INFLUENCE OF AVIAN MALARIA INFECTIONS ON MORPHOLOGICAL CHARACTERISTICS IN A MIGRATORY SONGBIRD, THE MOUNTAIN WHITE-CROWNED SPARROW (*ZONOTRICHIA LEUCOPHRYS ORIANTHA*)

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Abstract

Bird plumage is thought to serve many functions beyond warmth and protection. Ornithologists have proposed that feather color and quality facilitate communication among different members of a species by advertising an individual's condition and health. Understanding how a bird's plumage reflects its underlying health status can not only help us evaluate how avian communication functions, but can also open the door to assessing in a non-intrusive way the condition of a bird population. To test the relationship between health, nutrition and plumage, I investigated a population of White-crowned Sparrows (*Zonotrichia leucophrys*) in the Colorado Rocky Mountains. These birds live in a cold, food-limited environment and are infected by multiple species of vector-transmitted avian malaria. I used a combination of long-term observational data and short-term experimental field manipulations (food supplementation and antimalarial drug administration) to test if plumage traits would be reduced as a result of avian malaria infection, and if the benefits of food supplementation and antimalarial drugs would be reflected in increased plumage traits.

I found that bird plumage traits (head crown whiteness, tail and wing length) reflect the status of a bird in several unexpected ways. The relationship between malaria infection and plumage characteristics varied based on a bird's sex, the parasite species it was infected with, and the size of the parasite population in the blood. Whereas the most virulent pathogens do indeed diminish a bird's plumage quality, other less pathogenic species appear to have the opposite effect -- in this case, plumage quality actually advertises a bird's ability to survive with infection. I also found that food supplementation that consists mostly of enhancing caloric intake rather than nutrients does not appear to affect plumage traits.

Introduction

Avian plumage has several physical functions, such as regulating temperature, protecting skin, and aiding flight, but birds also use aspects of plumage to communicate sex, dominance, willingness to mate, and even condition and overall health. Feather colors and patterns serve to identify not only an individual's species, but also an individual's sex in species with plumage variation between the sexes. Often plumage characteristics such as feather length or the size of color patches fluctuate with an individual's breeding status and health (Hamilton & Zuk, 1982). Comparing these changes in plumage with the presence or absence of disease can provide researchers clues to how birds may use plumage features to communicate individual health. Research into how aspects of plumage reflect disease status in a variety of bird species increases the scientific knowledge of avian disease, and presents the opportunity for assessing avian population health through observation. The focal species of this study is the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*), which is a migratory songbird that nests in high-elevation habitats and is known to be infected with multiple Haemoparasites that cause avian malaria belonging to the genera *Plasmodium*, *Leucocytozoon*, and *Haemoproteus*. I used a combination of long-term observational data and short-term experimental field manipulations (food supplementation and antimalarial drug administration) to test if plumage traits would be reduced as a result of avian malaria infection, and if the benefits of food supplementation and antimalarial drugs would be reflected in increased plumage traits. The plumage characteristics of interest were crown-white, which is an honest signal in White-crowned Sparrows, as well as tail length and wing length, which are important for flight maneuverability and long-distance migration.

Honest Signals

Free-ranging vertebrates communicate through a variety of means, using auditory communication with visual signals; birds particularly rely on visual signals such as plumage coloration to communicate diverse aspects of health or social status. An honest signal in birds is a morphological or plumage characteristic that accurately reflects the quality of the bearer, varies based on health and fitness, and incurs a fitness cost to display (Hamilton & Zuk, 1982; Rohwer & Ewald, 1981). Such avian status signals or badges are specific plumage traits that individuals use to communicate information about health, including infection status, as well as dominance status and resource-holding potential (Chaine & Lyon, 2008; Rohwer & Ewald, 1981; Veiga, 1993). Costs of honest signals do not have to be physical or energetic, and could include exposure to increased intra-species aggression, and elevated predation risk. Communicating individual fitness in terms of dominance and subordinance allows birds to benefit from flocking behavior, which provides safety in numbers, while maximizing food-finding ability. Winter flocks of Harris's Sparrows (*Zonotrichia querula*) contain both dominant and subordinate individuals, where the dominant birds may benefit from the food-finding ability of many subordinates, and the subordinates may benefit from habitat defense by the most dominant bird, and avoid physical attacks that are generally directed toward dominant-signaling competitors (Rohwer &

Ewald, 1981). In addition, signaling fitness and dominance potential allows birds to avoid costly physical altercations when resource competition is high. For example, House Sparrow (*Passer domesticus*) badge size is correlated with physical condition, meaning more fit birds have larger badges, likely due to the energetic cost of producing and maintaining plumage badges (Veiga, 1993). Males with experimentally enlarged badges tend to acquire more nest sites, which supports the idea that conspecifics interpret badge size as a signal of body condition, often avoiding physical confrontations (Veiga, 1993). Additional examples of honest signals used in avian communication include multiple plumage ornaments in male Lark Buntings (*Calamospiza melanocorys*) used for intrasexual dominance, red wing patches in Red-winged Blackbirds (*Agelaius phoeniceus*) which can be either exposed to signal aggression or covered to indicate submissiveness in territorial disputes, and ultraviolet plumage coloration in Satin Bowerbirds (*Ptilonorhynchus violaceus*) which signals blood parasite infection intensity and body size to prospective mates (Chaine & Lyon, 2008; Hansen & Rohwer, 1986; Doucet & Montgomerie, 2003). Costs of enlarged badges include energy expenditure and physical injury due to increased aggression from competitors as a result of dominance signaling (Chaine & Lyo, 2008; Hansen & Rohwer, 1986; Rohwer & Ewald, 1981). Deciphering avian visual communication allows researchers to make important inferences about bird health and behavior that may otherwise be overlooked. In addition to helping us understand basic avian biology, this knowledge contributes to conservation and management efforts by allowing researchers access to the wealth of information that animals use when communicating with each other. For example, if aspects of plumage signal health status to other individuals of the same species, then researchers might likewise interpret the same information by evaluating plumage characteristics.

Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha)* are a subspecies of White-crowned Sparrow that breed at high elevations in western North America. White-crowned Sparrows have a brown-gray plumage that is offset by a highly visible black and white striped crown present in adults of both sexes. Recent research has demonstrated that the black and white head pattern of this species is an honest signal of an individual's status. Hence, individuals with a greater amount of white in their crown have greater reproductive success, and are less likely to be infected with malaria causing parasites (Laubach et al., 2013). Subsequent research has shown that the amount of white in the crown is used by both males and females in assessing mate quality, parenting decisions, and evaluating aggressive interactions (Laubach et al., 2015).

White feather color is caused by light scattering by keratin in the feather structure, and the density of keratin can determine feather brightness (Prum, Torres, Williamson & Dyck, 1999). Non-melanized plumage patches provide increased conspicuousness for signaling conspecifics when used as status signals (Galván, 2008). The importance of defined borders between melanized and non-melanized plumage patches has been shown to be an indicator of individual quality and to be correlated with reproductive success in both sexes of the Great Tit (*Parus major*) (Ferns & Hinsley, 2004). Research on Barn Swallows (*Hirundo rustica*), demonstrated

that non-pigmented feather patches enforce honesty in sexual signals, due to costs associated with the lack of pigment (Kose & Møller, 1999). White feathers tend to be structurally weaker than pigmented feathers, due to the absence of pigmentary granules in the feather micro-structures, and are more susceptible to abrasion and even breakage (Bonser, 1995; Kose & Møller, 1999). In Barn Swallows white patches in tail feathers host a larger number of feather-eating lice than the melanized sections of tail feathers (Kose & Møller, 1999). Likewise, research has demonstrated that white feathers are more vulnerable to feather degrading bacteria than melanized feathers, as evidenced by differences in bacteria activity on feathers of Domestic Geese (*Anser anser domesticus*) (Gunderston, Frame, Swaddle & Forsyth, 2008).

Avian Haemoparasites

Protozoan blood parasites are common in songbirds, and include the genera *Leucocytozoon*, *Haemoproteus* and *Plasmodium*. These microparasites typically circulate through their sexual stages in the peripheral blood stream, and are transmitted by various dipteran vector species (Valkiūnas, 2005). Different blood parasite species have different life cycles within the host, and can produce different deleterious effects on the host species depending on their life history and virulence. Blood parasite species that have been found in this White-crowned Sparrow population include *Plasmodium relictum*, *P. vaughani*, *Haemoproteus coatneyi*, *Leucocytozoon fringilinarum*, and *L. majoris* (Laubach et al., 2013). The cells of these pathogens reproduce in the bird's fixed tissues (e.g. lining of brain capillaries, spleen), and are transmitted to new hosts via bites of blood-feeding ectoparasitic vectors. In general, the newly injected parasite cells enter the host as sporozoites, and develop into merozoites in the organs, bone marrow or the lining of the brain capillaries; upon sexual maturation the adult stages (micro-/macroparasites) enter the peripheral bloodstream. *Haemoproteus* cells undergo merogony in the endothelial cells of the blood vessels in the organs, especially the lungs and heart; *Plasmodium* cells develop in white blood cells of organs and tissues, especially the liver and spleen, as well as in bone marrow and the brain, and *Leucocytozoon* cells develop in the cells of fixed tissues, specifically the liver and kidneys of the host (Valkiūnas, 2005). Each parasite species is spread through unique vectors, for *Haemoproteus* they are biting midges or sandflies (Family *Ceratopogonidae*) and louse flies (Family *Hippoboscidae*), for *Plasmodium* they are mosquitos (Family *Culicidae*), and for *Leucocytozoon* they are black flies (Family Simuliidae) (Valkiūnas, 2005).

Since the various blood parasites undergo life cycle stages in different internal systems of the host, it is expected that they will also have different effects on the host. Also, blood parasite infections are additive, and persist throughout a host's lifetime, so different blood parasite species should produce varying life history impacts on the host species (Bennett et al., 1995; Lachish, Knowles, Alves, Wood & Sheldon, 2011; Weatherhead & Bennett, 1991). Blood

parasites may affect their host in a diversity of ways, e.g. there can be effects on bird behavior, social interactions, resource holding potential, access to mates, and reproductive success. Lachish et al. (2011) conducted research on a population of Blue Tits (*Cyanistes caeruleus*) that compared the effects of 2 different *Plasmodium* species on survival, and found that infection virulence varied with parasite species, as did the effect on individual survival. In addition, a study looking at the influence of parasite species on White-crowned Sparrow singing behavior found that infection with *Leucocytozoon* or *Plasmodium* affected song consistency, and that birds infected with *Plasmodium* sang fewer songs in response to experimental playback (Gilman, Blumstein & Foufopoulos, 2007). Research into the effects of protozoan blood parasite on host species have shown that infected birds may exhibit reduced parental care (Buchanan, Catchpole, Lewis & Lodge, 1998), have lowered reproductive success (Marzal, De Lope, Navarro & Møller 2005; Marzal & Reviriego et al., 2013), and face an increased risk of mortality (Lachish et al., 2011).

Effects of Infection on Plumage

Given the diverse and pervasive effects of haemoparasites on their avian hosts, it is reasonable to ask whether there are also any effects on bird plumage. This is especially true for certain plumage traits known to be honest indicators of quality such as crown whiteness in White-crowned Sparrows. Birds usually grow in a completely new or partial plumage one to two times a year. Growing in new feathers is energetically costly, and it is thought that an individual must trade off resource and energy use between infection response and renewal of feathers. For example, previous studies have shown that infection with avian malaria parasites can influence feather growth in House Sparrows (*Passer domesticus*), and feather quality in Barn Swallows (*Hirundo rustica*) (Coon et al., 2016; Kose & Møller, 1999). Symmetry of feathers may indicate fitness level, as shown by a study on European Starlings (*Sturnus vulgaris*) where birds experiencing increased stress through poor nutrition and high energy costs produced asymmetrical feathers (Swaddle & Witter, 1994). A study on House Martins (*Delichon urbicum*) investigated how infections with multiple blood parasite taxa influenced the growth rate in tail feathers, and found that infection with multiple species resulted in a slower feather growth rate, and required a prolonged molt to produce the appropriate quality of feathers (Marzal & Asghar et al., 2013). Additional research has also shown that House Sparrows infected with avian malarial parasites also exhibited a reduced tail feather growth rate (Coon et al., 2016). An experimental study on House Sparrows infected with internal parasites provided medication to a treatment group, and then compared various measures of feather quality between the groups (Pap, Vágási, Bărbos, & Marton, 2013). Birds that did not receive medication had shorter wing lengths after they molted and poorer quality flight feathers, specifically shorter and thinner primaries, decreased vane and rachis size, and decreased stiffness (Pap et al., 2013). Karell et al. (2011) looked at how blood parasites exact different costs in Tawny Owls (*Strix aluco*) dependent on color morph. Administration of experimental medication reduced the overall

incidence of blood parasites, but there was a difference in body mass at the end of the breeding season for gray, or lightly pigmented females, compared to brown, or heavily pigmented females. The authors concluded that gray morph individuals suffer a higher cost of blood parasite infection, which is why the medication produced such a noticeable change in body condition for gray morph individuals (Karell et al., 2011). Based on a review of the literature, it is expected that in Mountain White-crowned Sparrows infection status would be significantly related to percent crown-whiteness, wing length and tail length and that these effects would be influenced by food supplementation or administration of anti-malarial drugs.

Food Supplementation

All wild organisms require sufficient food resources to survive, grow, and reproduce; research on avian nutrition has investigated the various effects of food availability and diet quality on plumage characteristics, reproductive success, individual health and survival (Jones, 2011; Martin, 1987; Robb, McDonald, Chamberlain & Bearhop, 2008). Probably the best way of testing these hypotheses is to experimentally manipulate food availability, which is typically done though food supplementations (Brommer, Karell & Pietiäinen 2004; Dawson & Bortolotti, 2002; Garcia, Merkle & Barclay, 1993; McGlothlin, Duffy & Henry-Freeman, 2007; Murphy & King, 1991; Wilcoxen et. al., 2015). In a review of the impacts of supplemental feeding of wild birds, Robb et al. (2008) reported that the type and amount of food provided can have varying effects on bird life history traits, especially when the supplemental foods provide nutrients not readily available naturally, and that these effects might not be evident until the following year. If morphological aspects of a bird's plumage change depending on an individual's access to food, then those same plumage traits could be used by potential mates to evaluate an individual's ability to locate resources and therefore successfully provision mates and offspring. This hypothesis has been tested by evaluating the effects of food availability on plumage through food supplementation experiments, where additional food is provided to randomly selected birds, and then specific plumage traits measured. For example, research by McGlothlin et. al (2007) has demonstrated that in Dark-eyed Juncos (*Junco hyemalis*) diet quality affects the size and brightness of tail-white patches, a known status signal in that species. Specifically, individuals that received a high-protein diet grew tail feathers with larger and brighter white patches than those on a low-protein diet. Since white plumage brightness is the result of keratin content in the feathers, it is possible that a high-protein diet could contribute to increased keratin density in the feathers, which would then result in improved light scattering and therefore brighter feathers (McGlothlin et al., 2007; Prum et al., 1999). In a study of White-crowned Sparrows (*Zonotrichia leucophrys gambelii*), birds that were experimentally restricted to a very low-protein diet (containing 5% protein) experienced a protracted molt that produced shorter primaries on average than those in higher protein diet groups, and the most severe protein deficiency was shown to affect molt and feather quality (Murphy & King, 1991). A study by Wilcoxen et. al. (2015) provided feeding stations to forest

birds for an entire year, covering two breeding seasons, and found that songbirds with access to feeders showed improved innate immune defense, improved body condition, and more rapid tail feather growth than those in territories without supplemental feeders. Research has discussed the influence of food supplementation, specifically the protein content and the amount of food provided, on plumage quality and growth, but it is not clear whether these changes result primarily from the increased nutrient availability (protein) or whether these benefits also derive simply from a boost in caloric intake. If the latter is the case, then one would expect that even high carbohydrate and low protein feed would result in feather quality improvements. Experimentally provisioning an energy limited, high-altitude population of songbirds (White-crowned Sparrows) with food containing a high percentage of carbohydrates, can help disentangle the importance of calories versus nutrients for proper plumage development.

In general, the bulk of nutrients acquired during the breeding season goes to reproductive effort, especially for females, with the remaining resources being directed towards somatic effort, such as maintenance of body condition, immune response, and feather growth (Martin, 1987). However, the energy demands during reproduction are different for each sex, with females generally having higher energy costs to produce and incubate eggs, and males having greater flexibility to balance the demands of somatic maintenance with reproductive investment. Males may maintain investment in certain plumage characteristics, such as tail length, for territorial defense or mate attraction, rather than divert energy resources to nesting behavior. These different reproductive investments can be offset by experimentally provisioning nesting birds to provide insight into the potential costs of food limitation for each sex. Multiple studies support the idea that reproduction is more energetically costly for females, as shown by their improved health and survival with improved access to food resources during the breeding season. For example, a study by Dawson and Bortolotti (2002) on American Kestrels (*Falco sparverius*) produced evidence that supplemental feeding directly benefited females, in this case by increasing survival, as reflected by higher return rates compared to control females; in contrast, there was no difference in return rate for males based on treatment. A similar sex-specific benefit was also found in a nest provisioning study on Ural Owls (*Strix uralensis*), where supplementing nests resulted in an improved body condition, specifically significantly higher weight, for females (Brommer et al., 2004). In a study on Mountain Bluebirds (*Sialia currucoides*), supplemented females maintained their body mass during the breeding season, while control females decreased in body mass, and males maintained body mass independent of treatment (Garcia et al., 1993). The results of food supplementation experiments indicate that the amount and quality of food influences plumage brightness, feather growth, body size and survival for a variety of bird species. Multiple studies have discussed the effects of food supplementation on breeding birds, highlighting the fact that resource availability is a limit on reproductive success, especially for females. However, the species involved in these studies represent a somewhat biased sample; e.g. these studies

involved birds of prey that depend on small mammal populations or captive birds that had no choice but to eat the supplemented food provided. In contrast we know much less about more typical species such as seed-eating songbirds living in arid or mountainous environments with unpredictable weather. In addition, in all cases, supplemental feeding provided both nutrients as well as energy and it is not clear to which extent these benefits can be attributed to the one versus the other component of food. As a result, it is not clear how birds in a cold, calorically demanding environment will be affected by access to a high-carbohydrate, but low-protein food supplement, and how any differences in responses may be affected by a bird's sex.

Drug Administration

Haemoparasites are pervasive across avian taxa, but their effects on birds are not well understood. Originally researchers compared specific metrics, such as mass, between infected and uninfected birds (Hamilton & Zuk, 1982). However, it was difficult for these studies to directly attribute infection status to any of the various life history traits since birds in poor health may have lower body mass anyway, and may be more likely to be infected with haemoparasites (Karell et al., 2011; Merino, Moreno, Sans & Arriero, 2000). To circumvent the causality issues, researchers can experimentally manipulate malaria health status by administering antimalarial drugs. Controlling for blood parasite infection by reducing or eliminating parasitemia allows researchers to investigate whether or not blood parasites affect host fitness. Medication can reduce parasitemia or completely clear infections, allowing researchers to measure changes in morphological characteristics, and track changes to life history that occur after treatment. Past research has looked into the effects of experimentally administered drugs on reducing blood parasitemia, and consequently improving body condition, plumage quality, and overall fitness in several bird species (Aguilar, Maia, Santos & Macedo, 2007; Karell et al., 2011; Knowles, Palinauskas, & Sheldon, 2010; Marzal et al., 2005; Merino et al., 2000). One of the first studies of this type was the pioneering work by Merino et al. (2000) who provided evidence for costs of sub-lethal blood parasite infections in wild birds. The authors did so by randomly administering antiprotozoal medication to a population of Blue Tits (*Cyanistes caeruleus*) that reduced the infection intensity in *Haemoproteus* and the infection prevalence in *Leucocytozoon*. Birds that received medication had both lower infection intensity as well as higher body mass scores relative to those that did not. Following this study, Marzal et al. (2005) similarly treated a House Martin (*Delichon urbicum*) population with medication, and found that treated birds showed a reduction in both intensity and prevalence of *Haemoproteus* infection. In a similar study of wild-caught Blue-black Grassquits (*Volatinia jacarina*), experimentally administered medication eliminated coccidian infection in both sexes, and allowed researchers to directly compare morphological differences between infected and healthy individuals (Aguilar et al., 2007). Untreated males had shorter average wing length and no wing growth, as well as smaller body size than treated males, indicating an increased somatic cost to infection, though there were no detectable differences in female plumage

measurements. Both infected and cured males showed a decrease in the size of the white wing patch, which is considered to be a breeding ornament, relative to the otherwise pigmented wing plumage, possibly due to the inherent cost in maintaining white plumage (Aguilar et al., 2007). Additional research investigating the differential impacts of parasitemia based on host sex found that Blue Tits naturally infected with multiple haemoparasites (*Haemoproteus* and *Leucocytozoon*) and treated with antimalarials showed a drug-induced reduction of parasitemia which occurred only in females, and not males, and only in the intensity of *Haemoproteus* infection (Martínez-de la Puente et al., 2010). Medicated females also exhibited increased survival compared to control females. The results of drug administration experiments indicate that appropriate medication can reduce or even eliminate the intensity and prevalence of parasitemia in wild birds. This diversity of studies has demonstrated how, by experimentally controlling haemoparasite infections, researchers can compare differences in body size, feather growth, plumage quality and survival for treated versus untreated birds to understand how the effects of infection vary for each sex. However, these studies used a variety of drug treatments with various combinations and amounts of active ingredients, to treat a range of micro- and macroparasites in several bird species with divergent life history traits. All of these studies have focused on investigating the effects of parasitism on birds living in relatively stable, non-challenging environments. In contrast little is known about the effects of haemoparasite infection on birds living in challenging, high-elevation environments. In order to examine how the additional environmental stressors of a high-altitude mountain habitat (unpredictable weather, extreme temperatures, arid environment) compound the fitness costs of haemoparasite infection (*Plasmodium* and *Leucocytozoon*), we conducted an antiparasitic medication experiment on a population of Mountain White-crowned sparrows. We hypothesized that birds treated with antimalarial drugs and provided access to supplemental food would have improved health, which would be reflected in increased plumage traits, with greater amounts of crown-whiteness, longer tail feathers, or longer wing feathers than birds that did not receive drug or food treatment, and that these plumage features would be reduced in birds based on infection status.

Methods

The study site was located in the East River Valley of the Colorado Rocky Mountains, at approximately 2,900 m elevation, near the Rocky Mountain Biological Laboratory in Gothic, Colorado (38˚ 95’ N, 106˚ 98’ W; **Fig. 1**). Birds were trapped at one of four established study plots. Study plots were approximately 200 m by 400 m, and were separated from each other by 200-300 m wide buffer gaps. The habitat on the plots was a matrix of alpine meadows interspersed with low willow thickets near the wet valley bottoms (See **Fig. 2**). Potter traps were set out in the same locations each year, with 15-30 traps per site. Traps were baited with

millet seed to attract the sparrows, and were locked open when not in use. Trapping hours were between 0600 and 1200 h during the breeding season, from the middle of May to early August. All open traps were checked every 50 minutes and captured birds were removed by hand from the traps. Unbanded birds received a metal US Fish and Wildlife Service band (Bird Banding Laboratory, Patuxent, MD, USA) plus a unique combination of color bands for visual identification in the field. Morphological measurements, as well as sex and age characteristics were recorded for each individual. All unbanded adult birds were considered to be 1 year old on first capture. Morphological measurements of interest included weight (grams), fat on abdomen and furcula (using a scale from 0 = no fat to 5 = bulging), height and width of cloacal protuberance (*mm*), development of brood patch (using a scale from 0 = absent to 3 = extensive denudement with blistering), left wing chord (*mm*), tail length (*mm*), and left tarsus length (*mm*). Additional plumage measurements include the width of the crown, measured from the outer black edges of the crown at the height of the eyes, and the width of the white stripe in the center of the crown, measured in line with the center of the eyes, to the nearest 0.1 *mm* (See **Fig. 3**). Crown whiteness score for each bird was calculated as the width of the central stripe divided by the width of the crown multiplied by 100. As a result, this score did not express absolute size of a bird's crown but rather which percentage of the crown was white. Blood samples were taken from the brachial vein of each individual and stored on snow. A maximum of two micro-capillary tubes at 60 microliters each was taken, with no more than 360 microliters taken every 2 weeks for birds caught multiple times. Blood was then also used to prepared standard thin smear microscope slides at the field station laboratory. The air-dried slides were stained with a Fisher Hema 3 Stat pack™ (Fisher Diagnostics, Middletown, VA, USA). Each slide was examined for haemoparasite infection for 20 minutes, using a compound microscope at 1,000x magnification, with a minimum of 10,000 red blood cells examined.

Food Supplementation and Drug Administration Methods

To test the hypothesis that access to supplemental food would increase plumage traits, half of the study plots were designated as food supplementation sites each year, and these sites received additional millet seed (White Proso millet) at each trap site, whereas the non-supplemented sites received only the bare minimum of millet needed to bait sparrow traps. Food supplemented sites received millet, at least a large handful per trap site, sufficient to provide an additional food source to birds with territories in the vicinity of the supplemented trap sites. In addition, to test the hypothesis that drug treatment would increase plumage traits, half of the study birds received antimalarial drugs. Birds with odd-numbered USFWS bands, i.e. half of all handled birds, received an antiprotozoal drug cocktail each time they were captured, at a dose based on bird weight, with birds less than 25 grams receiving 0.1 cc of drug, those between 25-30 grams receiving 0.13 cc, and those over 30 grams receiving 0.15 cc. The anti-protozoal drug was an aqueous solution of sulfadimethoxine (50 *mg/kg*) and pyrimethamine (1 *mg/kg*). Birds who did not belong to the drug treatment group received

instead a placebo of an equal amount of water. The drug cocktail was given to the birds by placing liquid drops on the corner of the beak, allowing the bird to drink the liquid on its own.

Statistical Methods

I used multivariate linear regression to examine the effects of infection status, food supplementation, and drug administration on specific plumage traits based on sex and age. Linear models were created for each plumage trait, (crown-whiteness, tail length, and wing length), based on general infection status (whether or not a bird was infected with the Haemoparasites Plasmodium, Leucocytozoon, and *Haemoproteus*, including immatures that could not be identified to species), and infection status based on parasite species (*Plasmodium* and *Leucocytozoon*). Linear models were also created based on whether or not a bird had access to supplemental food, or whether or not a bird received antiprotozoal drugs.

Results

An initial multivariate regression analysis of general infection status (whether or not a bird is infected with *Plasmodium*, *Leucocytozoon*, *Haemoproteus* or asexual cells not identified to species) for both sexes pooled, showed that sex had a statistically significant effect on the percent crown-whiteness, with males having on average 2.48 units higher crown-whiteness % score than females ($p = 0.002$; **Table 1A**). In contrast, neither age ($p = 0.10$) nor general infection status ($p = 0.13$) were related to crown-whiteness. In a follow-up analysis I investigated the effects of individual parasite genera (*Plasmodium, Leucocytozoon*) on percent crown-whiteness for both sexes combined. Reflecting the previous analyses, a strong significant effect of sex on crown-whiteness was evident ($p=0.0001$). The corresponding pooled-sex analysis showed that the differences between the mean crown-whiteness were significant for *Plasmodium* ($p = 0.01$) and *Leucocytozoon* ($p = 0.02$) infection status, and that these differences varied based on sex, with significant interactions between sex and *Plasmodium* ($p = 0.037$), and between sex and *Leucocytozoon* ($p = 0.037$) (**Table 2A**).

An initial multivariate regression analysis of general infection status, for both sexes combined, showed that infection status ($p = 0.72$) was not significantly related to tail length, though the relationships with age ($p = 0.01$) and sex ($p < 0.001$) were significant (**Table 8A**). Males had on average significantly longer tails than females by 3.18 *mm*. When average parasitemia (i.e. a metric of parasite population in the blood), rather than general infection status, was considered for both sexes pooled, multivariate analysis showed that parasitemia ($p = 0.028$) and age ($p = 0.01$) were significantly related to tail length, and that sex ($p < 0.001$) also had a significant effect, with males having significantly longer tails (**Table 9A**). In a follow-up analysis I investigated the distinct effects of individual parasite genera (*Plasmodium*, *Leucocytozoon*) on

tail length, first by pooling both sexes together. Reflecting the previous analyses, a significant effect of sex ($p < 0.001$) and age ($p = 0.009$) was again evident (**Table 10A**). In this pooled sex analysis, neither *Plasmodium* infection status ($p = 0.13$), nor *Leucocytozoon* infection status ($p = 0.10$) were significantly related to tail length. Since average parasitemia was shown to be significantly related to tail length, I also investigated the relationship of average parasitemia based on infection species; this allowed us to look at the effects of intensity of infection (parasite population in the blood, i.e. parasitemia) on tail length while distinguishing between different parasite species. Restricting the analysis to birds of both sexes infected with solely *Plasmodium*, there was no significant relationship between average parasitemia ($p = 0.32$) and tail length, and there was no significance for age ($p = 0.20$), though sex continued to be significant ($p = 0.002$) (**Table 11A**). For individuals of both sexes infected with solely *Leucocytozoon*, no significant effect was detected between tail length and average parasitemia ($p = 0.38$), nor between tail length and age ($p = 0.13$), although the significant relationship to sex ($p < 0.001$) persisted (**Table 11B**).

An initial multivariate regression analysis, for both sexes combined, showed that sex ($p < 0.001$) was significantly related to wing length, but that general infection status ($p = 0.82$) was not. Wing length depended on sex; males had on average wings that were longer than females wings by 3.96 *mm*. Age was only marginally significant ($p = 0.058$) (**Table 14A**). When average parasitemia, rather than general infection status was considered, multivariate regression analysis for both sexes showed that parasitemia was significantly related to wing length ($p = 0.02$), with higher amounts of parasitemia correlating with shorter wing lengths, and that sex ($p < 0.001$) remained significant (**Table 15A**). In a follow-up analysis I investigated the distinct effects of individual parasite genera (*Plasmodium*, *Leucocytozoon*) on wing length, first by combining both sexes. Reflecting the previous analyses, a significant effect of ($p < 0.001$) was again evident (**Table 16A**). Age ($p = 0.047$) and *Plasmodium* infection status ($p = 0.026$) were also significantly related to wing length, but *Leucocytozoon* infection status ($p = 0.32$) was not. Individuals infected with *Plasmodium* had shorter wings than uninfected individuals, while older birds tended to have longer wings.

Crown-whiteness

A. Observational Data

(i.) General infection status

I conducted a multivariate regression analysis of general infection status (whether or not a bird is infected with *Plasmodium*, *Leucocytozoon*, *Haemoproteus* or asexual cells not identified to species) compared to percent crown-whiteness for each sex. For males I found neither an effect of age ($p = 0.41$) nor of general infection status ($p = 0.29$) on percent crown-whiteness

(**Table 1B**). Similarly, for females, neither age (p = 0.11) nor general infection status (p = 0.13) had a significant effect on percent crown-whiteness (**Table 1C**).

(ii.) Effects of specific parasite genera

Because the associations between infection status and percent crown-whiteness differed by sex, I conducted separate analyses for males and females. For males, neither age (p = 0.40), nor *Plasmodium* infection status (p = 0.64), nor *Leucocytozoon* infection status (p = 0.57) appeared to be significantly related to percent crown-whiteness (**Table 2B**). In contrast, for females, both *Plasmodium* infection status (p = 0.015) and *Leucocytozoon* infection status (p = 0.03) were significantly related to percent crown-whiteness, though age was not significant (p = 0.13) (**Table 2C**, **Figures 4, 5**). Hence, females infected with *Plasmodium* had on average a greater percent crown-whiteness than *Plasmodium*-healthy females by 2.76%. Similarly, females infected with *Leucocytozoon* had a greater percent crown-whiteness than *Leucocytozoon*-healthy females by 1.74 % on average. To further elucidate the causes of these relationships, I analyzed them relative to a female's reproductive status (whether they were experienced breeders, i.e. were more than 2 years old). Whether a female was an experienced breeder or not, had in itself, not a significant effect on crown whiteness (p = 0.45). However, the significant effects of *Leucocytozoon* infection (p =0.002) varied depending on the birds' experienced breeder status (interaction term p = 0.02), though the significant effects of *Plasmodium* infection (p = 0.03) did not vary based on experienced breeder status (interaction term p = 0.39) (**Table 3, Fig. 6**). Consequently, first-year *Leucocytozoon*-infected females had on average crown-whiteness scores that were elevated by 3.72% relative to uninfected ones; this difference disappeared in older females (**Fig. 7**). When average parasitemia (i.e. intensity of infection), rather than general infection status (1/0) was considered, multivariate regression analysis for both sexes showed that parasitemia was not significantly related to crown-whiteness (p = 0.55) (**Table 4**).

To determine if heavier birds had whiter crowns, we compared body condition, which is how heavy a bird is for its size, using the residuals from a regression of body mass versus tarsus length, as well as body frame size (measured as tarsus length in *mm*) to percent crown-whiteness. According to the pooled-sex multivariate-regression analysis, there was a significant relationship of percent crown-whiteness to body condition (p = 0.027) and sex (p = 0.009), but not to tarsus length (p = 0.34) (**Table 5A**). Further analysis indicated that for males, body condition (p = 0.018), but not tarsus length (p = 0.40), significantly influenced percent crown-whiteness (**Table 5B**). This relationship was not evident for females, where neither body condition (p = 0.37), nor tarsus length (p = 0.44) showed significance (**Table 5C**).

B. Effects of experimental manipulations on crown whiteness

Linear regression analysis showed that food penetration (i.e. the amount of food a bird received based on the number of visits to the trap/feeding side) received the previous year did not have a statistically significant effect on percent crown-whiteness for neither males (p = 0.32) nor females (p = 0.84) (**Tables 6A**, **6B**). Likewise, the amount of drug received the previous year did not produce a statistically significant effect on percent crown-whiteness for males (p = 0.92) nor females (p = 0.18) (**Tables 7A**, **7B**).

Tail Length

A. Observational Data

(i.) General infection status

I conducted a multivariate regression analysis of general infection status for each sex compared to tail length. The differences in male mean tail length based on age were significant (p = 0.008), with tail length increasing with age, but it was marginally not significantly related to general infection status (p = 0.077) (**Table 8B**). However, for females, neither age (p = 0.44), nor general infection status (p = 0.19) were significantly related to tail length (**Table 8C, Fig. 8**).

In a follow-up analysis I investigated the effect of average parasitemia (i.e. a metric of parasite population in the blood), separately for males and females. For males, there was no significance of average parasitemia (p = 0.97), though age continued to be significant (p = 0.007) (**Table 9B**). For females, the pattern was reversed, with average parasitemia (p = 0.018) showing a significant relationship to female tail length, and age (p = 0.60) showing none (**Table 9C**). Hence, females with higher levels of parasitemia had shorter tail lengths on average compared to females with lower levels of parasitemia.

(ii.) Effects of specific parasite genera

Because the associations between infection status and tail length differed by sex, I conducted separate analysis for males and females. For males, age continued to show a significant effect (p = 0.009), and the analysis highlighted a relationship between tail length and *Leucocytozoon* infection status (p = 0.04), though *Plasmodium* infection status (p = 0.62) was not significant (**Table 10B; Figures 9**, **10**). Males infected with *Leucocytozoon* had longer tails than uninfected males. For females, neither *Plasmodium* (p = 0.09), nor *Leucocytozoon* (p = 0.95), nor age (p = 0.42) were significantly related to tail length (**Table 10C**).

B. Effects of experimental manipulations on Tail Length

Linear regression analysis on the experimental data showed that the amount of food penetration received the previous year did not have a statistically significant effect on the change in tail length the following year for males (p-value = 0.52) nor females (p-value = 0.60) (**Tables 12A**, **12B**).

Likewise, the amount of drug received the previous year did not have a significant effect on the change in tail length the following year for males (p-value = 0.51), nor for females (p-value = 0.08) (**Tables 13A**, **13B**).

Wing Length

A. Observational Data

(*i*.) Morphological associations and general infection status

I conducted a multivariate regression analysis of general infection status for each sex compared to wing length. In males, wing length was positively correlated with age (p = 0.02) but was not related to a bird's infection status (p = 0.14) (**Table 14B**). For females, a parallel analysis did not detect any differences based on age (p = 0.88) nor general infection status (p = 0.22) (**Table 14C, Figure 11**).

I investigated the effect of average parasitemia separately for males and females. For males, multivariate regression showed that average parasitemia was not significantly related to wing length (p = 0.19), but age (p = 0.02) was significant, and positively correlated, with older males having longer wings (**Table 15B**). For females, multivariate regression analysis indicated a significant relationship between average parasitemia and wing length (p = 0.005), with higher amounts of parasitemia correlating with shorter wings, but there was no significance of age (p = 0.90) (**Table 15C**).

(*ii*.) Effects of specific parasite genera

Because wing length differed by sex, I also conducted separate analysis for males and females (**Figures 12, 13**). For males, age (p = 0.02) continued to show a significant effect, but neither *Plasmodium* infection status (p = 0.36), nor *Leucocytozoon* infection status (p = 0.11) was significantly related to wing length (**Table 16B**). For females, *Plasmodium* infection status (p = 0.02) showed significance, while neither *Leucocytozoon* infection status (p = 0.55), nor age (p = 0.84) were significantly related to wing length (**Table 16C**). There was a negative correlation

between female *Plasmodium* infection status and wing length, with infected females having wings that were shorter by 1.02 *mm*.

B. Effects of experimental manipulations on Wing Length

Linear regression analysis on the experimental data showed that the amount of food penetration the previous year had a marginally significant effect on the change in wing length the following year for males (p = 0.053) (**Table 17A**). On average, males who visited feeding stations more often had a negative change in wing length the following year. For females, there was no significant effect of food penetration (p = 0.94) on change in wing length (**Table 17B**). The amount of drug received the previous year also did not produce a statistically significant effect on the change in wing length for males (p-value = 0.59) nor females (p-value = 0.55) (**Tables 18A**, **18B**).

Discussion

Percent Crown-whiteness

This study revealed a relationship between infection with specific parasite species (*Plasmodium* and *Leucocytozoon*) and percent crown-whiteness for females only, but found no similar pattern in male crown-whiteness. Whether a bird was healthy or infected (i.e. its general infection status, irrespective of pathogen identity) was not reflected in the extent of crown-whiteness for either sex. However, a more specific analysis showed that within females, an individual's *Plasmodium* infection status was significantly related to her percent crown-whiteness, with animals infected with *Plasmodium* showing a greater percent crown-whiteness. These results were also mirrored in infections with *Leucocytozoon* in females only. These patterns were mostly driven by first-year females who were the only subgroup among the whole population that showed a clear relationship between infection and crown-whiteness, although in the opposite direction of what one would expect; that is, infected birds had higher crown-whiteness scores. Since first-year females did not breed the previous season, it is possible they were able to direct their resources into somatic investment, and therefore were better equipped to produce higher quality status signals despite infection with *Leucocytozoon*. In addition, poor-quality first-year females may have been more likely to die during the acute, early phase stage of infection rather than survive their first year. As a result, the infected first year birds may represent the high-quality adults that were able to survive the initial *Leucocytozoon* infection. In contrast, those that were not infected with *Leucocytozoon* may represent the more average individuals who had not yet come in contact with the parasite

vector (Valkiūnas, 2005). Therefore, while uninfected birds had average crown-whiteness scores, the infected ones represented the high-quality individuals (with whiter crowns) that survived the infection. In addition, it is expected that the additive negative effects of blood parasite infection should be much more pronounced in older females (Weatherhead & Bennett, 1991).

No relationship was detected between access to supplemental food nor to anti-malarial medication and percent crown-whiteness. The effectiveness of treating chronic infections, as well as different parasite species with a single medication can vary depending on parasitemia and parasite species (Martínez-de la Puente et al., 2010; Valkiūnas, 2005). Specific medications may better treat certain infections types than others, and birds infected with multiple haemoparasite species may not fully benefit from treatment with a single medication, depending on the infection species. For example, anti-malarial drugs given to Blue Tits (*Cyanistes caeruleus*) infected with multiple haemoparasite species reduced parasitemia in *Haemoproteus* infection but not in *Leucocytozoon* infection (Martínez-de la Puente et al., 2010). It is also likely that access to winter resources has a greater influence on molt that occurs over winter than food availability during the breeding season. Recent research in Swamp Sparrows (*Melospiza georgiana*) has revealed that the condition of individuals plus food availability on the wintering ground, rather than on the breeding ground, influences the quality of crown feathers produced (Danner, Greenberg, Danner & Walters, 2015). This occurs because of the alternate molt cycle in sparrows, which in general consists of replacement of the head feathers, including the crown feathers, and takes place during the non-breeding season (Pyle & Howell, 1997). In White-crowned Sparrows, the alternate molt occurs on the wintering ground and precedes migration to the breeding location (Pyle & Howell, 1997). Since crown-whiteness influences intra-species conflict over access to resources for White-crowned Sparrows, even in winter plumage, less dominant individuals may have restricted access to limited food resources during the winter due to competition with more dominant individuals (Fugle, Rothstein, Osenberg, & McGinley, 1984). An individual with a lower amount of white crown feathers may have difficulty competing with more dominant individuals on the wintering ground, and may therefore be unlikely to noticeably increase the amount of crown-whiteness produced for the subsequent breeding season. This may explain why neither anti-malarial drugs nor food supplementation on the breeding ground produced any significant influence on percent crown-whiteness in either sex. Also, it is simply expected that after so many months, the benefits of food or infection eradication fade out; for example, the bird may acquire new infections over the course of late summer or fall.

Wing Length & Tail Length

Tail length has been shown to be an important secondary display for many songbird species, and although wing length generally reflects body size, it also is considered an important aspect of health in terms of plumage quality (Andersson, 1982; Møller, 1988). We found that males

had longer tails and longer wings than females, and male tail and wing length tended to increase with age. In contrast we saw little relationship between general infection status and tail length or wing length for either sex. However, average parasitemia was significantly related to tail and wing length for females, but not for males. Therefore, females with higher levels of parasitemia had shorter tails and shorter wings on average compared to females with lower levels of parasitemia. For females, there seemed to be a trade-off between an up-regulated immune response to control parasite populations, and investment in feather growth, while a similar tradeoff does not appear to exist for males. Coon et al. (2016) documented the trade-off that occurs in House Sparrows (*Passer domesticus*) between feather growth rate and health maintenance as a result of malaria infection, and found that infected birds had significantly reduced growth rate in tail feathers. The authors determined that a bird's ability to prolong molt in order to maintain sufficient quality feathers highlights, rather than masks, the physiological trade-off induced by malaria infection. This is because a prolonged molt means a bird must endure the associated stressors, such a diverting energy to growing feathers, for a longer period of time. In addition, it is possible that females are more susceptible to the costs of infections with more than one parasite species than males, as infection with two parasite lineages has been shown to slow feather growth rate in House Martins (Marzal & Asghar et al., 2013). *Leucocytozoon* infection status had a significant relationship to tail length for males, but not for females. Males infected with *Leucocytozoon* had tails that were significantly longer than *Leucocytozoon*-healthy males. While this result may appear to be counter-intuitive, it is possible that perhaps only the healthiest, highest quality males can survive the acute stage of *Leucocytozoon* infection, so that males that are not infected with *Leucocytozoon* have not yet encountered an infected vector and are more representative of the overall population variation in average tail length (Valkiūnas, 2005). There was no significant relationship between tail length and *Plasmodium* infection status for either sex, possibly because the immune response to chronic *Plasmodium* infection does not impact tail length, such as reported by a similar study on Barn Swallows (*Hirundo rustica*) in Italy (Romano et al., 2018). However, I did find a significant relationship of *Plasmodium* infection to female -but not to male- wing length, with *Plasmodium*-infected females having shorter wings; this reflects again the previously mentioned negative influence of parasitemia levels on female plumage characteristics. The difference of effects on females versus on males may simply be a result of different reproductive schedules and demands. Studies from other birds (e.g. Wiehn and Korpimäki 1998) show that females shoulder the main costs of reproductive effort, and it is therefore possible that the trade-offs between infection and reproduction are much harder to avoid.

Counterintuitively, we found that birds that received food supplementation showed poorer feather growth the subsequent year. The amount of food received the previous year was marginally related to male wing length, with males receiving more food having on average the lowest growth in wing length over the following year. While these results may appear to be unexpected, they can be probably explained by the set-up of the food supplementation

treatment. Food was provided on randomly assigned study plots, but the extent to which a bird visited a feeding site was an individual's decision and indeed varied a great deal between the different sparrows in the population (Robb et al., 2008; Wilcoxen et al., 2015). As a result, it is possible that birds in poorer condition or of poor-quality, were more likely to take frequent and repeated advantage of available food, resulting in higher food penetration scores, yet their underlying poorer body condition was still reflected in decreased wing length or tail length the following year (Wilcoxen et al., 2015). In addition, the supplementary food that we provided was high in carbohydrates but low in protein, and only protein has been shown to be a valuable nutrient for feather growth and plumage quality (McGlothin et al, 2007; Murphy & King, 1991). Therefore, birds in poorer health may not have gained any long-term benefits in terms of improvements in plumage quality from our low-protein food supplementation. This suggests that what determines plumage quality is less the amount of calories needed to produce it, and more the nutritional content of the food.

In regard to the drug administration treatment, the lack of observed antimalarial drug effects may be traced by the potentially toxic side effects of antiprotozoal agents which may impact plumage characteristics of the birds. A study by Knowles et al. (2010) identified an increased risk for nest abandonment by medicated Blue Tit (*Cyanistes caeruleus*) females compared to similarly handled, but untreated females, which suggests a potentially negative influence of antiprotozoal drugs. Another explanation is that in the case of low-virulence pathogens, drug administration may not produce many observable benefits for the host (Valkiūnas, 2005). Lack of effects may further be caused by the significant and variable time elapsed between treatment and response measurement (Marzal et al., 2005). Lastly, the infection rate for each bird is comprised of multiple blood parasite species (*Haemoproteus*, *Plasmodium* and *Leucocytozoon*), as well as immature or asexual cells that cannot be identified to species, so there could be varying effects on plumage characteristics based on the combination of blood parasite species and the asexual and reproductive stages that each species is undergoing in the individual (Knowles et al., 2010; Valkiūnas, 2005).

TABLES

Dependent Variable: Crown-whiteness (%)

1A. ALL BIRDS	**df=516, R^2_{mult} =0.0248, p=0.0111**			**1B. MALES**	**df= 287, R^2_{mult} =0.0066, p=0.387**			**1C. FEMALES**	**df= 228, R^2_{mult}=0.02, p =0.10**		
Variable	***Estimate±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	27.08±0.67	40.05	**<.001**	**Intercept**	29.33±0.71	41.04	**<.001**	**Intercept**	27.41±0.83	33.137	**<.001**
Age	-0.33±0.20	-1.66	0.097°	Age	-0.20±0.25	-0.83	0.406	Age	-0.52±0.32	-1.60	0.111
Sex	2.48±0.81	3.05	**0.002**								
Status	1.13±0.73	1.53	0.126	Status	-0.71±0.67	-1.06	0.288	Status	1.15±0.76	1.513	0.132
Sex*Status	-1.826±1.00	-1.82	0.069°								

Table 1. Results of multivariate analysis of age, sex, general infection status (whether a bird is infected with blood parasites, including asexual or immature cells) and the interaction between sex and infection status on percent crown-whiteness for both sexes combined **(A = all birds)**. Results of multivariate analysis of age, and general infection status (whether a bird is infected with blood parasites, including asexual or immature cells) on percent crown-whiteness for males **(B = males)** and females **(C = females)**. (Bold **values** indicate significance <0.05. values˚ indicates marginal significance, gray values indicate non-significance.)

2A. ALL BIRDS	**df=514, R^2_{mult} =0.0413, p=0.0013**			**2B. MALES**	**df= 286, R^2_{mult} =0.0049, p=0.7056**			**2C. FEMALES**	**df= 227, R^2_{mult}=0.06, p =0.0044**		
Variable	***Estimate±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	26.93±0.57	47.25	**<.001**	**Intercept**	29.05±0.61	47.45	**<.001**	**Intercept**	27.25±0.75	36.57	**<.001**
Age	-0.32±0.20	-1.63	0.105	Age	-0.21±0.25	-0.85	0.399	Age	-0.49±0.32	-1.54	0.126
Sex	2.32±0.60	3.87	**0.0001**								
Plasm	2.72±1.10	2.46	**0.014**	Plasm	-0.49±1.05	-0.47	0.641	**Plasm**	2.76±1.13	2.45	**0.150**
Leuco	1.77±0.78	2.28	**0.023**	Leuco	-0.37±0.65	-0.57	0.568	**Leuco**	1.74±0.80	2.18	**0.030**
Sex:Plasm	-3.21±1.53	-2.09	**0.037**								
Sex:Leuco	-2.13±1.02	-2.09	**0.037**								

Table 2. Results of multivariate analysis of age, sex, *Plasmodium* infection status, *Leucocytozoon* infection status, and the interaction between each infection species and sex on percent crown-whiteness for both sexes combined **(A = all birds)**. Results of multivariate analysis of age, *Plasmodium* infection status, and *Leucocytozoon* infection status on percent crown-whiteness for males **(B = males)** and females **(C = females)**.

3. FEMALES	df=225, R^2_{mult} =0.0758, p=0.0031		
Variable	*Estimate±SE*	*t-val*	*P*
Intercept	25.99±0.64	40.32	**<.001**
Age2plus	0.68±0.89	0.76	0.445
Plasm	3.72±1.67	2.23	**0.027**
Leuco	3.42±1.07	3.20	**0.0016**
Age2plus:Plasm	-1.94±2.25	-0.86	0.389
Age2plus:Leuco	-3.72±1.60	-2.33	**0.021**

Table 3. Results of multivariate analysis of female reproductive status (whether a female is age 1 or is older than 1, represented as Age2plus), *Plasmodium* infection status, *Leucocytozoon* infection status, and the interaction effect between reproductive status and *Plasmodium* and *Leucocytozoon* infection on percent crown-whiteness for females.

4. ALL BIRDS	df=516, R^2_{mult} =0.0192, p=0.0401		
Variable	*Estimate±SE*	*t-val*	*P*
Intercept	27.73±0.52	53.76	**<.001**
Age	-0.32±0.197	-1.62	0.105
Sex	1.33±0.50	2.63	**0.009**
Avg.Parasitemia	0.005±0.009	0.60	0.547
Sex:Avg.Parasitemia	-0.001±0.04	-0.03	0.980

Table 4. Results of multivariate analysis of age, sex, average parasitemia (the number of infected cells per 10,000 red blood cells), and the interaction effect between sex and average parasitemia on percent crown-whiteness for both sexes combined.

5A. ALL BIRDS	df=505, R^2_{mult} =0.0273, p=0.0029			5B. MALES	df= 279, R^2_{mult} =0.0223, p=0.0429			5C. FEMALES	df= 224, R^2_{mult}=0.0063, p =0.4925		
Variable	*Estimate±SE*	*t-val*	*P*	*Variable*	*Estim±SE*	*t-val*	*P*	*Variable*	*Estim±SE*	*t-val*	*P*
Intercept	34.70±7.75	4.48	**<.001**	**Intercept**	36.29±9.34	3.89	**<.001**	**Intercept**	38.26±14.3	36.57	**0.008**
Resid	0.29±0.13	2.22	**0.027**	**Resid**	0.45±0.19	2.38	**0.018**	Resid	-0.16±0.18	0.90	0.368
Sex	1.41±0.54	2.62	**0.009**								
Tarsus	-0.28±0.29	-0.97	0.335	Tarsus	-0.29±0.34	-0.84	0.403	Tarsus	-0.42±0.54	-0.78	0.437

Table 5. Results of multivariate analysis of body condition (residuals from a linear regression of body mass (*g*) versus tarsus length (*mm*), represented as resid), sex, and body size (tarsus length in *mm*) on percent crown-whiteness for both sexes combined **(A = all birds).** Results of multivariate analysis of body condition (residuals from a linear regression of body mass (*g*) versus tarsus length (*mm*), represented as resid), and body size (tarsus length in *mm*) on percent crown-whiteness for males **(B = males)** and females **(C = females).**

6A. MALES	df=76, R^2_{mult} =0.0129, p=0.3219			6B. FEMALES	df= 46, R^2_{mult} =0.0009, p=0.8403		
Variable	***Estimate±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	0.04±0.84	0.05	0.964	Intercept	-0.17±1.12	-0.16	0.878
Food.1	-174.54±175.06	-0.997	0.322	Food.1	-52.16±257.32	-0.20	0.840

Table 6. Results of multivariate analysis of amount of food penetration in year 1 (the amount of food a bird received based on the number of visits to the trap/feeding side) on percent change in crown-whiteness between year 1 and year 2 for males **(A = males)** and females **(B = females).**

7A. MALES	df=76, R^2_{mult} =0.0001, p=0.9216			7B. FEMALES	df= 46, R^2_{mult} =0.0397, p=0.1746		
Variable	***Estimate±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	-0.41±0.92	-0.45	0.655	Intercept	-0.72±1.19	0.60	0.550
Drug.1	0.23±2.28	0.099	0.922	Drug.1	-3.95±2.87	-1.38	0.175

Table 7. Result of multivariate analysis of the amount of drug received in year 1 (*cc*) on percent change in crown-whiteness between year 1 and year 2 for males **(A = males)** and females **(B = females).**

<u>Dependent Variable: Tail Length (*mm*)</u>

8A. ALL BIRDS	df=517, R^2_{mult} =0.259, p=<.001			8B. MALES	df= 287, R^2_{mult} =0.0359, p=0.0053			5C. FEMALES	df= 228, R^2_{mult}=0.0099, p =0.3227		
Variable	***Estimate±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	72.47±0.30	242.87	**<.001**	**Intercept**	75.13±0.37	204.50	**<.001**	**Intercept**	73.07±0.41	177.28	**<.001**
Sex	3.18±0.24	13.03	**<.001**								
Status	0.09±0.26	0.36	0.717	Status	0.61±0.34	1.78	0.077˚	Status	-0.50±0.38	-1.33	0.185
Age	0.25±0.10	2.54	**0.011**	**Age**	0.34±0.13	2.66	**0.008**	Age	0.12±0.16	0.77	0.444

Table 8. Results of multivariate analysis of sex, general infection status (whether a bird is infected with blood parasites, including asexual or immature cells) and age on tail length (*mm*) for both sexes combined **(A = all birds).** Results of multivariate analysis of general infection status (whether a bird is infected with blood parasites, including asexual or immature cells) and age on tail length (*mm*) for males **(B = males)** and females **(C = females).** (Bold **values** indicate significance <0.05. values˚ indicates marginal significance, gray values indicate non-significance).

9A. ALL BIRDS	**df=517, R^2_{mult} =0.2657, p=<.001**			**9B. MALES**	**df= 287, R^2_{mult} =0.0253, p=0.0253**			**9C. FEMALES**	**df= 228, R^2_{mult}=0.0256, p =0.0170**		
Variable	***Estimate ±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	72.62 ±0.26	279.25	**<.001**	**Intercept**	75.5 ±0.30	253.70	**<.001**	**Intercept**	72.92 ±0.36	208.56	**<.001**
Sex	3.14±0.24	12.89	**<.001**								
Avg. Parasitemia	-0.009 ±0.04	-2.20	**0.028**	Avg. Parasitemia	0.0008 ±0.02	0.04	0.966	**Avg. Parasitemia**	-0.001 ±0.004	-2.34	**0.020**
Age	0.25±0.10	2.48	**0.014**	**Age**	0.35±0.13	2.73	**0.007**	Age	0.09±0.16	0.53	0.597

Table 9. Results of multivariate analysis of sex, average parasitemia (the number of infected cells per 10,000 red blood cells), and age on tail length (*mm*) for both sexes combined **(A = all birds).** Results of multivariate analysis of average parasitemia (the number of infected cells per 10,000 red blood cells), and age on tail length (*mm*) for males **(B = males)** and females **(C = females).**

10A. ALL BIRDS	**df=516, R^2_{mult} =0.2653, p=<.001**			**10B. MALES**	**df= 286, R^2_{mult} =0.0394, p=0.0093**			**10C. FEMALES**	**df= 227, R^2_{mult}=0.0148, p =0.3348**		
Variable	***Estimate±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	72.46 ±0.27	269.17	**<.001**	**Intercept**	75.32 ±0.31	240.07	**<.001**	**Intercept**	72.87 ±0.38	193.06	**<.001**
Sex	3.13±0.24	12.86	**<.001**								
Plasm	-0.60 ±0.39	-1.52	0.128	Plasm	-0.26 ±0.54	-0.49	0.623	Plasm	-0.97 ±0.57	-1.70	0.090˚
Leuco	0.42±0.26	1.63	0.104	**Leuco**	0.67±0.33	2.04	**0.043**	Leuco	-0.03 ±0.40	-0.07	0.949
Age	0.26±0.10	2.62	**0.009**	**Age**	0.33±0.13	2.64	**0.009**	Age	0.13±0.16	0.82	0.415

Table 10. Results of multivariate analysis of sex, *Plasmodium* infection status, *Leucocytozoon* infection status, and age on tail length (*mm*) for both sexes combined **(A = all birds).** Results of multivariate analysis of *Plasmodium* infection status, *Leucocytozoon* infection status, and age on tail length (*mm*) for males **(B = males)** and females **(C = females).**

11A. *Plasmodium* (all birds)	**df=21, R^2_{mult} =0.4695, p=0.0035**			**11B. *Leucocytozoon* (all birds)**	**df= 136, R^2_{mult} =0.3517, p=<.001**		
Variable	***Estimate±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	70.33±1.52	46.19	**<.001**	**Intercept**	72.49±0.51	143.45	**<.001**
Sex	4.59±1.27	3.61	**0.002**	**Sex**	3.65±0.44	8.21	**<.001**
Avg.Parasitemia	-0.05±0.05	-1.01	0.325	Avg.Parasitemia	0.03±0.04	0.89	0.377
Age	0.79±0.53	1.31	0.203	Age	0.28±0.18	1.53	0.128

Table 11. Results of multivariate analysis of sex, average parasitemia (the number of infected cells per 10,000 red blood cells), and age for birds infected with only *Plasmodium* on tail length (*mm*) for both sexes combined **(A = all birds, *Plasmodium*).** Results of multivariate analysis of sex, average parasitemia (the number of infected cells per 10,000 red blood cells), and age for birds infected with only *Leucocytozoon* on tail length (*mm*) for both sexes combined **(B = all birds, *Leucocytozoon*).**

12A. MALES	**df=73, R^2_{mult} =0.0058, p=0.5146**			**12B. FEMALES**	**df= 45, R^2_{mult} =0.0063, p=0.5978**		
Variable	***Estimate±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	1.01±0.66	1.53	0.131	Intercept	0.59±0.56	1.05	0.299
Food.1	-89.13±136.10	-0.66	0.515	Food.1	-67.99±127.96	-0.53	0.598

Table 12. Results of multivariate analysis of amount of food penetration in year 1 (the amount of food a bird received based on the number of visits to the trap/feeding side) on change in tail length (*mm*) between year 1 and year 2 for males **(A = males)** and females **(B = females).**

13A. MALES	**df=73, R^2_{mult} =0.0059, p=0.5112**			**13B. FEMALES**	**df= 45, R^2_{mult} =0.0680, p=0.0767**		
Variable	***Estimate±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	0.52±0.73	0.71	0.478	Intercept	1.08±0.59	1.85	0.071˚
Drug.1	1.16±1.76	0.66	0.511	Drug.1	-2.54±1.40	-1.81	0.077˚

Table 13. Result of multivariate analysis of the amount of drug received in year 1 (*cc*) on change in tail length (*mm*) between year 1 and year 2 for males **(A = males)** and females **(B = females).**

Dependent Variable: Wing Length (*mm*)

14A. ALL BIRDS	**df=517, R^2_{mult} =0.4575, p=<.001**			**14B. MALES**	**df= 287, R^2_{mult} =0.0270, p=0.0198**			**14C. FEMALES**	**df= 228, R^2_{mult}=0.0067, p =0.4654**		
Variable	***Estimate±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	75.15±0.23	320.47	**<.001**	**Intercept**	78.70±0.29	271.23	**<.001**	**Intercept**	75.64±0.32	234.73	**<.001**
Sex	3.96±0.19	20.65	**<.001**								
Status	0.05±0.20	0.23	0.819	Status	0.40±0.27	1.49	0.138	Status	-0.37±0.30	-1.24	0.218
Age	0.15±0.08	1.90	0.058˚	**Age**	0.23±0.10	2.33	**0.021**	Age	0.02±0.13	0.15	0.884

Table 14. Results of multivariate analysis of age, sex, and general infection status (whether a bird is infected with blood parasites, including asexual or immature cells) on wing length (*mm*) for both sexes combined **(A = all birds).** Results of multivariate analysis of age, and general infection status (whether a bird is infected with blood parasites, including asexual or immature cells) on wing length (*mm*) for males **(B = males)** and females **(C = females).**

15A. ALL BIRDS	**df=517, R^2_{mult} =0.4632, p=<.001**			**15B. MALES**	**df= 287, R^2_{mult} =0.0252, p=0.0257**			**15C. FEMALES**	**df= 228, R^2_{mult}=0.0336, p =0.0204**		
Variable	***Estimate ±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	75.26 ±0.20	368.61	**<.001**	**Intercept**	78.9 ±0.23	337.10	**<.001**	**Intercept**	75.56 ±0.27	278.02	**<.001**
Sex	3.92±0.19	20.52	**<.001**								
Avg. Parasitemia	-0.008 ±0.003	-2.34	**0.020**	Avg. Parasitemia	0.02 ±0.02	1.30	0.195	**Avg. Parasitemia**	-0.01 ±0.003	-2.81	**0.005**
Age	0.14±0.08	1.82	0.069˚	**Age**	0.23±0.10	2.34	**0.020**	Age	-0.02±0.13	-0.13	0.899

Table 15. Results of multivariate analysis of age, sex, and average parasitemia (the number of infected cells per 10,000 red blood cells) on wing length (*mm*) for both sexes combined **(A = all birds)**. Results of multivariate analysis of age and average parasitemia (the number of infected cells per 10,000 red blood cells) on wing length (*mm*) for males **(B = males)** and females **(C = females).**

16A. ALL BIRDS	**df=516, R^2_{mult} =0.4633, p=<.001**			**16B. MALES**	**df= 286, R^2_{mult} =0.0297, p=0.0343**			**16C. FEMALES**	**df= 227, R^2_{mult}=0.0245, p =0.1300**		
Variable	***Estimate±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	75.19 ±0.21	355.78	**<.001**	**Intercept**	78.86 ±0.25	318.10	**<.001**	**Intercept**	75.58 ±0.29	257.82	**<.001**
Sex	3.93±0.19	20.53	**<.001**								
Plasm	-0.68 ±0.31	-2.23	**0.026**	Plasm	-0.39 ±0.42	-0.92	0.361	**Plasm**	-1.02 ±0.44	-2.29	**0.023**
Leuco	0.20±0.20	0.99	0.323	Leuco	0.42±0.26	1.59	0.112	Leuco	-0.19 ±0.31	-0.59	0.553
Age	0.16±0.08	1.99	**0.047**	**Age**	0.23±0.10	2.31	**0.022**	Age	0.03±0.13	0.20	0.842

Table 16. Results of multivariate analysis of age, sex, *Plasmodium* infection status, and *Leucocytozoon* infection status on wing length (*mm*) for both sexes combined **(A = all birds).** Results of multivariate analysis of age, *Plasmodium* infection status, and *Leucocytozoon* infection status on wing length (*mm*) for males **(B = males)** and females **(C = females).**

17A. MALES	**df=76, R^2_{mult} =0.0484, p=0.0529**			**17B. FEMALES**	**df= 46, R^2_{mult} =0.0001, p=0.9431**		
Variable	***Estimate±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	0.93±0.25	3.72	**0.0004**	**Intercept**	0.82±0.35	2.34	**0.024**
Food.1	-102.28±52.01	-1.97	0.053˚	Food.1	5.78±80.54	0.07	0.943

Table 17. Results of multivariate analysis of amount of food penetration in year 1 (the amount of food a bird received based on the number of visits to the trap/feeding side) on change in wing length (*mm*) between year 1 and year 2 for males **(A = males)** and females **(B = females).**

18A. MALES	**df=76, R^2_{mult} =0.0038, p=0.5902**			**18B. FEMALES**	**df= 46, R^2_{mult} =0.0078, p=0.5509**		
Variable	***Estimate±SE***	***t-val***	***P***	***Variable***	***Estim±SE***	***t-val***	***P***
Intercept	0.78±0.28	2.81	**0.006**	**Intercept**	0.97±0.38	2.57	**0.013**
Drug.1	-0.37±0.69	-0.54	0.590	Drug.1	-0.55±0.91	-0.60	0.551

Table 18. Result of multivariate analysis of the amount of drug received in year 1 (*cc*) on change in wing length (*mm*) between year 1 and year 2 for males **(A = males)** and females **(B = females).**

Figures

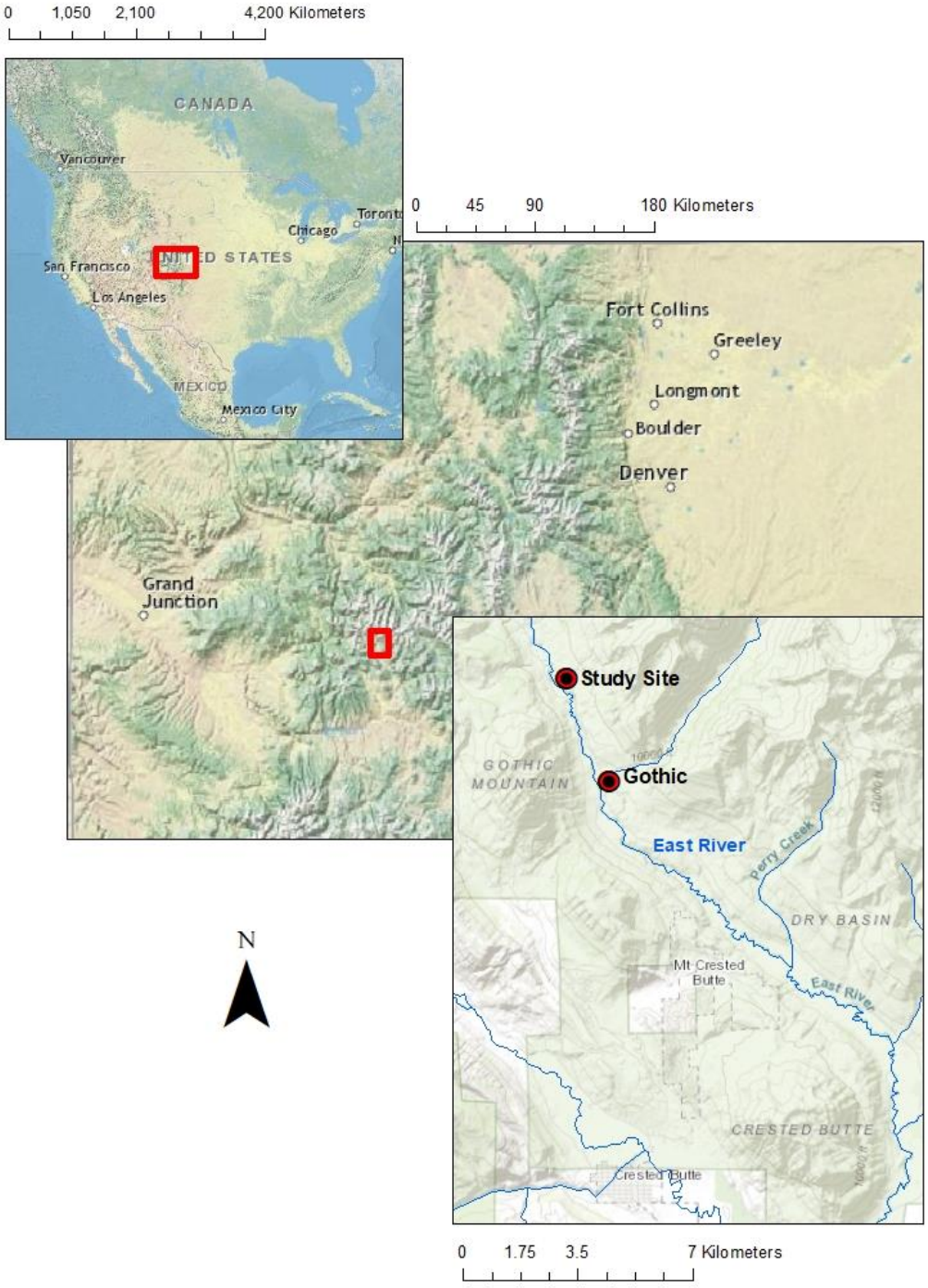

Figure 1. *Map of Research Area.* The study site was located in the East River Valley of the Colorado Rocky Mountains, at approximately 2,900 *m* elevation, near the Rocky Mountain Biological Laboratory in Gothic, Colorado (38˚ 95’ N, 106˚ 98’ W).

Figure 2. The habitat on the plots was a matrix of alpine meadows interspersed with low willow thickets near the wet valley bottoms. The study site was located in the East River Valley of the Colorado Rocky Mountains, at approximately 2,900 *m* elevation, near the Rocky Mountain Biological Laboratory in Gothic, Colorado (38˚ 95’ N, 106˚ 98’ W).

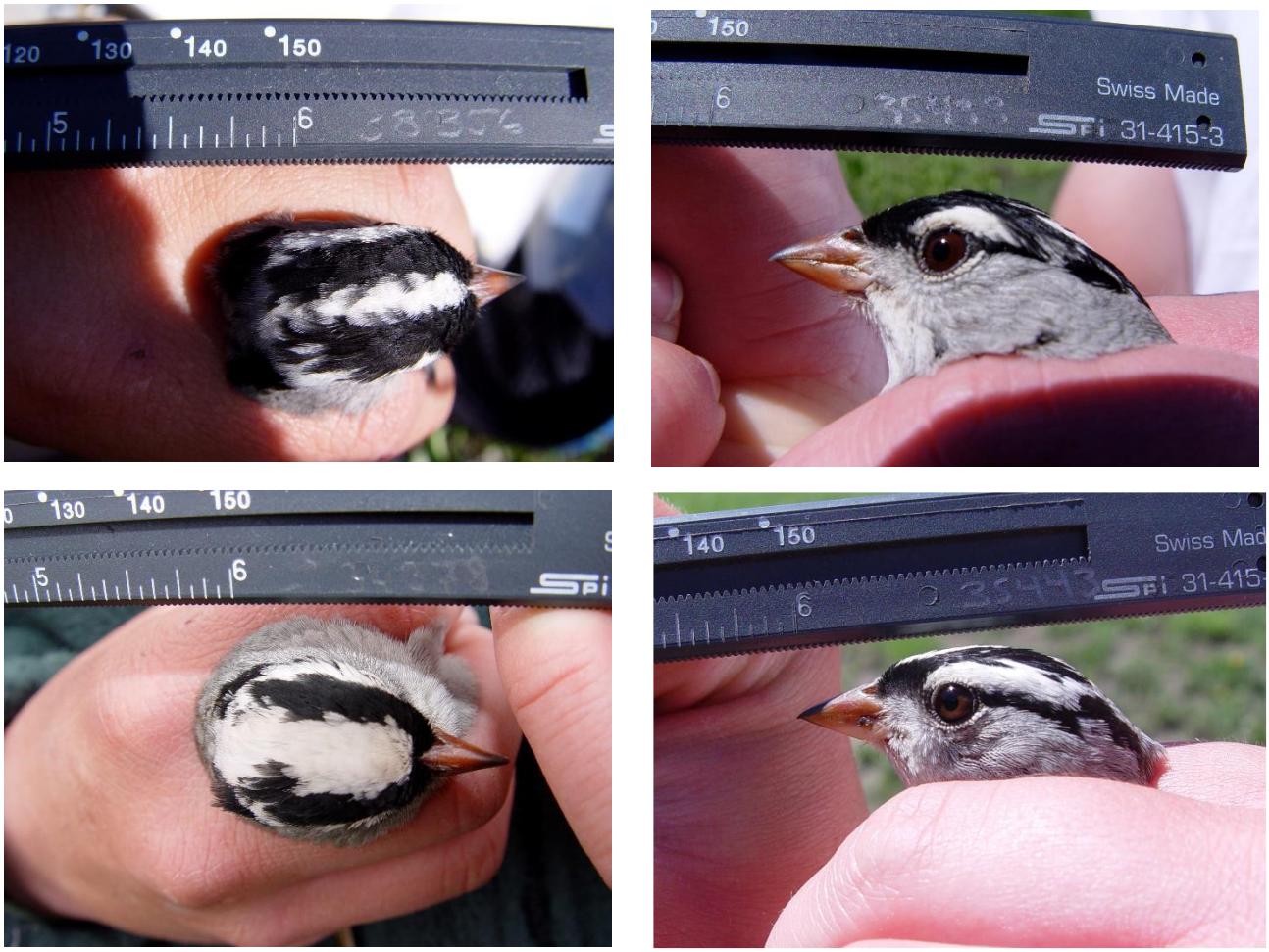

Figure 3. Images showing the head pattern of the White-crowned Sparrow and variation in the amount of white plumage in the center crown stripe. The width of the crown is measured from the outer black edges of the crown at the height of the eyes, and the width of the white stripe in the center of the crown is measured in line with the center of the eyes, to the nearest 0.1 *mm*.

Crown-white Figures

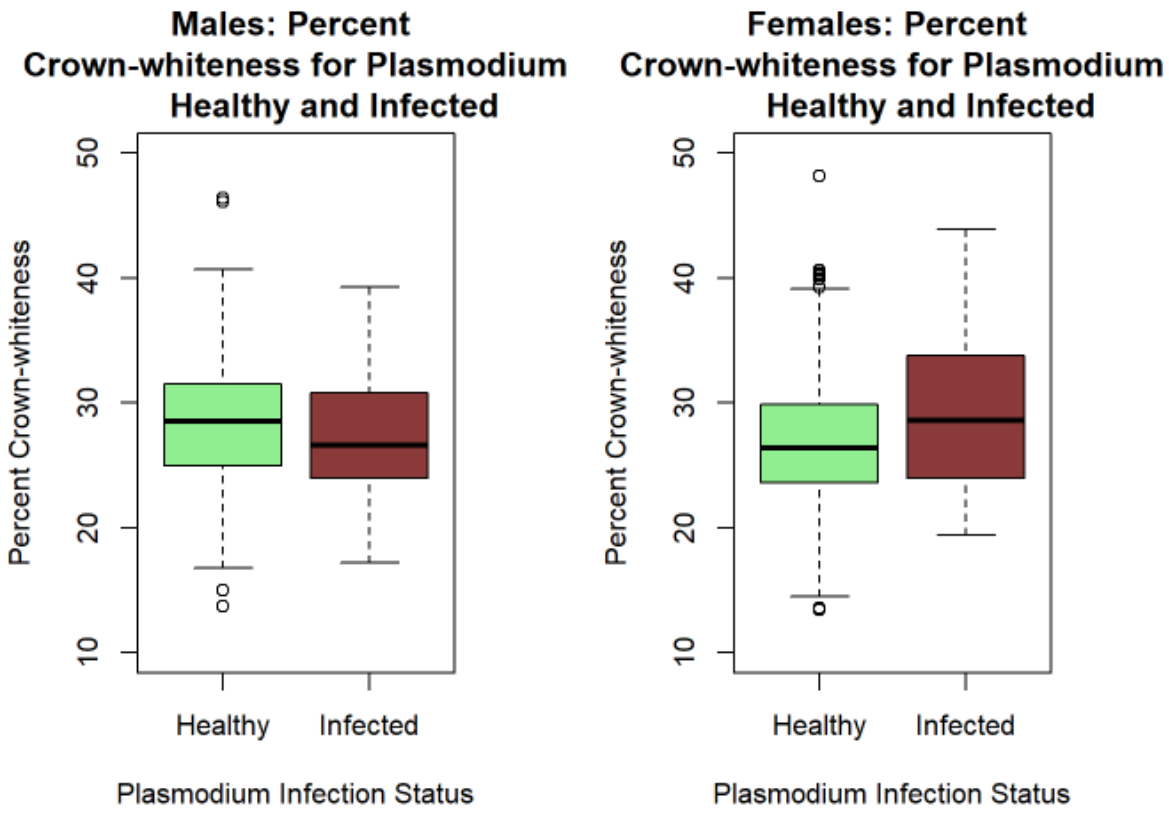

Figure 4. Percent crown-whiteness for *Plasmodium* healthy and infected individuals by sex. In males, the differences were not significant ($p = 0.64$, $n = 290$, linear regression), while for females infected birds had significantly higher crown-whiteness scores relative to uninfected birds ($p = 0.015$, $n = 231$, linear regression).

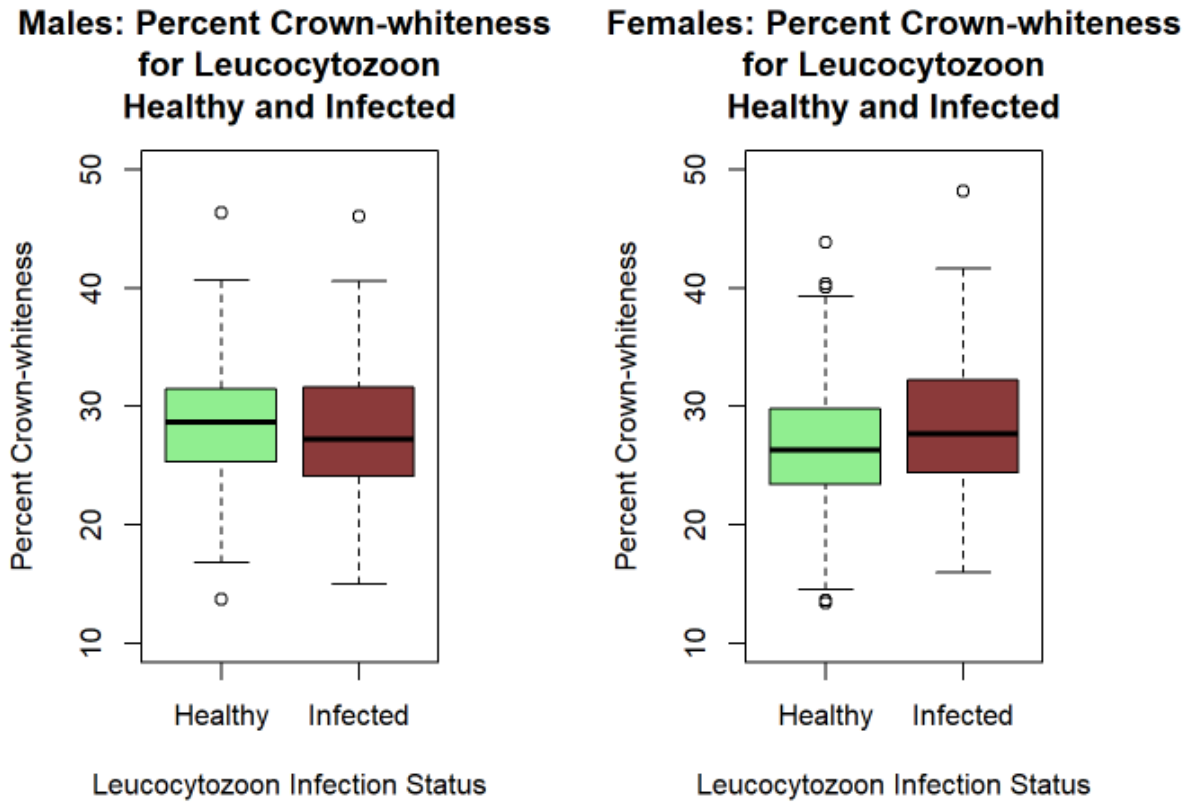

Figure 5. Percent crown-whiteness for *Leucocytozoon* healthy and infected individuals by sex. In males, the differences were not significant ($p = 0.57$, $n = 290$, linear regression), while for females infected birds had significantly higher crown-whiteness scores relative to uninfected birds ($p = 0.03$, $n = 231$, linear regression).

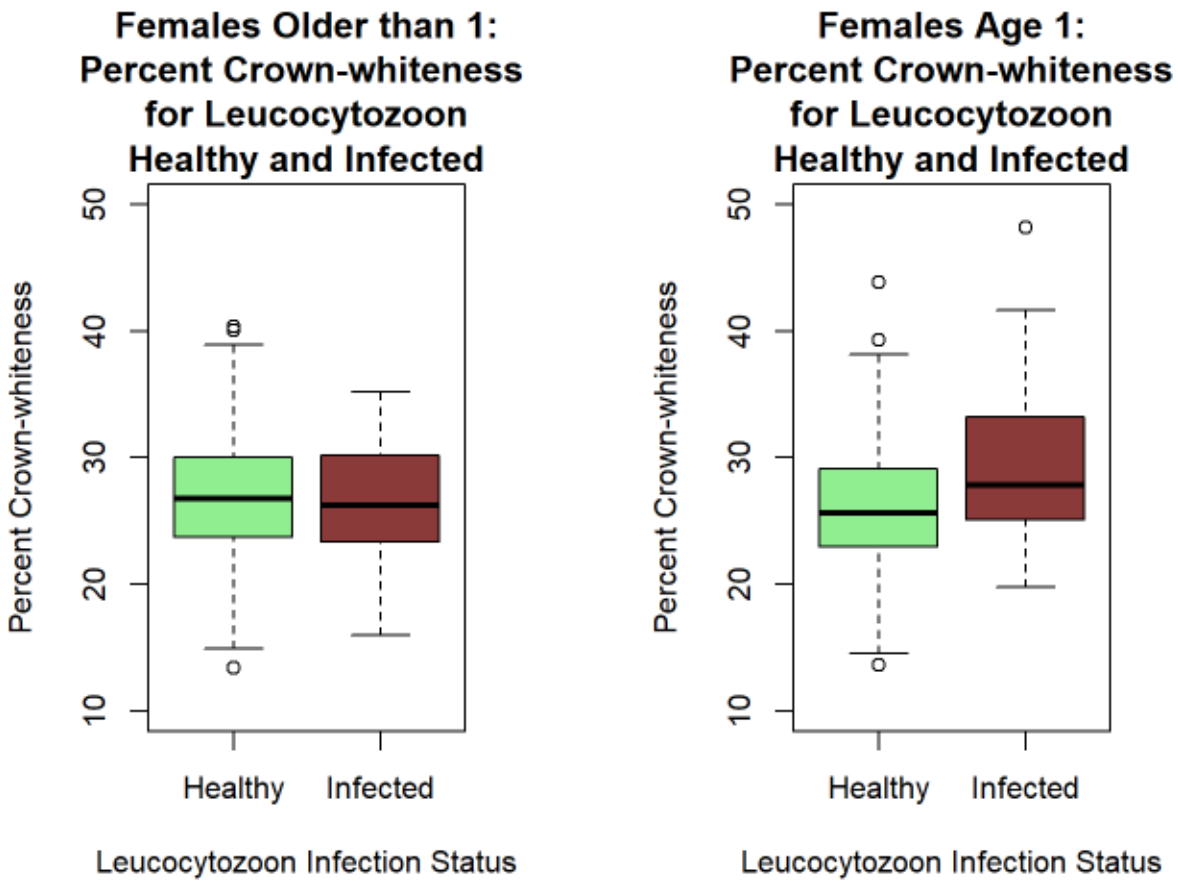

Figure 6. Interaction effects of *Leucocytozoon* infection status with reproductive status (whether they were experienced breeders, i.e. is more than 2 years old). For females age 2 and older, n = 115, with 28 females infected with *Leucocytozoon*; for females age 1, n = 116, with 40 females infected with *Leucocytozoon*. The significant effects of *Leucocytozoon* infection (p =0.002) vary dependent on the animals experienced breeder status (interaction term p = 0.02). Hence, first-year *Leucocytozoon*-infected females had on average crown-whiteness scores that were elevated by 3.72% relative to uninfected ones; this difference disappeared in older females.

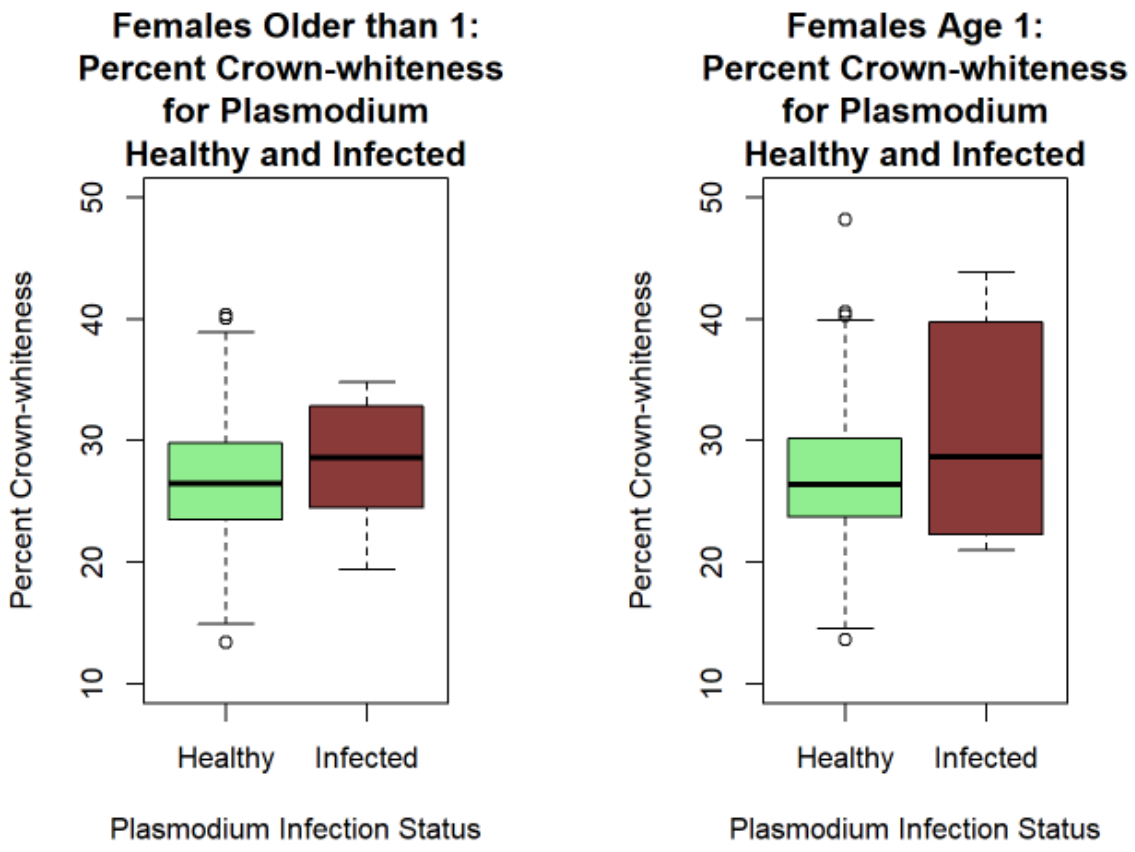

Figure 7. Interaction effects of *Plasmodium* infection status with reproductive status (whether they were experienced breeders, i.e. is more than 2 years old). For females age 2 and older, n = 115, with 15 females infected with *Plasmodium*; for females age 1, n = 116, with 12 females infected with *Plasmodium*. The significant effects of *Plasmodium* infection (p = 0.03) did not vary based on experienced breeder status (interaction term p = 0.39).

Tail Figures

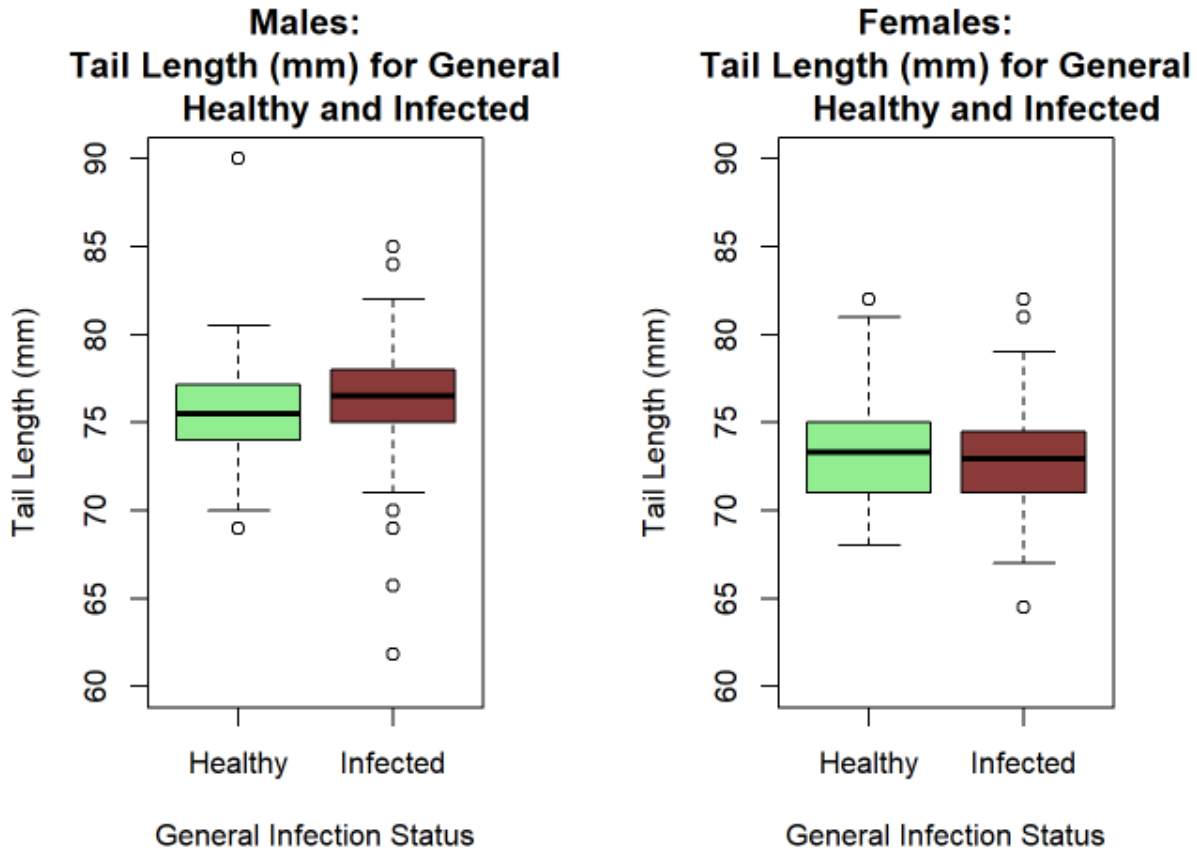

Figure 8. Tail length for general infection status (whether a bird is infected with blood parasites, including asexual or immature cells) by sex. The differences were not significant ($p = 0.08$, $n = 290$, linear regression) for males, nor for females ($p = 0.19$, $n = 231$).

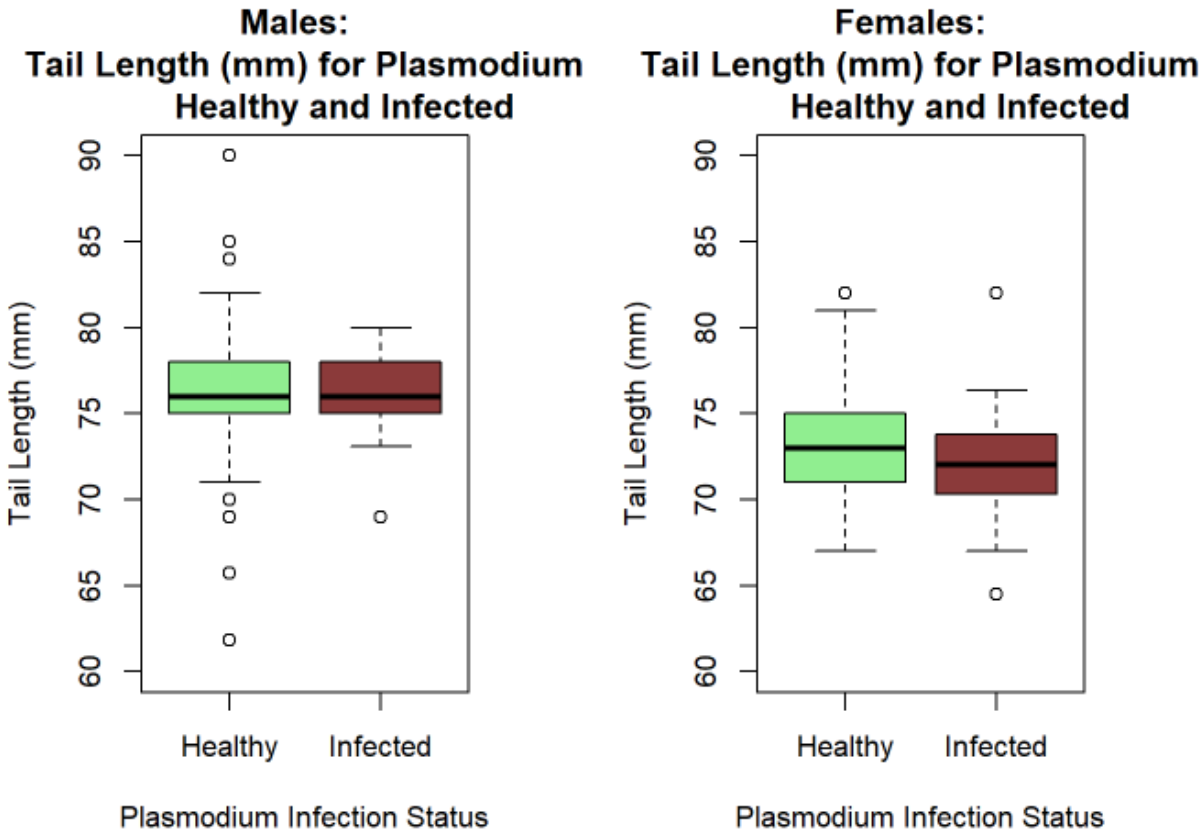

Figure 9. Tail length for *Plasmodium* infection status by sex. The differences were not significant (p = 0.62, n = 290, linear regression) for males, nor for females (p = 0.09, n = 231).

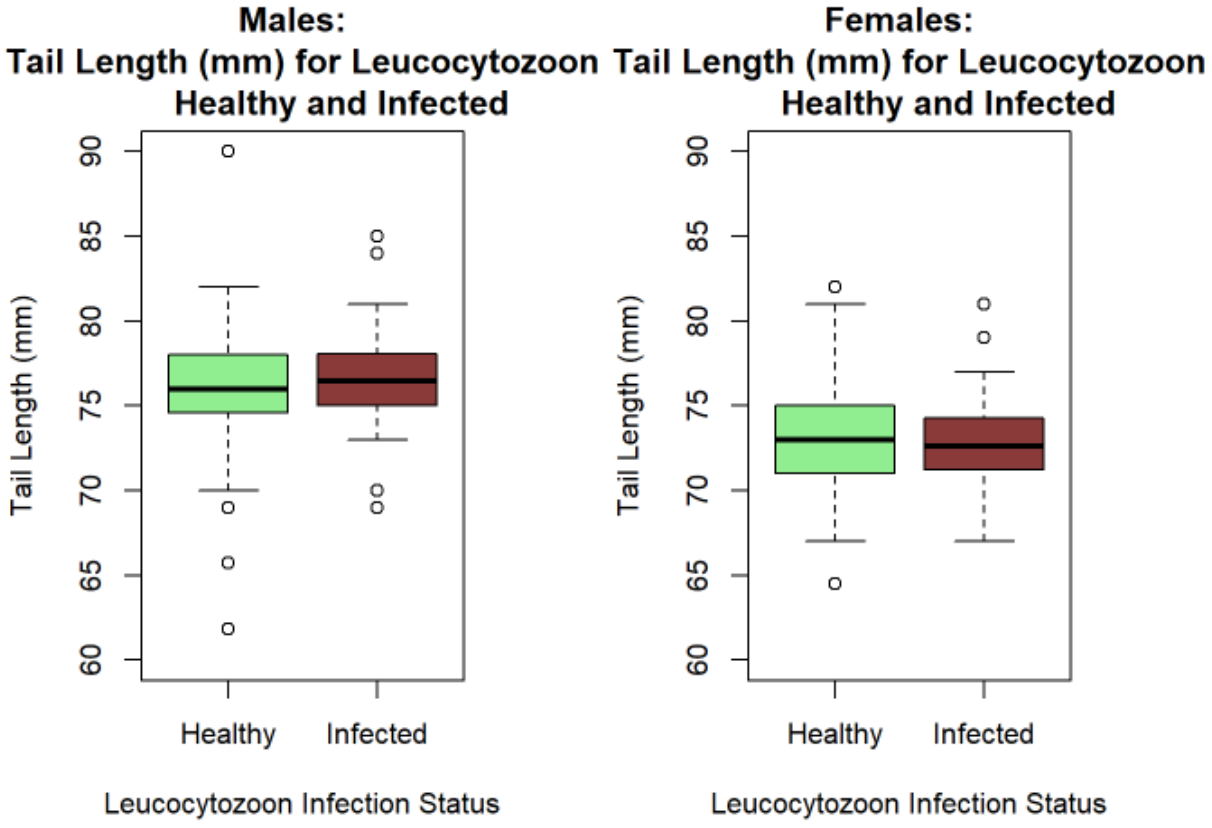

Figure 10. Tail length for *Leucocytozoon* infection status by sex. Infected males had significantly longer tails relative to uninfected males (p = 0.04, n = 290), while for females the differences were not significant (p = 0.95, n = 231).

Wing Figures

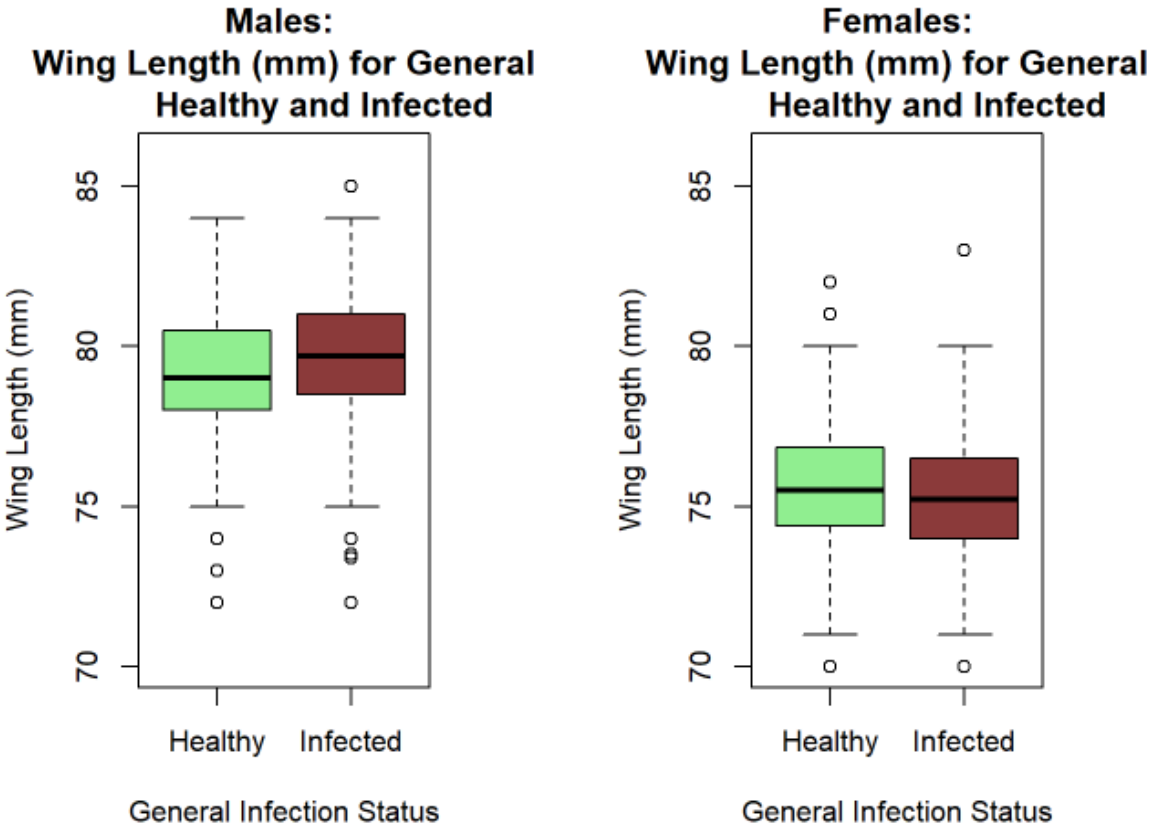

Figure 11. Wing length for general infection status (whether a bird is infected with blood parasites, including asexual or immature cells) by sex. The differences were not significant (p = 0.14, n = 290, linear regression) for males, nor for females (p = 0.22, n = 231).

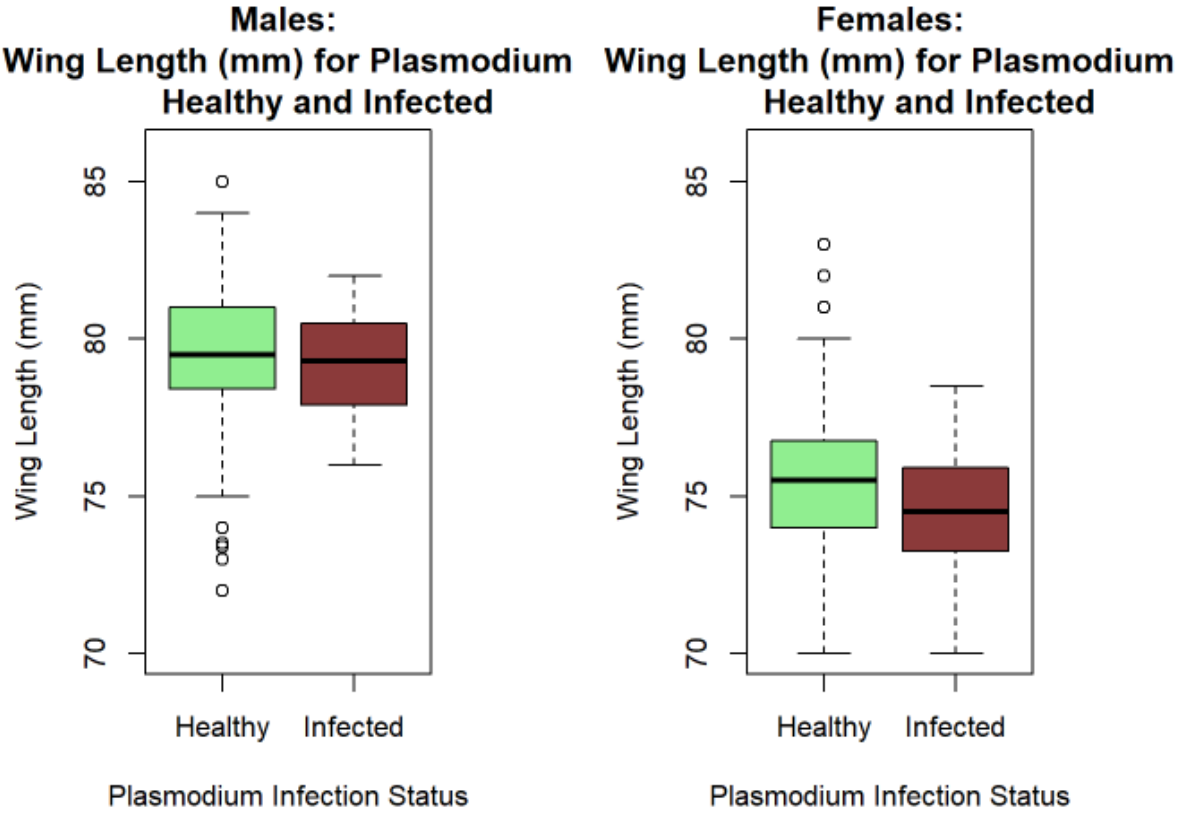

Figure 12. Wing length for *Plasmodium* infection status by sex. The differences were not significant (p = 0.36, n = 290, linear regression) for males, while infected females had significantly shorter wing lengths than non-infected females (p = 0.02, n = 231).

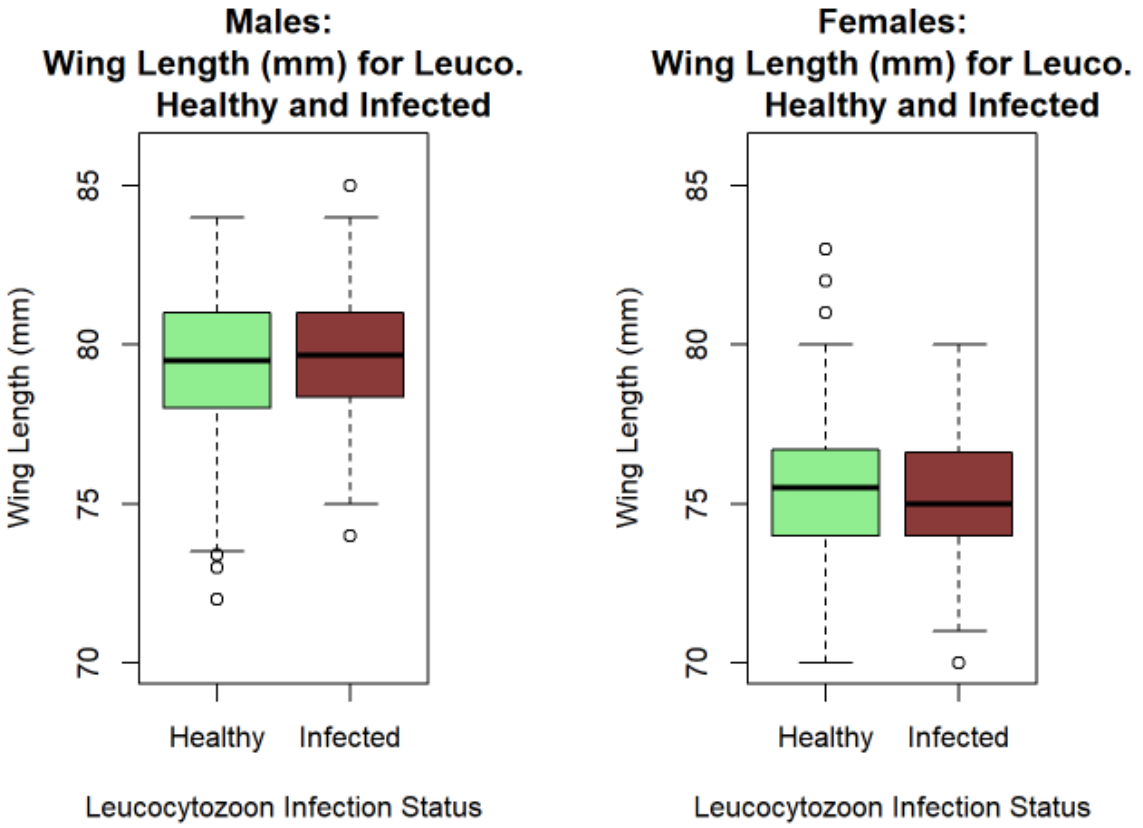

Figure 13. Wing length for *Leucocytozoon* infection status by sex. The differences were not significant (p = 0.11, n = 290, linear regression) for males, nor for females (p = 0.55, n = 231).

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