection) on wing, tail, tarsus, crown stripe width, and crown stripe proportion of infected and uninfected male Mountain White-crown sparrows. *Haemoproteus* x *Plasmodium* and *Leucocytozoon* x *Haemoproteus* x *Plasmodium* data is not shown because the samples of birds with those cross infections were too small to perform a statistical test. Values significant for $p < 0.05$ are bolded.

Effect	Dependent Variable	T-stat	p-value	Sample size
<i>Leucocytozoon</i>	Wing Length	0.178	0.8591	115
	Tail Length	0.4374	0.6626	114
	Tarsus Length	1.663	0.0990	117
	Crown-stripe Width	1.386	0.1681	128
	Crown-stripe Proportion	0.9057	0.3669	119
<i>Haemoproteus</i>	Wing Length	.5835	0.5607	115
	Tail Length	2.1245	0.03577	117
	Tarsus Length	.4280	0.6694	118
	Crown-stripe Width	0.1134	0.9099	128
	Crown-stripe Proportion	0.1066	0.9152	119
<i>Plasmodium</i>	Wing Length	0.3500	0.7	118
	Tail Length	0.08499	0.9324	116
	Tarsus Length	0.6161	0.5390	117
	Crown-stripe Width	0.3541	0.7238	128
	Crown-stripe Proportion	0.6247	0.5334	119
<i>Leucocytozoon</i> x <i>Haemoproteus</i>	Wing Length	0.4558	0.6494	118
	Tail Length	0.8029	0.4237	118
	Tarsus Length	0.4099	0.6826	116
	Crown-stripe Width	1.329	0.1906	45
	Crown-stripe Proportion	0.1436	0.8864	45
<i>Leucocytozoon</i> x <i>Plasmodium</i>	Wing Length	1.0247	0.372	148
	Tail Length	0.4493	0.6539	148
	Tarsus Length	1.535	0.127	148
	Crown-stripe Width	0.7457	0.4572	128
	Crown-stripe Proportion	1.876	0.06300	128

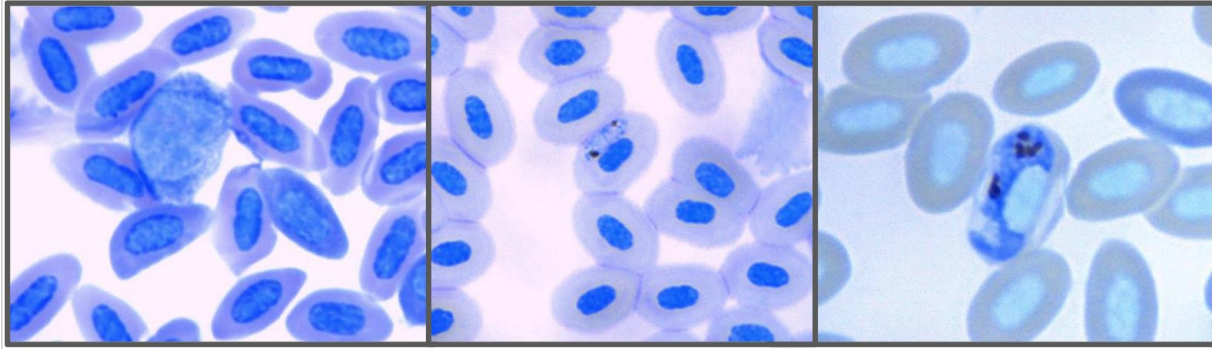


Figure 1 – Blood-slide images of the three genera of Hemosporidian blood parasites, taken from blood samples from Mountain White-crown Sparrows. On the left is *Leucocytozoon majoris*, in the middle is *Plasmodium vaughani*, and on the right is *Haemoproteus coatneyi*.

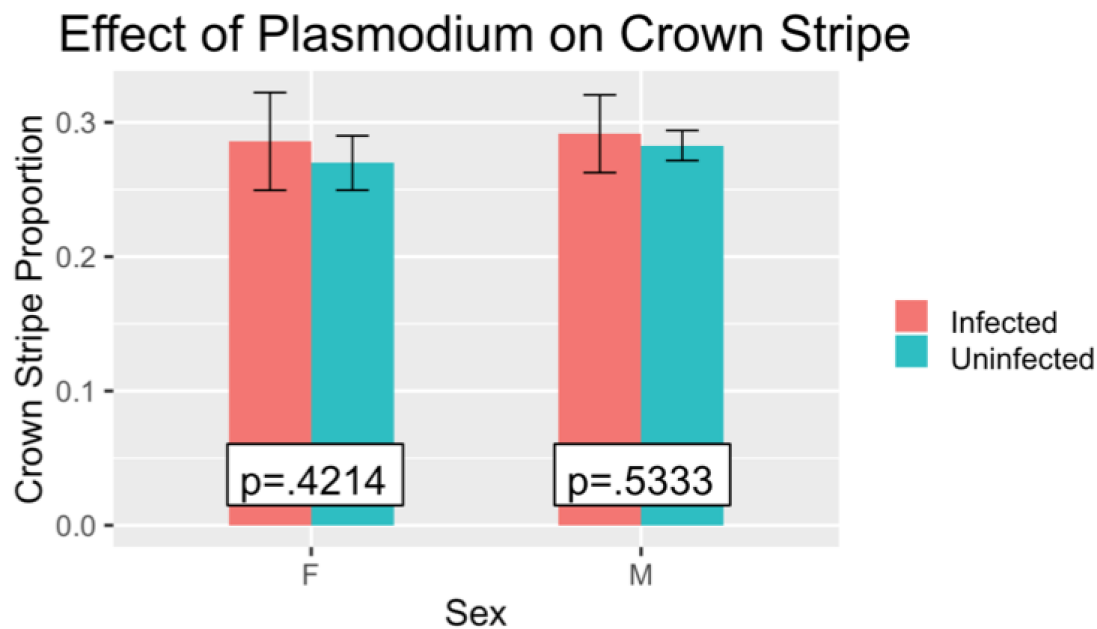


Figure 2 – Mean Crown-stripe Proportion (CSP) of *Plasmodium*-infected and uninfected male and female Mountain White-crown sparrows. The black bars indicate 95% confidence interval. There is no significant difference in crown-stripe proportion between infected and uninfected birds.

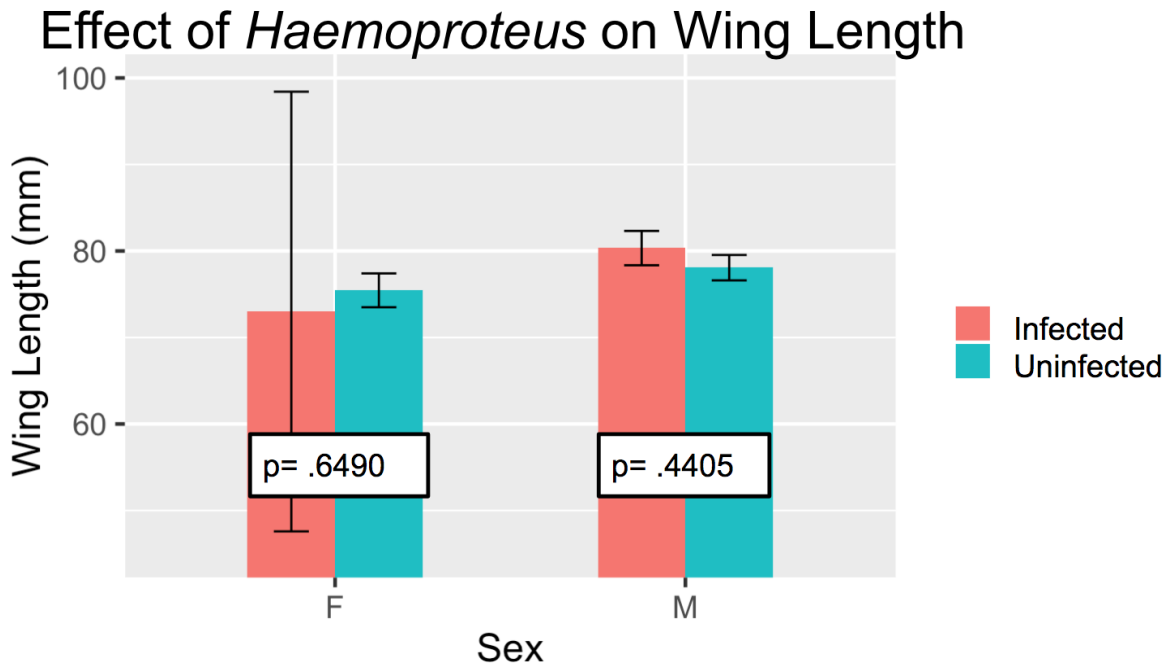


Figure 3 – Wing length (mm) of *Haemoproteus*-infected and uninfected male and female Mountain White-Crowned sparrows. The black bars indicate 95% confidence interval. There is no significant difference in wing length between infected and uninfected birds.

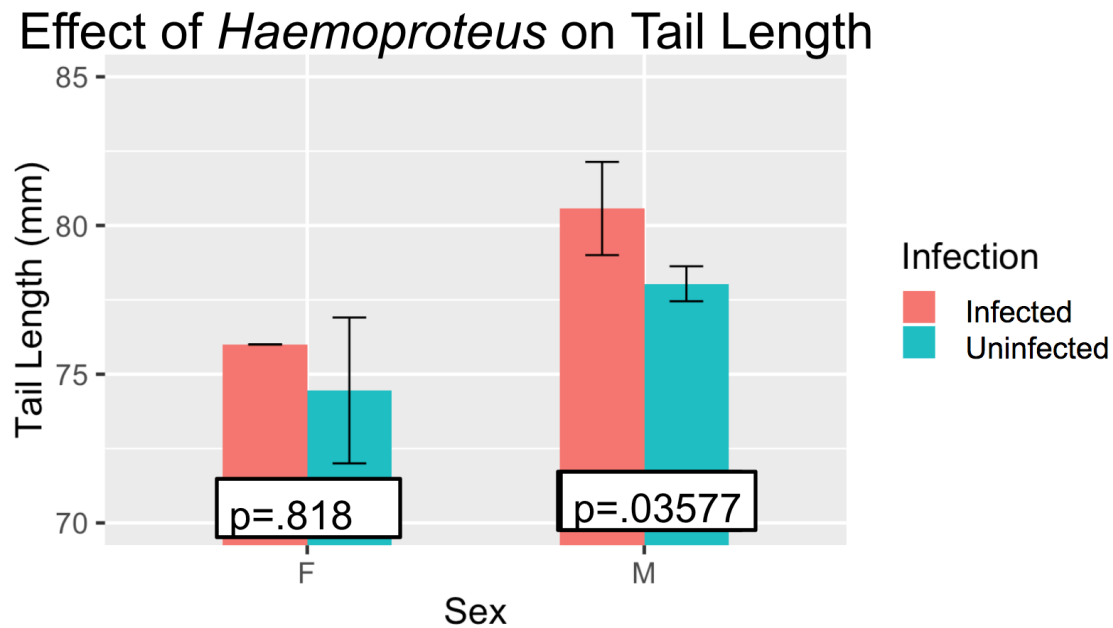


Figure 4 – Mean tail length (mm) of *Haemoproteus*-infected and uninfected males and female Mountain White-crown sparrows. For males, tail length is significantly different between

infected and uninfected individuals, with $p < 0.05$. The black bars indicate 95% confidence intervals.

Effect of *Leucocytozoon* x *Plasmodium* on Tail Length

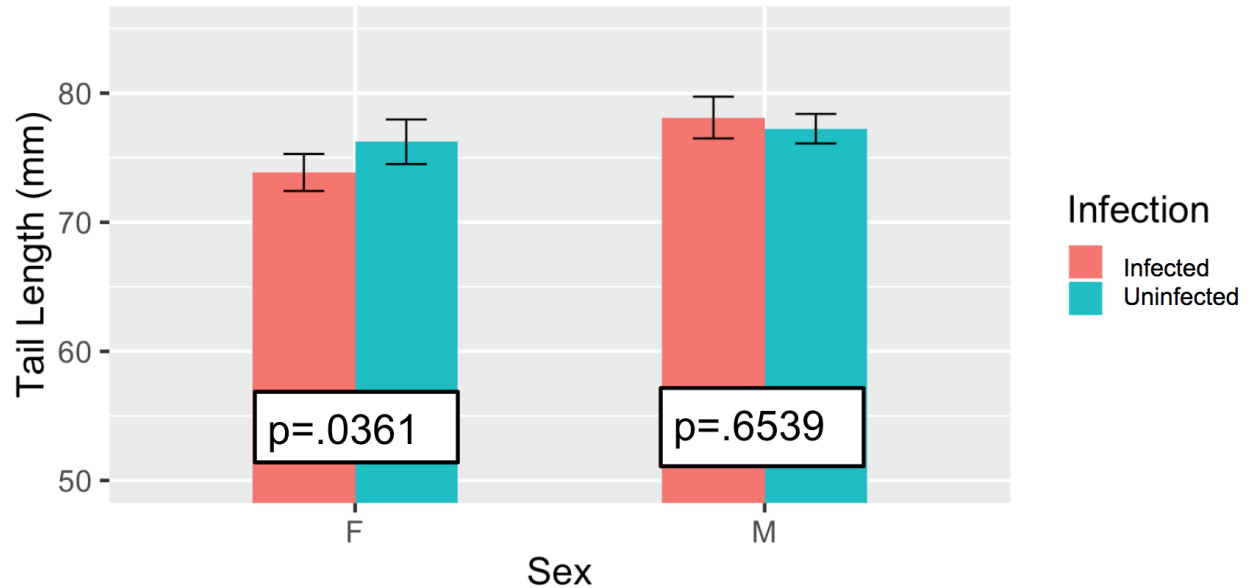


Figure 5 – Mean tail length (mm) of *Leucocytozoon* x *Plasmodium* cross-infected and uninfected males and female Mountain White-crown sparrows. For females, tail length is significantly different between infected and uninfected individuals, with $p < 0.05$. The black bars indicate 95% confidence intervals.

Mountain White-Crown Sparrow Research Sites 2018

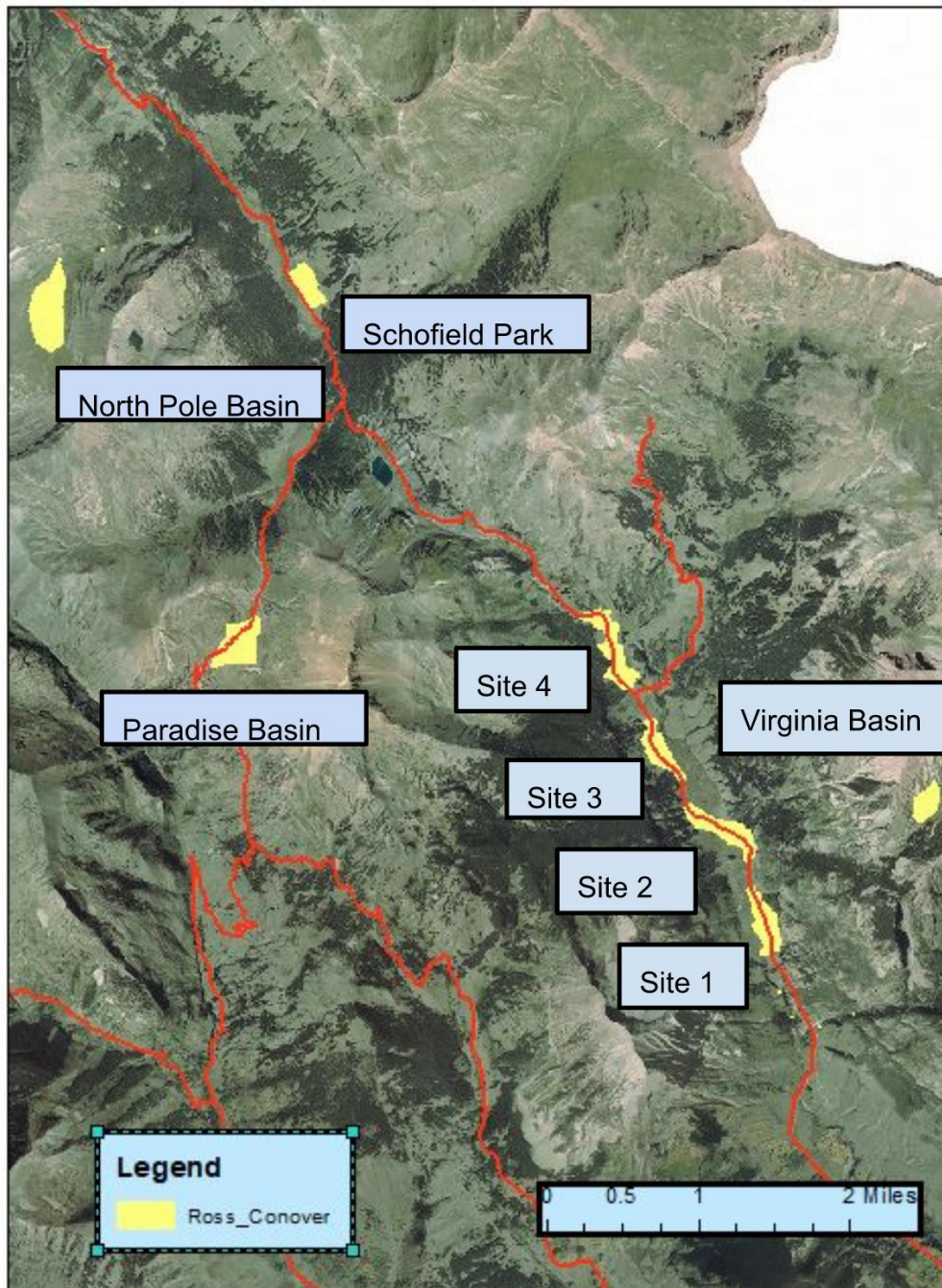


Figure 6 – Map of study sites surrounding the Rocky Mountain Biological Laboratory. Low elevation sites include Sites 1, 2, 3, and 4 (2924 - 2991 m). Mid-elevation site at Schofield Park is at 3167 m, and high elevation sites at North Pole, Paradise, and Virginia Basin reach 3550 m.

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