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**The Relationship Between Parasite Infection, Body Condition, and
Migration in White-Crowned Sparrows and California Towhees**

A Thesis Presented

by

Madeline Galbraith

To the Keck Science Department

of

Claremont McKenna, Scripps, and Pitzer Colleges

In Partial Fulfillment of

The Degree of Bachelor of Arts

Senior Thesis in Biology

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Table of Contents

TABLE OF CONTENTS	2
ABSTRACT.....	3
ACKNOWLEDGEMENTS.....	4
INTRODUCTION	5
MIGRATION.....	5
MIGRATION AND INFECTION.....	5
BODY CONDITION AND INFECTION	8
MIGRATION, BODY CONDITION, AND INFECTION	10
RESEARCH QUESTIONS AND HYPOTHESIS.....	13
METHODS.....	15
BIRD CAPTURING.....	15
PARASITE FECAL EGG COUNTS	16
DATA CLEANUP	17
ANALYSIS	18
RESULTS.....	22
QUESTION 1: DOES MIGRATION EFFECT BODY CONDITION?	23
<i>Season and Species</i>	25
<i>Age and Sex in WCSPs</i>	26
QUESTION 2: DOES MIGRATION EFFECT INFECTION STATUS?	29
<i>Coccidia</i>	30
<i>Eimeria</i>	31
<i>Isospora</i>	32
QUESTION 3: WHAT IS THE RELATIONSHIP BETWEEN INFECTION AND BODY CONDITION? DOES MIGRATION INCREASE WITH THE COST OF INFECTION?	33
<i>Coccidia</i>	35
<i>Eimeria</i>	38
<i>Isospora</i>	40
DISCUSSION	43
WORKS CITED	49
APPENDIX A: PHOTOS OF PARASITES	54
APPENDIX B: DOES THIS EFFECT OF INFECTION ON BODY CONDITION VARY BY SEASON OR SPECIES?	56

Abstract

Long-distance animal migration plays a large role in the spread of infectious disease, potentially causing an increase or a decrease in infection. These outcomes can be serious, as infection has the ability to induce a variety of effects on the host, all which may impact their overall health. The consequences of infection on a host can be measured using body condition. Changes to an individual's body condition are central to the mechanisms involved in migration's ability to both increase (ex: susceptibility) and decrease infection (ex: migratory culling). Therefore, when assessing potential migratory effects, it is important to consider relationships between infection and body condition. To determine migration's role in infection-body condition dynamics, we studied measures of coccidia infection and body condition in a migratory species, White-crowned Sparrows (WCSPs), and controlled for migration using a non-migratory species, CA Towhees. Data was collected in Claremont, CA twice per year for each species, once after WCSP migration in the fall and once before their migration in the spring. We analyzed two data sets, one with both condition and parasite data, and one much larger data set that lacked infection data. Overall, we found significant differences in body condition across species, but only in the subset of individuals with infection data did we see significant seasonal variations and a significant interaction effect of season and species on body condition. Additionally, infection status significantly differed across species, and infected birds were found to be in greater condition than those uninfected. Future research needs to address any potential biases found in the data set with infection data, in addition to increasing sample sizes, to truly understand migration's role in the relationships between infection and body condition.

Acknowledgements

If you had told me four years ago that my Senior Thesis would be a culmination of a year and a half's work of analyzing bird feces and doing research I didn't even know existed, I probably would have transferred on the spot, intimidated by what was in store for me.

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Words cannot express my gratitude to my family for their unconditional love and unwavering support. This endeavor would not have been possible without them. Special thanks to my friends for providing immense encouragement throughout this process. Lastly, I'd like to recognize the CMC community for helping me along this journey. I am incredibly lucky to call CMC my home.

Introduction

Migration

Every year billions of animals undergo long distance seasonal migrations. Individuals typically migrate in search of food, a more suitable climate, or for reproductive success. For example, humpback whales (*Megaptera novaeangliae*) migrate in the summer to feeding grounds rich in krill and small fish near the polar. In the winter, they migrate back to warmer waters and raise their offspring (National Geographic Society 2022). Some individuals migrate to an area with climate conditions better suited for their survival, thus avoiding seasonally enhanced mortality (Binning et al., 2017). This is common for avian species, as research shows that severe winter weather can increase these population's mortality rates, so they migrate elsewhere for a greater chance of survival (Shaw et al., 2019). Thirdly, migration can facilitate an animal in spawning, finding a mate, or raising their offspring, enhancing their reproductive success (National Geographic Society 2022). This is observed in Pacific salmon (*Onorhynchus* spp.) who migrate from the ocean to their natal rivers (National Geographic Society 2022), which are better suited for reproduction, to spawn (Cooke, et al. 2011). As a whole, migration aims to be ultimately beneficial for an individual, however, it can come with unintended consequences.

Migration and Infection

As essential and remarkable migration is for many species, it can play a large role in the spread of infectious disease (Altizer et al. 2011). For example, migratory events have caused spikes in the prevalence of the parasites involved in raccoon rabies (Russell et al. 2005) and human influenza (Viboud et al. 2006). In fact, studies show that between 30-50% of animal species can be classified as parasites and that almost all free-living animals carry at least one parasite species (Poulin and Morand 2000). Additionally, in a study of 10,356 fecal samples of

different avian birds, researchers found 33.4% of these birds to be infected with parasites (Globokar et al. 2017). Given that parasite infection is so common, it is not surprising that relationships exist between infection and such an extensive behavior like migration. However, these relationships can be incredibly consequential, as parasites have the ability to manipulate the host's biology and behavior (Binning et al. 2017). As a result, infection can potentially induce a variety of broad and far-reaching effects on both overall ecosystems (Hatcher et al. 2012), and on individuals (Binning et al. 2017). This makes it incredibly important to understand the relationship between migration and infection.

There are many different ways in which migration can cause either an increase or decrease in infection in a migrating individual (Altizer et al. 2011). Some of these relationships are demonstrated in Figure 1. Decreased infection can occur through migratory escape or

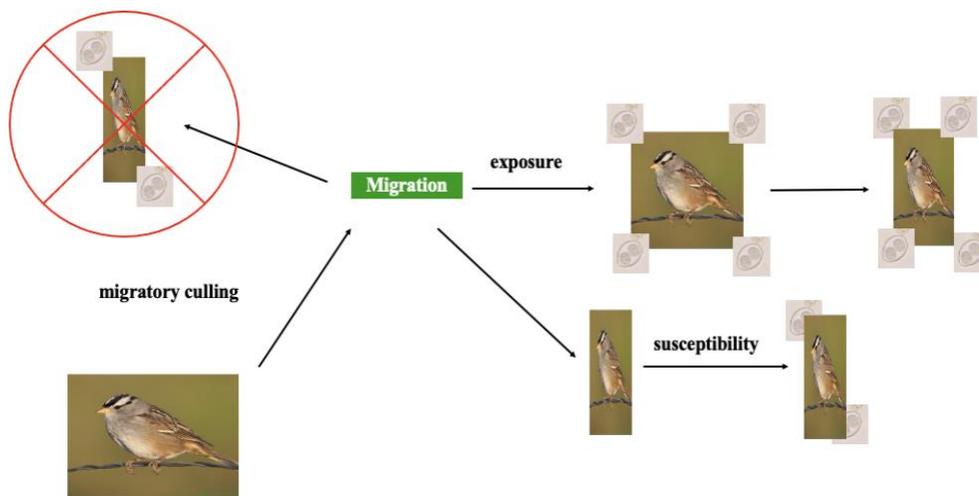


Figure 1. Migration can either increase or decrease infection in the migrant, and body condition may mediate some of these relationships (greater body condition indicated by the increased width of the birds (WCSPs), whereas a narrower WCSP is representative of worse body condition; parasite infection demonstrated by the coccidia oocyte photo overlaying the WCSP).

migratory culling. In migratory escape, infected individuals migrate away from highly-infected environments, reducing their infection risk (Altizer et al. 2011). Migratory culling is when infected individuals die along the migratory journey, and are thus removed from the population, resulting in successful migrants who are relatively less infected (Bradley and Altizer 2005). These are just two of the mechanisms involved in the effect of migration on infection.

On the other hand, migration can increase infection by increasing the migrant's parasite exposure or by increasing their susceptibility to infection. Throughout the migratory journey, migrants interact with different host species and habitat types, thereby increasing their chances of encountering parasites (Altizer et al. 2011). Migrants typically have stopover points along their journey to refuel, and these stops are home to many different migratory species at once, increasing chances of infection transmission (Altizer et al. 2011). In a study of migratory waterfowl, researchers found that individuals who flew longer distances, and thus had more stopover points and opportunities for exposure, were infected with a greater number of parasites and parasite species than those who flew shorter distances (Figuerola and Green 2000). Lastly, migration is one of the most physiologically demanding activities animals can endure (Weber and Stilianakis 2007), and these high migratory costs can weaken immune responses, and result in increased infection susceptibility (Altizer et al. 2011). Overall, this increased infection can cause a variety of significant impacts on the host.

The ability for migration to either increase or decrease infection, and the many of methods involved in each, makes it difficult to fully understand the effect of migration on infection. However, these relationships can be simplified with body condition, which represents an individual's overall health and energetic state (Sánchez et al. 2018). Body condition can mediate the effect of migration on infection and it is often used to measure the consequences of

infection on a host (Sánchez et al. 2018). Specifically, body condition is central to the effect of migration on infection through the mechanisms of migratory culling and susceptibility.

Therefore, when studying migratory effects, it is imperative to consider the relationships between infection and body condition. However, we are going to first remove migration from this framework and decipher the relationships between infection and body condition. We will then be able to better determine the role of migration.

Body Condition and Infection

There is some existing literature on the effect of infection on body condition. For example, one study found that swans and mallard ducks naturally infected with low pathogenic avian influenza virus had a lower body mass, and thus lower body condition, than those individuals uninfected (van Dijk et al. 2015). Interestingly, in another study researchers studying blood parasites in White-crowned Sparrows (*Zonotrichia leucophrys*) noted that infection can decrease body condition and indirectly decrease survival rates (Blanco et al. 2001). Contrary to the swan and mallard duck study, they concluded that infection was not a main contributor to the poor body condition observed in White-crowned Sparrows, however (Blanco et al. 2001).

Overall, there is conflicting research regarding the relationship between infection and condition, and we will try to best synthesize these discrepancies by separately describing negative, positive, and null body condition-infection relationships. A visual depiction of these relationships is demonstrated in Figure 2.

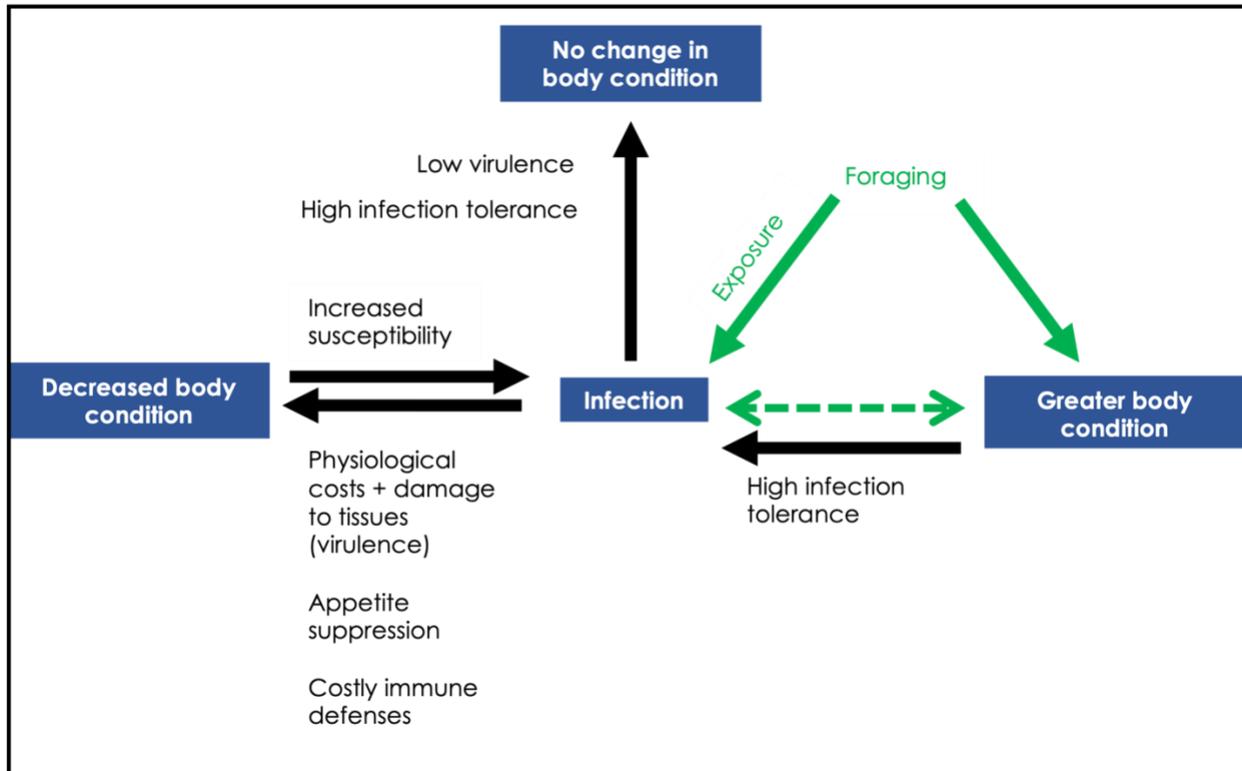


Figure 2. The potential relationships between infection and body condition, in addition to the impact of foraging (green). Solid arrows indicate direct effects and the dashed arrow represents indirect effects.

Parasites exploit the host's resources (Combes 2001), which can decrease body condition and result in a negative body condition and infection relationship. Parasites may employ physiological costs, such as causing lethargy, and damaging the host's tissues and functions (Binning et al. 2017). Infection can also limit foraging activity, potentially as a way to conserve energy, thereby worsening condition (Binning et al. 2017). Additionally, costly immune responses can negatively impact condition. Endotherms, such as house finches (*Carpodacus mexicanus*), have been found to experience even greater energetic costs when fighting infection given the energy required to both fight infection and thermoregulate (Hawley et al. 2012). Just as infection can worsen condition, poor condition can cause susceptibility, predisposing an individual to infection. Those in worse condition may have weak immune defenses, and experience a higher parasite load or a longer infection duration (Beldomenico and Begon 2010).

However those in greater condition may have more robust immune systems and be less susceptible to infection (Sánchez et al. 2018). This generates a feedback loop between infection and condition.

Foraging can indirectly drive a positive condition-infection relationship. In a study of Great Tits (*Parus major*), those more dominant within the social hierarchy foraged more, and were thus in greater condition (Carrascal et al. 1998). However, foraging increases exposure to parasites, seemingly promoting infection in individuals with better condition (Sánchez et al. 2018). Tolerance, in which an infected individual is able to offset the consequences of infection on fitness, may also contribute to a positive infection-condition relationship (Roy and Kirchner 2000). For example, those in good condition with robust immune systems may be able to tolerate high parasite loads, resulting in this positive relationship (Sánchez et al. 2018). There can also be null infection-condition relationships, also due to high infection tolerance or low parasite virulence. Bats, for instance, are often infected with parasites that are highly virulent in other species, but for whatever reason these specific parasites are not very virulent for the bat, resulting in them asymptotically carrying the parasites (Wynne and Wang 2013). Their body condition does not change as a result of infection.

Now that we have broken down the various body condition and infection relationships, we can re-introduce migration to these dynamics, specifically to explain the mechanisms of migratory culling and increased susceptibility.

Migration, Body Condition, and Infection

The relationships between infection and body condition provide the basis for our understanding of migration's role in these dynamics. As mentioned above, the effects of migration on infection are often mediated by body condition, as seen in migratory culling, and increased susceptibility. In migratory culling, the cost of infection on the migrant reduces their

ability to complete migration (Sánchez et al. 2018). This limited migratory ability may be due to the parasite causing decreased endurance (Bradley and Altizer 2005), or even problems in limb function (Thomas and Poulin 1998). The reduction in migratory ability is regarded as a worsening in body condition, as a result of infection. Decreased body condition increases the infected individual's chances of mortality throughout the migratory journey.



Figure 3. Migratory culling results in the mortality of those infected and in poor condition, resulting in decreased infection and greater body condition among the surviving migrants.

Therefore, individuals who successfully migrate will inevitably be less infected and in greater body condition relative to the deceased (Peacock et al. 2020), and this is depicted in Figure 3.

Migration is also able to increase infection by increasing an individual's susceptibility to infection, as seen in Figure 4. Migration is known to be one of the most physiologically demanding activities animals can endure (Weber and Stilianakis 2007). The associated high energetic demands can worsen body condition and compromise host immunity, such that they have fewer resources available for an immune response, and their immune defenses are more costly. As a result, these individuals are highly susceptible to infection, and they may experience higher parasite loads or a longer infection duration than those less susceptible and in better condition (Weber and Stilianakis 2007). This highlights the negative feedback mechanism

between condition and infection, specifically that infection decreases body condition, increases susceptibility and infection, which in turn can decrease condition (Sánchez et al. 2018). This cycle will repeat itself, which suggests the interconnected nature of infection, body condition, and migration. These overlaps make researching these relationships very difficult, specifically the impact of migration on infection and body condition.

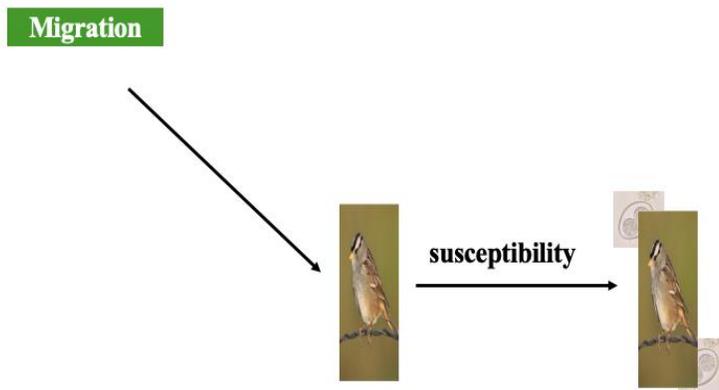


Figure 4. Migratory demands can reduce body condition, weakening immune responses and resulting in increased infection susceptibility.

To study the role of migration in the relationships between infection and body condition, we used two different species of birds - one migratory species, White-crowned Sparrows (*Zonotrichia leucophrys*; WCSP), and one non-migratory species, CA Towhees (*Melozone crissalis*). CA Towhees are non-migratory species that exist year-round on the pacific coast from Southern Oregon to Baja California, Mexico (Benedict et al. 2020). WCSPs migrate in the fall

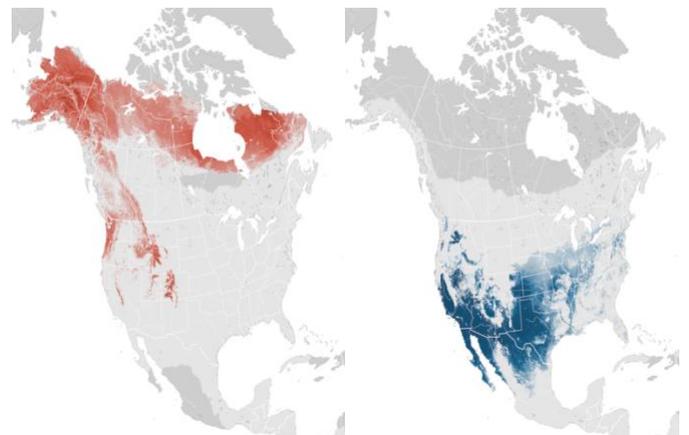


Figure 5. WCSP distribution before (red) and after (blue) fall migration. [Adapted from (Auer 2022)].

from the arctic circle to the Pacific Southwest, and return back north in the spring (Figure 5) (Lisovski et al. 2019). We focused on the common intestinal protozoa, coccidia, as it has been found to be the most common parasite infection in avian species (Figure 6) (Globokar et al. 2017). We were able to analyze the relationships between infection, body condition, and migration by comparing the infection and body condition of both species caught in the fall (after WCSP migration) and in the spring (before WCSP) migration.

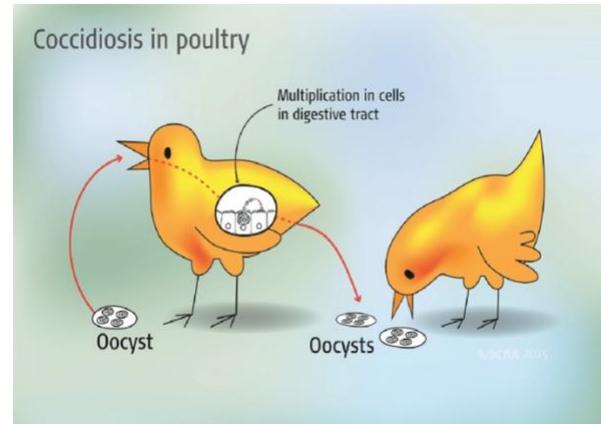


Figure 6. A life cycle diagram of coccidia infection in poultry (coccidiosis is the disease caused by coccidia infection). Host's ingest coccidia oocytes, which complete their life cycles within one host, and these oocytes are ultimately released in feces (Lu et al. 2021).

[Figure adapted from (Nesse et al. 2019)].

Research Questions and Hypothesis

We had three main research questions:

1. *Does migration effect body condition?*

Given the cost of migration, we hypothesized WCSPs would be in worse condition overall. Specifically, we expected that their body condition would be worse in the fall after the taxing migratory journey, than in the spring after overwintering and preparing for migration.

2. *Does migration effect infection status?*

If migratory culling was occurring, we would expect WCSPs to be less infected in the fall. The high costs of migration and infection would cause the removal of most of the infected WCSPs from the population during the fall migration. As a result, CA Towhees and WCSP would likely have similar infection statuses.

If migration increased the exposure of WCSPs to parasites, we would expect WCSPs to be more infected than CA Towhees. Additionally, if migration led to increased susceptibility, we would also likely find more infection in WCSPs as a result of the cost of migration on body condition, leading to their increased susceptibility to infection.

3. *What is the relationship between infection and body condition? Does migration increase the cost of infection?*

We predicted that those in worse condition would have a greater parasite prevalence and intensity, either due to the cost of infection on body condition or due to poor body condition predisposing them to infection. If migration does increase the cost of infection, we would expect the reason for their increased susceptibility to be due to the migratory costs on body condition. However, if migratory culling occurs, we would see that WCSPs would be in better condition (and less infected) in the fall than in the spring.

Methods

Bird Capturing

White-crowned Sparrows and CA Towhees were captured at the Bernard Field Station (BFS) in Claremont, California between October 2016 and March 2022. Baited traps (8x8x8 inch, made of hard-ware cloth) were open 2-3 days per week for 2-3 hours per day for 3 weeks in October and 3 weeks in February/March. This resulted in the traps being open for approximately 24 hours in the fall and 24 hours in the spring. Traps were checked every 15 minutes for captured birds. The captured birds were put in a light-weight cotton bag for about 5 minutes until standard measurements could be taken. Birds caught for the first time were banded with a USGS aluminum band that had a unique 9-digit identification number and recaptured birds retained this band from their first capture. Sex was only determined for White-crowned Sparrows. Using a 26-gauge needle and a capillary tube, 25 up to 45 μL of blood was taken from the brachial wing veins of the WCSPs. Several drops of blood were taken and stored on Whatman FTA Classic Cards for future sexing using PCR. Only 269 birds (all new captures) out of the 347 White-crowned Sparrows (both first time and recaptured birds) examined had sex data, which was provided to us by Professor Elise Ferree.

Age could also only be determined for White-crowned Sparrows. Overall, young birds had brown feathers and adult birds had white feathers on the crowns of their heads. Age classes are distinguished by single-digit numeric codes. We found 4 different classes amongst our captured birds. These classes were: 1 (After Hatching Year), 2 (Hatching Year), 5 (Second Year), and 6 (After Second Year). Those with age codes of 1 in the fall or 6 in the spring were likely in their second winter in the BFS. Moreover, those with age codes of 2 in the fall or 5 in the spring were likely in their first winter at the BFS. For the purposes of our analyses, we

categorized the birds with an age code of 1 and 6 to be “Adults” and 2 and 5 to be “Young” (DeSante et al. 2022).

The bird mass was measured using a spring scale while the bird was in the bag, and the weight of the bag was subtracted from this value to determine the bird’s mass. The wing chord length was measured with a wing ruler. We calculated the ratio of each observation’s mass and wing chord length. This mass to wing chord ratio controls for the effect of size on the body, and was used as our measurement of body condition in later analyses (Sánchez et al. 2018). Similar size-corrected mass ratios have been used in the past as measurements of body condition, for example in studies of Anatidae and coots (*Fulica atra*) (Mateo et al. 1998) and in red knot shorebirds (*Calidris cantus rufa*) (Duijns et al. 2017). A greater ratio value indicates better body condition, and thus better overall health and energy reserves of an individual (Sánchez et al. 2018). Finally, the bird bags were examined for fecal samples and any samples found were collected in plastic containers for future analysis for parasites. All birds were then released back in the BFS. This data was entered into an Excel sheet termed “capture data.”

Parasite Fecal Egg Counts

To measure the parasite load of the host, fecal egg counts were performed on the fecal samples collected at the bird capturing events. These fecal samples were refrigerated until they were weighed to later calculate the fecal egg counts per gram of feces. The fecal weight was calculated by subtracting the weight of the empty plastic container storing the feces from the combined weight of the feces and container. The samples were then stored in formalin until examination to preserve the sample. The solution of the fecal sample and the formalin was poured into the body of the fecalyzer device. Fecazol was added to the device to enable the parasite eggs to float up to the top of the fecalyzer. An insert inside the device was twisted back and forth for 90 seconds to crush the fecal samples, release the oocytes, and mix the solution.

More Fecasol was added to create a meniscus on the top of the device, and a cover slip was then placed on top of the meniscus. The coverslip was left on the meniscus for 10-15 minutes for the water near the top of the device to cling to the coverslip and transfer the oocytes to the slide. The cover slip was then transferred to a microscope slide.

The cover slip on the microscope slide was examined with a microscope at 20x magnification to examine the parasitic content in each sample. The number of coccidia, specifically *Eimeria*, *Isospora*, *Caryospora*, *Cryptosporidium*, and *Sarcocystis*, was recorded. The number of nematodes, specifically *Capillaria* and *Strongylids*, was also recorded. Lab members were trained on how to identify the parasites visually and they inputted the data into the parasite data Excel sheet (see Appendix A). To measure infection, we determined the presence or absence of a parasite in each observation, parasite prevalence (proportion of individuals infected with a parasite), and parasite intensity (the average number of individual parasites in an infected host) (Shaw et al. 2018). To specifically measure intensity, we calculated the number of parasites per gram of feces for each sample.

Data Cleanup

The bird capture and parasite data entries were double checked and cleaned up prior to running analyses. When we matched the observations in the parasite data to their corresponding entries in the capture data set, we found many mistakes and discrepancies between the two. There were many parasite observations that did not match an observation in the capture data and we then investigated the probable mistakes to ensure all parasite observations had a capture match. The most common mistake was typos in the recorded capture date of observations in both the parasite and capture data sets. Therefore, to determine the actual capture date of a particular tag number, we found its entry in scans of the handwritten capture sheets that were used at the BFS the day of the capture. We could then correct the data. There were also typos in many of the

tag numbers recorded in both data sets. To make the appropriate changes, we often had to find the indicated tag number's fecal sample tube, which was labeled with its corresponding tag number and capture date, and determine if the mistake in data entry was due to accidentally skipping digits when re-typing the tag number or due to difficulties in reading the handwriting on the sample tube. We ultimately fixed all the mistakes we found and this error checking was imperative to having complete and accurate data sets.

We then removed extreme outliers from the data sets because they likely indicated errors in data collection/recording. For example, WCSPs with a mass greater than 32 and Towhees with a mass greater than 52 were dropped from the capture data. In these cases, the mass of the bag was probably not subtracted from the total bird and bag weight. Some samples in the parasite data set did not have fecal weights, so the parasite eggs per gram calculation, our measurement of infection intensity, was unusable for these samples. Therefore, these observations were dropped from our infection intensity analyses but used for infection prevalence analyses.

After these edits, the capture data included data for 224 CA Towhees and 347 White-crowned Sparrows (both recaptured and new birds). We had mass and wing chord data for 191 of these CA Towhees and 320 of the WCSPs, so condition could be calculated. The capture and parasite data were then merged by the bird tag number and capture date using RStudio. Therefore, this merged data set only contained capture and parasite data for the birds we had parasite data for. We refer to this data set as the "combination data." The combination data included data for 50 CA Towhees and 99 White-crowned Sparrows. Forty-six Towhees and 93 WCSPs had mass to wing chord ratios.

Analysis

There were some birds caught multiple times and thus counted for twice in both the capture and combination data sets but represented as separate observations. We took these

repeated measurements into account by including tag number, which remained the same throughout recaptures, as a random effect in our statistical analyses. We generated histograms for both the capture and combination data sets to determine how many recapture events were present in our data sets. RStudio was used for all statistical analyses and graphs. An alpha level of 0.05 was used for all statistical tests and as mentioned above, the mass to wing chord ratio was used as our measurement of body condition.

A linear mixed effects model (LMM) was performed to determine the effect of species, season, and their interaction (season:species) on body condition. Tag number was included in the models as a random effect. This analysis was run twice, once with the capture data (n=511) and once with the combination data (n=139). We used both data sets in this analysis to determine if the same statistical conclusions could be made from both data sets. It was important to determine if the combination data, the only data set used in the parasite analyses, was unbiased and an accurate representation of the data in the capture data set. We would then be better able to verify our prediction that WCSPs would be in worse condition and more infected than CA Towhees as a result of migration.

We determined the potential effect of covariates, such as sex, age, and season, on body condition in WCSPs. We did not have age or sex data for CA Towhees, so only WCSPs were included in these analyses. LMM analyses were performed for the capture data set only and tag number was included as a random effect. However only WCSP observations that included both age and sex data were used in the analysis. Out of the 347 observations in the capture data, only 269 had sex data and 235 had age data, but only 181 observations had both age and sex data to be used in the analysis.

Next, we tested for differences in infection between WCSPs and CA Towhees and by season. We performed three separate analyses to determine the effect of season, species, and their interaction (season:species) on infection presence -- one for coccidia presence, one for *Eimeria* presence, and one for *Isospora* presence. All three analyses were binomially distributed so we assessed these effects with general linear mixed models. Tag number was included as a random effect and the combination data set was used for all three analyses (n=149).

Because we found differences in infection in the above analyses, we next determined the effect of infection (both the presence and intensity) on body condition for both seasons and species. In addition to coccidia, we also studied the two main types of coccidia infection: *Eimeria* and *Isospora*. We ran three separate LMM analyses of infection presence -- one for coccidia presence, one for *Eimeria* presence, and one for *Isospora* presence -- to determine the effect of each, in addition to the effect of season, species, and their interaction (season:species), on body condition. All three analyses included tag number as a random effect and used the combination data set (n=139). To assess if the effect of infection on body condition varies by season or season, we included the interaction of infection presence and species (coccidia/*Eimeria*/*Isospora* presence:species) and the interaction of infection presence and season (coccidia/*Eimeria*/*Isospora* presence:season) in the three separate analyses. However, the effect of these interactions was not significant and thus dropped from the analyses (see Appendix B).

We ran three separate general linear mixed models (GLMER) for coccidia intensity, *Eimeria* intensity, and *Isospora* intensity, and determined the effect of each parasite intensity, in addition to the effect of the season, species, and their interaction, and the interaction of infection intensity and season and species on body condition. The three models all had negative binomial

distributions and thus the mass to wing chord ratios for all three analyses were converted to integers.

Intensity was measured by the count of specific parasite eggs per gram of fecal weight. However, fecal weights were absent for some infected individuals and thus dropped from infection intensity analyses. Sixty four out of 91 coccidia infected observations, 41 out of 62 *Eimeria* infected observations, and 49 out of 56 *Isospora* infected observations were used in each intensity analysis. Additionally, there was no *Eimeria* intensity data from the spring and thus season was dropped from the *Eimeria* intensity analysis. Tag number was included as a random effect and the combination data set was used (n=139) for all three models.

Results

Although we were not focused specifically on recaptured birds, we took repeated measurements into account by including tag number as a random effect in our statistical analyses. Thus, we were interested in determining exactly how much of our data set was comprised of recaptured birds and how many of these observations were actually repeated measurements. To do this, we calculated the number of birds per frequency of recapture events (Figure 7). Recapture events in the capture data ranged from 1 to 9 recaptures and 38.2% of the capture data observations were recaptures. Recapture events in the combination data ranged from 1 to 5 events and 16.7% of observations were recaptures.

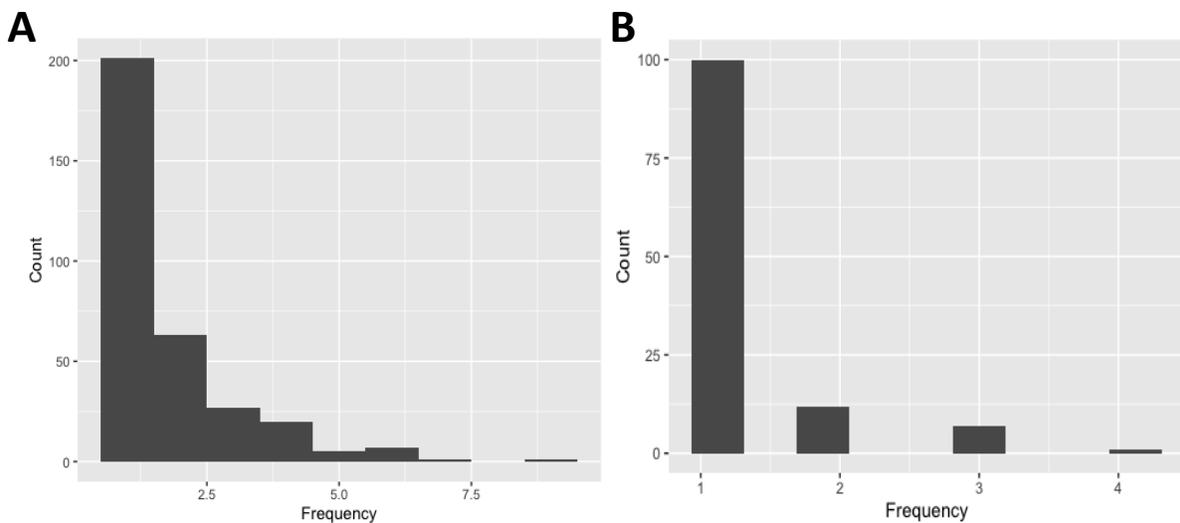


Figure 7. The number of birds caught per frequency of recapture events in the full capture data set (A) and the smaller combination data set for which infection data were available (B).

Question 1: Does migration effect body condition?

To assess the effect of season and species on body condition in WCSPs, we used both the capture and combination data sets. We used both data sets to assess if the combination data set was unbiased and representative of the capture data set. This helped inform later analyses in our study that required parasite data and thus only the combination data could be used for those analyses. However only the full capture data set was used for analyses of age and sex given its larger sample size. Sample sizes differed slightly in each analysis and thus the total number of observations are broken down into the specific characteristics assessed. This is demonstrated in Table 1 for the capture data and Table 2 for the combination data.

Table 1. Sample sizes of characteristics assessed in the capture data to answer Question 1.

	White-crowned Sparrow	California Towhee	Grand Total
Fall	131	110	241
Unknown Sex	32		
Adult	20		
Young	8		
Unknown Age	4		
Female	50		
Adult	28		
Young	12		
Unknown Age	10		
Male	49		
Adult	34		
Young	8		
Unknown Age	7		
Spring	189	81	270
Unknown Sex	37		
Adult	10		
Young	10		
Unknown Age	17		
Female	75		
Adult	21		
Young	21		
Unknown Age	33		
Male	77		
Adult	32		
Young	11		
Unknown Age	34		
Grand Total	320	191	511

Table 2. Sample sizes of characteristics assessed in the combination data to answer Question 1.

	White-crowned Sparrow	California Towhee	Grand Total
Fall	63	34	97
Spring	30	12	42
Grand Total	93	46	139

Season and Species

We were interested in determining the overall body condition, measured by the mass to wing cord ratio, for CA Towhees and White-crowned Sparrows in the fall and in the spring. We used both the capture data and the

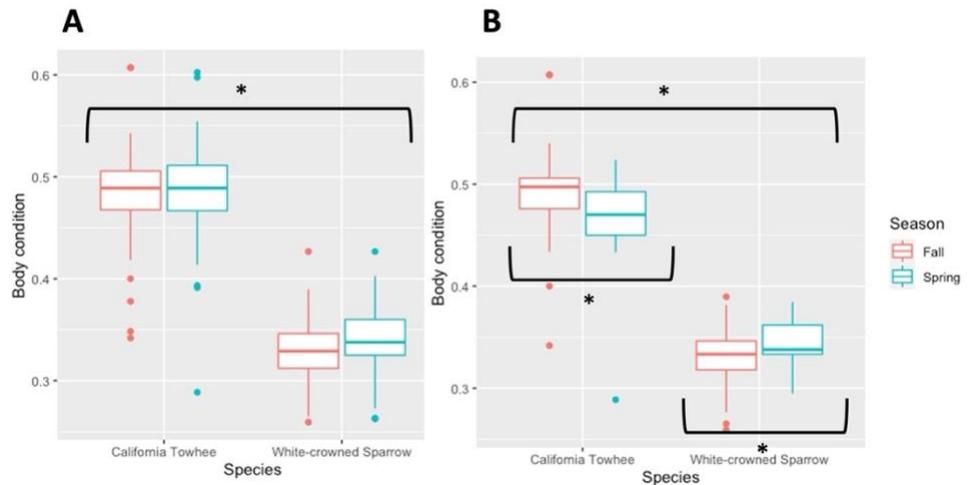


Figure 8. There was a significant interaction effect of season and species on BC in the smaller combination data set ($p < 0.001$; B), but not in the capture data ($p = 0.116$; A). There were significant differences in BC across species ($p < 0.001$; A & B) but significant seasonal variations in BC were only found in the combination data ($p < 0.001$; B).

combination data in our analyses to ensure the combination data set was unbiased. In the capture data analysis, there was no significant interaction effect of season and species on body condition ($p = 0.116$; Table 3; Figure 8A). Towhees were in greater body condition than WCSPs ($p < 0.001$; Table 3). There was also no relationship between season and body condition ($p = 0.77$; Table 3).

Table 3. The effect of season, species, and the interaction of season and species on body condition using the capture data set (511 observations for 317 individuals).

	Estimate \pm SE	df	t-value	p-value
Species	-0.155 \pm 0.00437	438	-35.5	<0.001
Season	0.00140 \pm 0.00473	501	0.295	0.768
Season:Species	0.00931 \pm 0.00597	500	1.57	0.116

Interestingly, when the same analyses were run with the combination data, there was a significant interaction effect of season and species on body condition ($p < 0.001$; Table 4; Figure 8B). Towhees were in greater body condition than WCSPs ($p < 0.001$; Table 4; Figure 8B) and there was a significant relationship between season and condition ($p < 0.001$; Table 4).

Table 4. The effect of season, species, and the interaction of season and species on body condition using the combination data set (139 observations for 115 individuals).

	Estimate±SE	df	t-value	p-value
Species	-0.163±0.00777	125	-21.0	<0.001
Season	-0.0425±0.0113	133	-3.77	<0.001
Species:Season	0.0635±0.0133	127	4.80	<0.001

Age and Sex in WCSPs

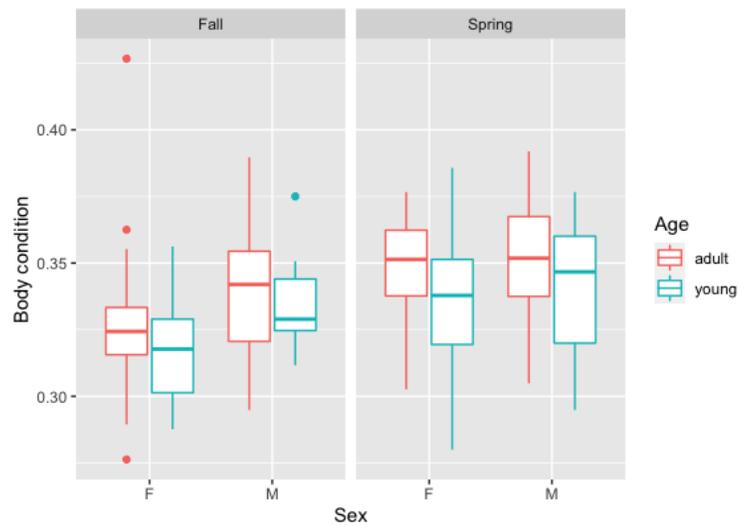


Figure 9. The relationship between sex (F=female, M=male), season (fall and spring), and age on body condition in WCSPs using the capture data.

We were interested in determining the relationships between potential covariates, such as age, sex, and season on body condition in WCSPs. We only used the capture data set for these analyses given the larger sample size. There was no sex or age data recorded for Towhees so only WCSPs were included. Table 5 reports the results of this analysis. As seen in Figure 9, body condition varied by sex, season, and age in WCSPs, and although our statistical model included all three of these factors, we decided to generate single factor figures to better visualize the statistical results (Figure 10).

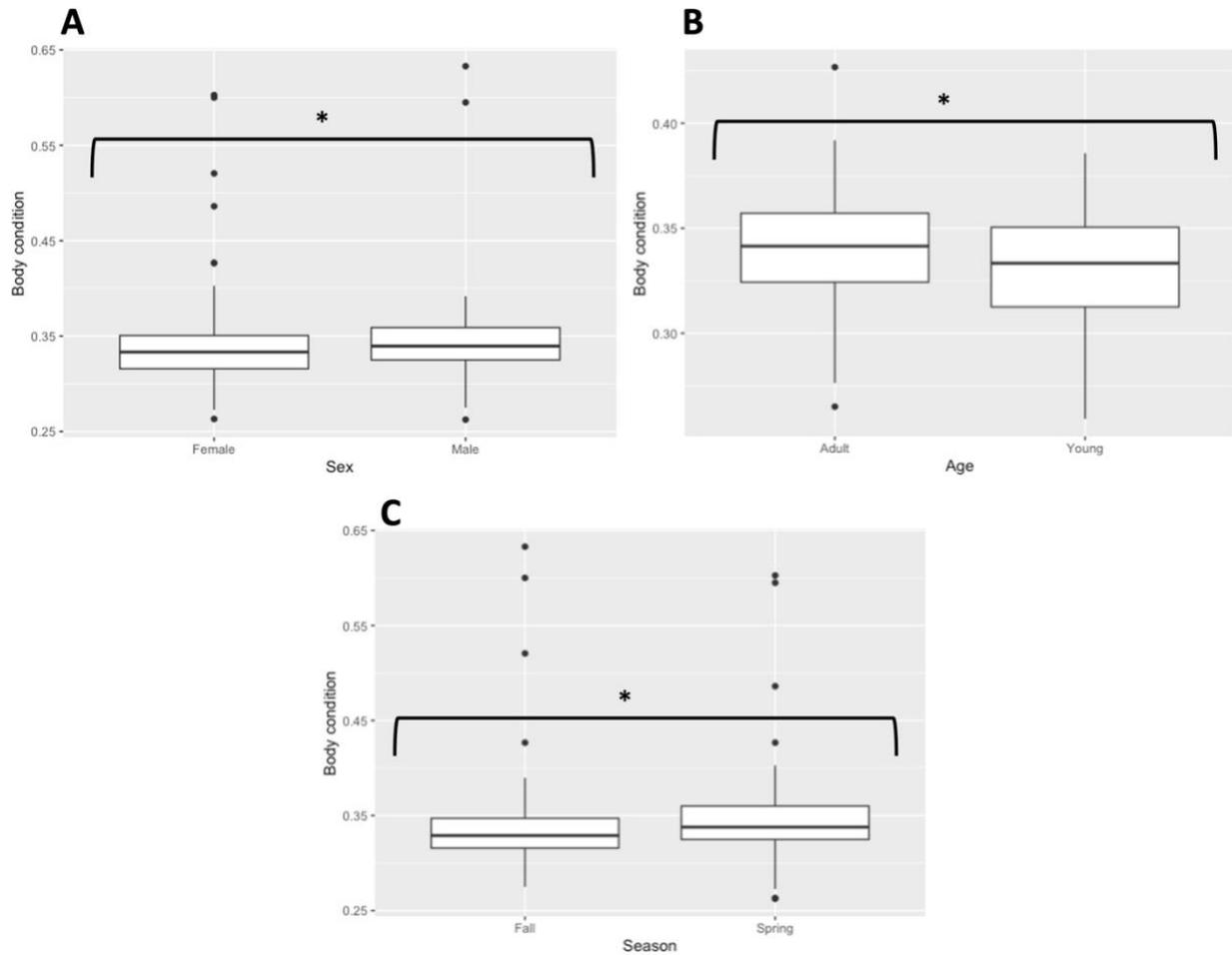


Figure 10. There were significant differences in body condition across sex ($p=0.02$; A), age ($p=0.04$; B), and season ($p<0.001$; C) in WCSPs using the capture data.

Overall, there were significant seasonal differences in body condition, such that WCSPs in the spring were in greater body condition than those in the fall ($p<0.001$; Figure 9 & Figure 10C). Additionally, male WCSPs were in significantly greater body condition than females ($p=0.02$; Table 5; Figure 9 & Figure 10A), but greater body condition was exhibited for both sexes in the spring (Figure 9). Adult WCSPs had significantly greater body condition than did young WCSPs ($p=0.04$; Table 5; Figure 9 & Figure 10B), but both adult and young WCSPs were in greater body condition in the spring (Figure 9).

Table 5. The effect of sex, season, and age on body condition in WCSPs using the capture data (167 observations for 122 individuals).

	Estimate ± SE	df	t-value	p-value
Sex	0.00938±0.00385	91	2.44	0.0169
Age	-0.00877±0.00416	143	-2.11	0.0369
Season	0.0158±0.00375	162	4.21	<0.001

Question 2: Does migration effect infection status?

Before we analyzed body condition, we determined the species and seasonal differences in parasite infection. Because parasite data was required for these set of analyses, we could only use the combination data set. The sample sizes of observations assessed for Question 2 differs from those displayed in Table 2 because in these next set of analyses, our observations did not require body condition data, thereby increasing our sample size.

Table 6 Table 6 demonstrates the breakdown of the number of specific observations used in the analyses used to answer Question 2.

Table 6. Sample sizes of characteristics from the combination data assessed to answer Question 2.

	White-crowned Sparrow	California Towhee	Grand Total
Coccidia Presence			
Fall	69	38	107
No	18	19	37
Yes	51	19	70
Spring	30	12	42
No	14	7	21
Yes	16	5	21
Eimeria Presence			
Fall	69	38	107
No	37	22	59
Yes	32	16	48
Spring	30	12	42
No	18	10	28
Yes	12	2	14
Isospora Presence			
Fall	69	38	107
No	27	27	54
Yes	42	11	53
Spring	30	12	42
No	30	9	39
Yes	0	3	3
Grand Total	99	50	149

Coccidia

There was no significant interaction effect of season and species on the presence of coccidia infection ($p=0.58$; Table 7; Figure 11), nor was there a significant seasonal effect ($p=0.57$; Table 7). However, there was a significant difference in coccidia presence across species ($p=0.03$; Table 7). Due to variations in sample sizes, these species differences are better demonstrated in a graph of coccidia prevalence rather than of the count of infected individuals (Figure 11B). Overall, WCSPs were more infected with coccidia than CA Towhees.

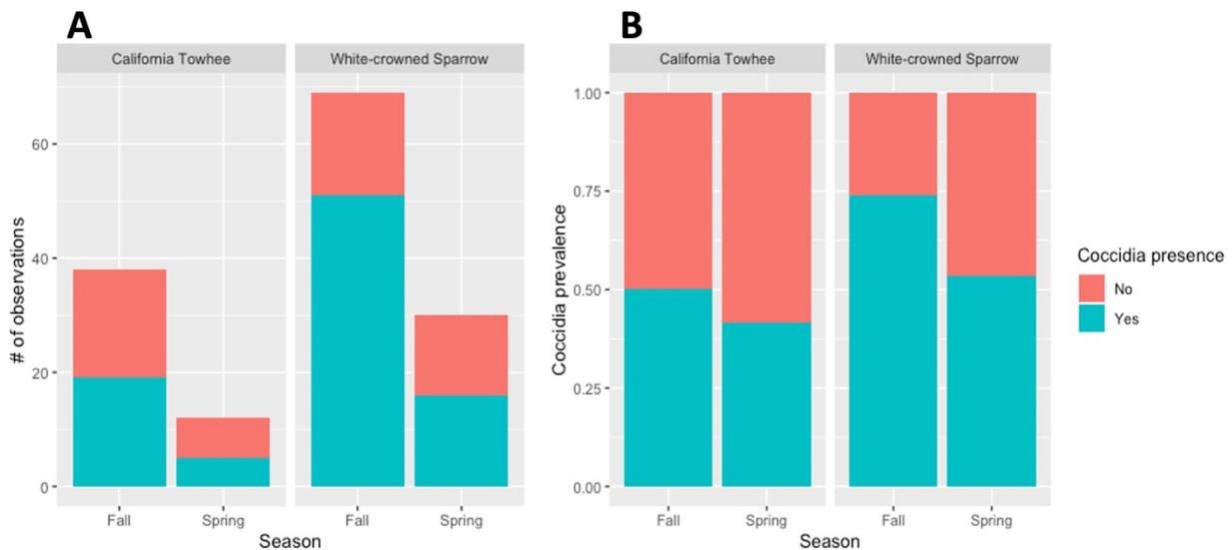


Figure 11. WCSPs were significantly more infected with coccidia than CA Towhees ($p=0.03$), as seen in measurements of the count of coccidia infected observations (A) and of coccidia prevalence (B) across season and species.

Table 7. The effect of season, species, and the interaction of season and species on coccidia presence (149 observations for 120 individuals).

	Estimate±SE	z-value	p-value
Season	-0.464±0.814	-0.570	0.569
Species	1.24±0.556	2.23	0.0255
Season:Species	-0.532±0.969	-0.549	0.583

Eimeria

Similar to coccidia infection, there was no significant interaction between season and species on *Eimeria* presence ($p=0.23$; Table 8; Figure 12). There were also no significant variations in *Eimeria* presence across season ($p=0.11$; Table 8) or species ($p=0.70$; Table 8), and this is exhibited in graphs of both the count of *Eimeria*-infected observations and of the prevalence of *Eimeria* infection (Figure 12).

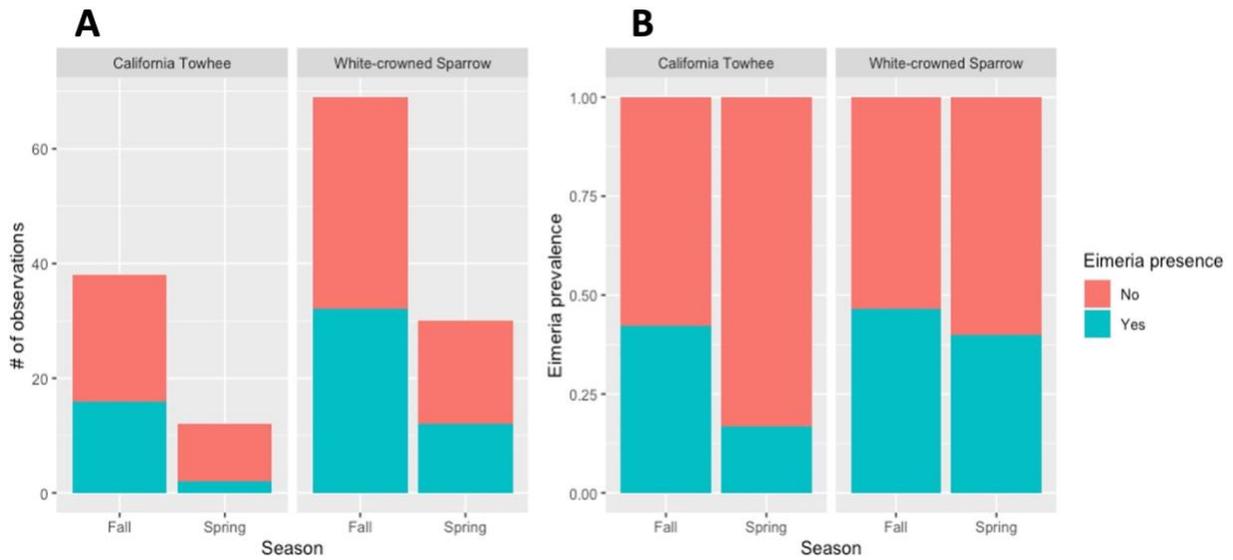


Figure 12. There was no significant interaction effect of season and species on *Eimeria* presence ($p=0.23$), nor were there significant seasonal ($p=0.11$) or species ($p=0.70$) differences in *Eimeria* presence.

Table 8. The effect of season, species, and the interaction of season and species on *Eimeria* presence (149 observations for 120 individuals).

	Estimate±SE	z-value	p-value
Season	-1.54±0.971	-1.59	0.112
Species	0.184±0.485	0.380	0.704
Season:Species	1.32±1.11	1.19	0.233

Isospora

There was no significant interaction effect of season and species on *Isospora* presence ($p=0.96$; Table 9; Figure 13), nor were there significant seasonal differences ($p=0.82$; Table 9; Figure 13). There were however significant differences in *Isospora* presence across species ($p=0.0055$; Table 9) as there were more WCSPs infected with *Isospora* than CA Towhees. Interestingly, there were no WCSPs in the spring infected with *Isospora*, but there were WCSPs infected with *Isospora* in the fall, which is depicted by both the count and *Isospora* prevalence graphs (Figure 13).

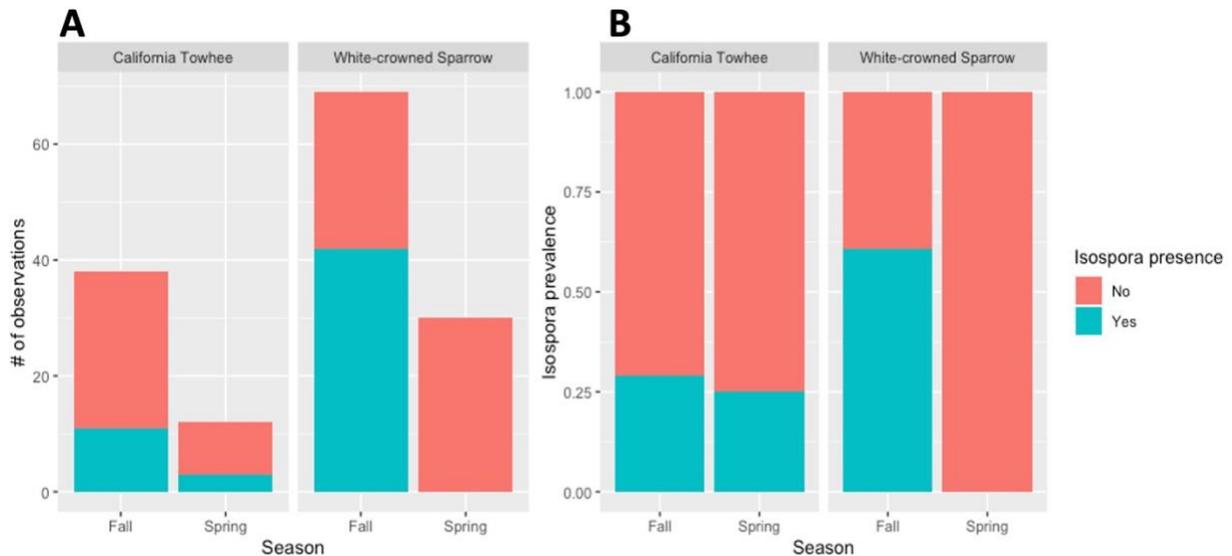


Figure 13. WCSPs were significantly more infected with *Isospora* than CA Towhees ($p=0.0055$), as seen in measurements of the count of *Isospora* infected observations (A) and of *Isospora* prevalence (B) across season and species.

Table 9. The effect of season, species, and the interaction of season and species on *Isospora* presence (149 observations for 120 individuals).

	Estimate±SE	z-value	p-value
Season	-0.181±0.801	-0.226	0.8212
Species	1.43±0.514	2.77	0.00554
Season:Species	-20.6±458	-0.0450	0.964

Question 3: What is the relationship between infection and body condition? Does migration increase with the cost of infection?

Similar to the analyses to answer Question 2, we only used the combination data set to answer Question 3. We specifically looked at the relationship between parasite presence and parasite intensity on body condition. However, the sample sizes changed slightly from those in Question 2's analyses because the infection presence and intensity analyses required observations that had body condition measurements. We also included analyses of coccidia, *Eimeria*, and *Isospora* presence. The sample sizes for our infection presence analyses are demonstrated in Table 10. Our intensity analyses differed in sample sizes because uninfected observations had to be dropped from these analyses, as only those with an eggs per gram value that was greater than 0 could be included.

Table 10. Sample sizes of observations included in presence analyses to answer Question 3.

	White-crowned Sparrow	California Towhee	Grand Total
Coccidia Presence			
Fall	63	34	97
No	17	18	
Yes	46	16	
Spring	30	12	42
No	14	7	
Yes	16	5	
Eimeria Presence			
Fall	63	34	97
No	34	21	
Yes	29	13	
Spring	30	12	42
No	18	10	
Yes	12	2	
Isospora Presence			
Fall	63	34	97
No	26	24	
Yes	37	10	
Spring	30	12	42
No	30	9	
Yes	0	3	
Grand Total	93	46	139

Table 11. Sample sizes of observations included in infection intensity analyses to answer Question 3.

	White-crowned Sparrow	California Towhee	Grand Total
Coccidia Intensity			64
Fall	46	15	
Spring	0	3	
Eimeria Intensity			41
Fall	29	12	
Spring	0	0	
Isospora Intensity			49
Fall	37	9	
Spring	0	3	

Coccidia

In our analysis of coccidia infection, we found a significant season by species interaction effect on body condition ($p < 0.001$; Table 12). Interestingly, infected and uninfected CA Towhee's both experienced a decrease in body condition in the spring, whereas infected and uninfected WCSPs had an increase in body condition in the spring (Figure 14). Coccidia infection presence did

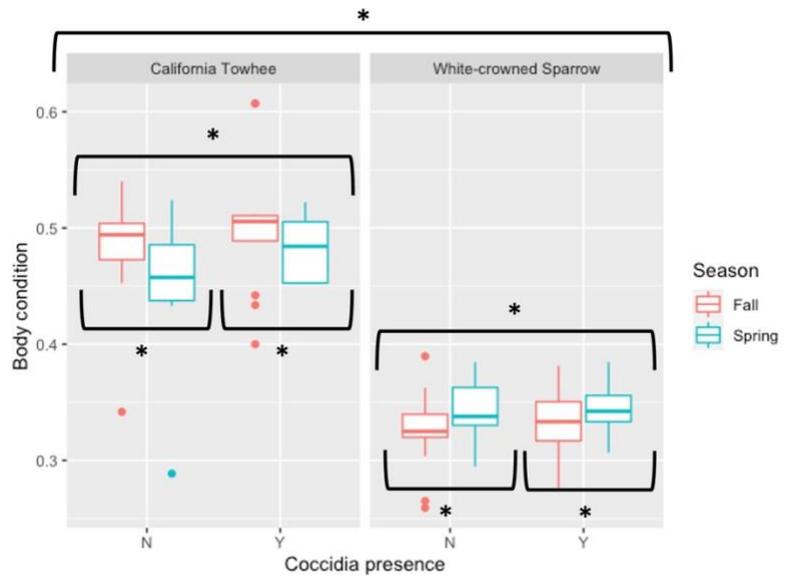


Figure 14. Variation in body condition by coccidia presence ($p=0.046$) (N=no, Y=yes), season ($p < 0.001$), and species ($p < 0.001$).

have a significant relationship with body condition ($p=0.046$; Table 12). Specifically, greater body condition was observed in infected observations (Figure 15). There were also significant differences in body condition by season ($p < 0.001$; Table 12) and species ($p < 0.001$; Table 12).

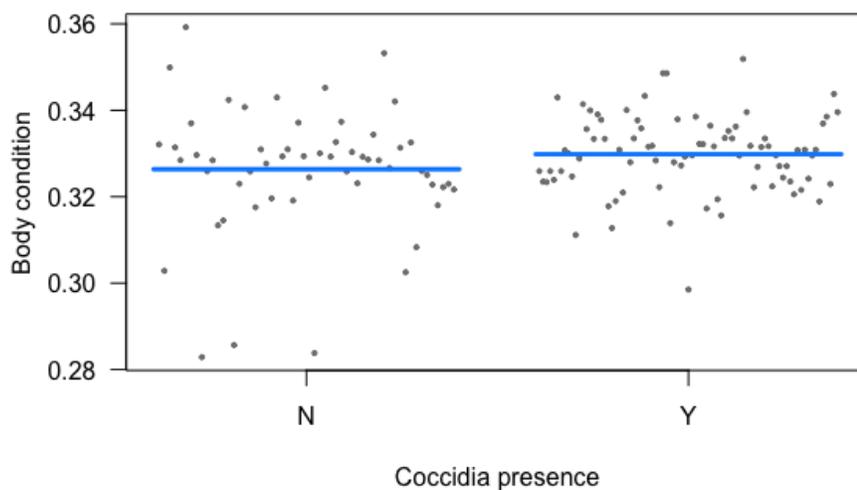


Figure 15. Greater body condition was observed in coccidia infected birds ($p=0.046$) (N=no/uninfected, Y=yes/infected).

Table 12. The effect of coccidia presence, season, species, and the season by species interaction on body condition in WCSPs and CA Towhees (139 observations, 115 individuals).

	Estimate ± SE	df	t-value	p-value
Coccidia presence	0.0116±0.0057	118	2.02	0.0461
Season	-0.0408±0.0112	132	-3.63	<0.001
Species	-0.166±0.00784	127	-21.2	<0.001
Season:Species	0.0638±0.0130	124	4.90	<0.001

Coccidia infection intensity was also analyzed for both seasons and species for its relationship with body condition (Figure 16). There was a significant interaction of coccidia intensity and season on body condition ($p < 0.001$; Table 13) and significant seasonal ($p < 0.001$; Table 13), and species differences ($p < 0.001$; Table 13). However, the interaction effect of coccidia infection intensity and species was not significant on body condition ($p = 0.50$; Table 13), nor was coccidia intensity ($p = 0.33$; Table 13). Interestingly, there were no WCSPs in the spring with coccidia eggs per gram values greater than zero.

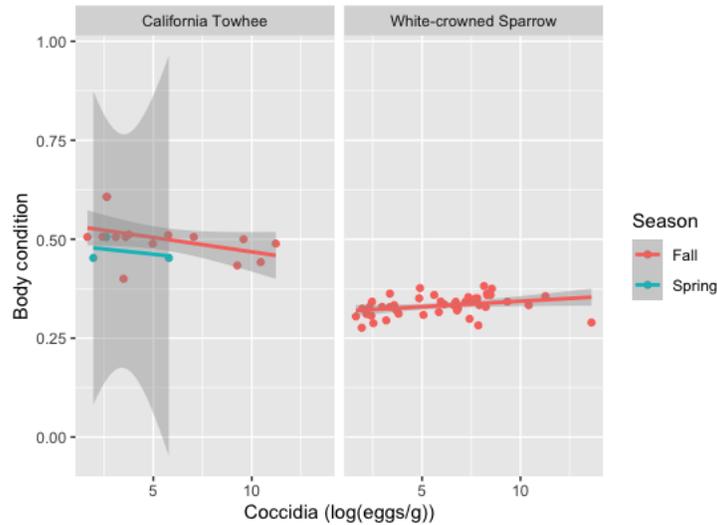


Figure 16. There was a significant interaction effect of coccidia intensity and season on body condition ($p < 0.001$), in addition to significant species ($p < 0.001$) and seasonal ($p < 0.001$) differences. There were no significant differences in coccidia infection intensity (measured in the log of coccidia eggs per gram) on body condition ($p = 0.11$).

Table 13. The effect of coccidia intensity on body condition and the effect of season, species, and the interaction effect of this infection intensity and season and species on body condition (64 observations for 56 individuals).

	Estimate \pm SE	z-value	p-value
Coccidia intensity	- 0.0488 \pm 0.049 8	-0.981	0.327
Season	-2.69 \pm 0.137	-19.6	<0.001
Species	- 0.408 \pm 0.0235	-17.4	<0.001
Coccidia intensity:Species	0.0338 \pm 0.050 3	0.673	0.501
Coccidia intensity:Season	-16.1 \pm 0.633	-25.5	<0.001

To specifically determine the cost of coccidia on body condition, we studied the two main types of coccidia: *Eimeria* and *Isospora*.

Eimeria

Unlike coccidia presence, *Eimeria* presence did not have a significant effect on body condition ($p=0.319$; Table 14). However, there was a significant interaction effect of season and species on body condition ($p<0.001$; Table 14). There were also significant variations in body condition across season ($p<0.001$; Table 14; Figure 17) and species ($p<0.001$; Table 14; Figure 17). Specifically, CA Towhees were in significantly greater body condition than WCSPs (Figure 17).

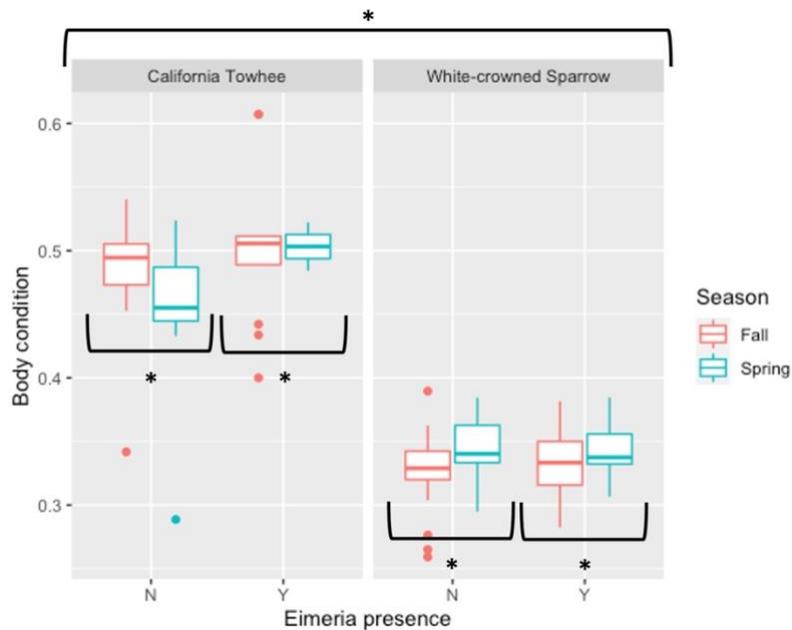


Figure 17. *Eimeria* presence (N=no, Y=yes) did not have a significant effect on body condition ($p=0.319$) but there was variation in body condition by season ($p<0.001$) and species ($p<0.001$).

Table 14. The effect of *Eimeria* presence, season, species, and the season by species interaction on body condition (129 observations for 115 groups).

	Estimate ± SE	df	t-value	p-value
<i>Eimeria</i> presence	0.00564±0.00564	116	1.00	0.319
Season	-0.0404±0.0115	133	-3.52	<0.001
Species	-0.164±0.00778	125	-21.1	<0.001
Season:Species	0.0618±0.0133	127	4.63	<0.001

There was a significant interaction of *Eimeria* intensity and species on body condition ($p=0.028$; Table 15; Figure 18), in addition to significant species differences in body condition ($p<0.001$; Table 15). Interestingly, there were no birds in the spring with *Eimeria* eggs per gram values greater than zero, so season was not taken into account in this analysis. There was also a significant relationship between *Eimeria* intensity and body condition observed ($p=0.046$; Table 15).

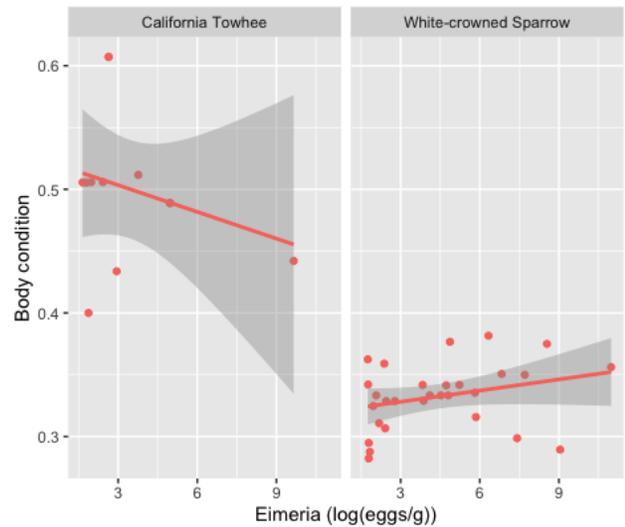


Figure 18. The interaction of *Eimeria* intensity (measured in the log of *Eimeria* eggs per gram) and species was significant on body condition ($p=0.038$), as was species ($p<0.001$), and *Eimeria* intensity ($p=0.046$) on body condition. This plot only displays data from the fall for both species.

Table 15. The relationship between *Eimeria* intensity, species, and the interaction of *Eimeria* intensity and species on body condition (41 observations for 34 individuals).

	Estimate ± SE	z-value	p-value
<i>Eimeria</i> intensity	-0.0749± 0.0375	-2.00	0.0455
Species	-0.405±0.0298	-13.6	<0.001
<i>Eimeria</i> intensity:Species	0.0853±0.0389	2.19	0.0283

Isospora

Isospora presence did not have a significant impact on body condition (p=0.30; Table 16). There was a significant season by species interaction effect on body condition (p<0.001; Table 16) and significant differences in body condition across season (p<0.001; Table 16; Figure 19) and species (p<0.001; Table 16; Figure 19). However, there were no WCSPs infected with *Isospora* in the spring.

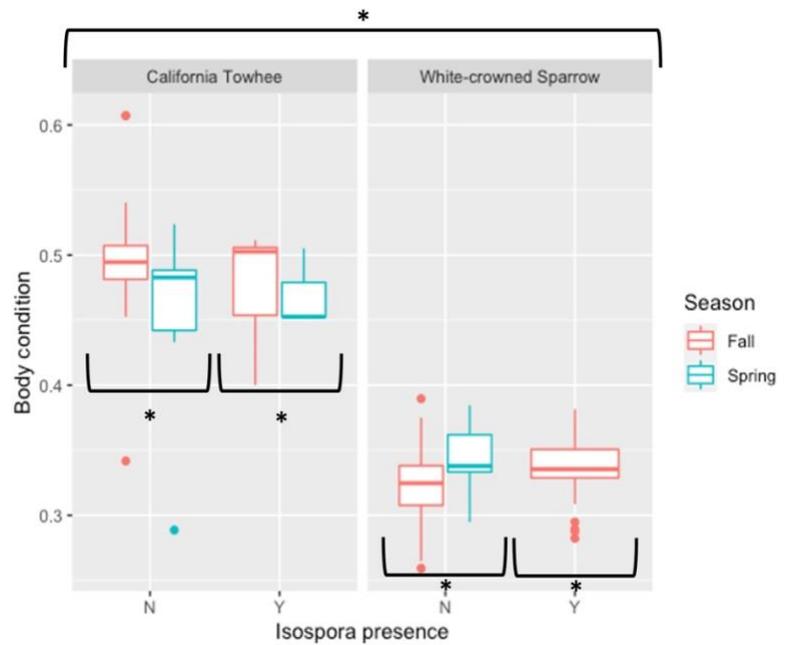


Figure 19. *Isospora* presence (N=no, Y=yes) did not have a significant effect on body condition (p=0.30), but there was variation in body condition by season (p<0.001) and species (p<0.001).

Table 16. The effect of *Isoospora* presence, season, species, and the season by species interaction on body condition (139 observations for 115 individuals).

	Estimate ± SE	df	t-value	p-value
<i>Isoospora</i> presence	0.00659±0.00635	110	1.04	0.302
Season	-0.0428±0.0113	131	-3.79	<0.001
Species	-0.165±0.00798	128	-20.7	<0.001
Season:Species	0.0669±0.0135	121	4.94	<0.001

There was a significant interaction of *Isoospora* intensity and season on body condition ($p < 0.001$; Table 17; Figure 20), and significant differences in body condition across species ($p < 0.001$; Table 17) and season ($p < 0.001$; Table 17). However, there was no significant interaction of *Isoospora* intensity and species ($p = 0.70$; Table 17), nor was there a significant relationship between *Isoospora* intensity and body condition ($p = 0.98$; Table 17). Interestingly, there were no WCSPs in the spring with *Isoospora* eggs per gram values greater than zero.

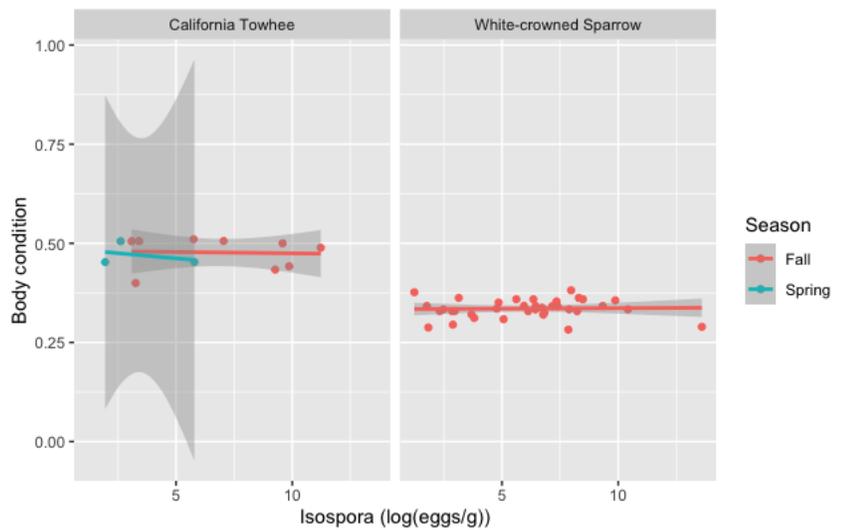


Figure 20. There was a significant interaction of *Isoospora* intensity (measured in the log of *Isoospora* eggs per gram) and season on body condition ($p < 0.001$). Season ($p < 0.001$) and species ($p < 0.001$) also had significant differences in body condition.

Table 17. The relationship between *Isoospora* intensity, species, season, the interaction of *Isoospora* intensity and species and season on body condition (49 observations for 44 individuals).

	Estimate ± SE	z-value	p-value
<i>Isoospora</i> intensity	0.00139±0.05 54	0.025	0.980
Species	- 0.363±0.0239	-15.2	<0.001
Season	-3.17±0.0645	-49.2	<0.001
<i>Isoospora</i> intensity:Species	- 0.0213±0.055 9	-0.381	0.703
<i>Isoospora</i> intensity:Season	-18.3±0.284	-64.5	<0.001

Discussion

This study assessed migration's role in the relationships between infection and body condition. We first looked at the effect of migration on body condition and we found significant species and seasonal variations in body condition. As expected, CA Towhees were in overall greater body condition than WCSPs. In the combination data set, WCSPs were in greater body condition in the spring than after their migration in the fall. Additionally, the interaction of season and species on body condition was only significant in the combination data set. We next analyzed the effect of migration on infection. We found significant differences in coccidia and *Isospora* presence across species, specifically that there were more infected WCSPs than CA Towhees. Finally, we determined the relationship between infection and body condition. We found that the impact of infection intensity on body condition differed across seasons (for both coccidia intensity and *Isospora* intensity) and species (only for *Eimeria*). There were also significant differences in body condition due to the presence/absence of coccidia, and in fact, we found greater body condition in coccidia-infected individuals.

The seasonal-specific demands of migration can help explain the seasonal variations in body condition we observed (Macías-Torres et al. 2022). Preparations for the spring migration may be one explanation for the increase in body condition in the spring for WCSP. WCSPs have been found to be under pressure in the spring to arrive to their breeding locations in a timely manner (Lisovski et al. 2019). In doing so, they enhance their opportunities to find mates (Duijns et al. 2017), thus facilitating their reproductive success (Lisovski et al. 2019). Therefore, it is likely WCSPs use a “time minimization” strategy during the spring migration (Duijns et al. 2017) – an extra efficient migration with the fewest number of stops necessary (Hedenström and Ålerstam 1997). There is evidence of this, as in the spring, the average migration duration for WCSPs is 32 days, with only two to three stopover stops in total, whereas WCSPs in the fall

average 44 days for their migration and have about two to six stopover spots (Lisovski et al. 2019). However, this speedy spring migration likely requires preparation.

WCSPs must be in high body condition to undergo spring migration (Duijns et al. 2017), and it has been found that prior to migration, WCSPs enhance their fuel reserves by consuming in excess ("pre migratory hyperphagia") (King and Farner 1965). This is supported by other researchers who found that WCSPs can gain up to 6.5% of their initial body mass on day one of this process, and reach their maximum weight gain on day eight, the final day of this process (King and Farner 1965) Research has also shown that WCSPs have greater energy reserves in the spring than in the fall, with maximum lipid indices of 27% and 22%, respectively (King 1963). Thus, the increased body condition of WCSPs in the spring that we observe may be due to their attempt to optimize their migratory success for the intense spring migration. Additionally, migration has high physiological and energetic demands, which can negatively impact body condition in the migrant (Bowlin et al. 2010). Therefore, this is one explanation for the decreased body condition observed in the fall for WCSPs, and is indicative that migration is likely driving the interaction effect of season and species on body condition.

However, it was striking that this interaction effect on body condition was only found in the combination data set and not in the capture data set. We expected that the conclusions drawn from the combination data set would be the same as those from the capture data set, as the combination data set is meant to be a subset of the capture data. Additionally, the capture data set has more statistical power given its larger sample size, and thus we anticipated it would demonstrate the interaction effect. Although it is likely migration is the cause of this interaction effect, we cannot be sure given the discrepancies between the combination and capture data sets.

We are unsure why there were such differences but the capture data set had more outliers than the combination data set, which may explain some of these differences.

Our results provide evidence of migration's ability to increase infection, as we found more WCSPs infected than CA Towhees. Our study does not distinguish between increased exposure (Altizer et al. 2011) or increased susceptibility (Weber and Stilianakis 2007) as the driving mechanism. However, in a study of three different species of thrushes, researchers found that in their migratory season, they had poorer immunity and body condition, suggesting that increased susceptibility may be the cause of enhanced infection in WCSPs (Owen and Moore 2006). We surprisingly did not find seasonal variations in infection status, but this was likely due to small sample sizes and the large variations in sample sizes by season.

We have evidence that migration increases infection, however our study also indicates the potential role of migratory culling, as we unexpectedly found greater body condition in those infected with coccidia. It is possible that the WCSPs we studied were in high body condition to overcome the combined cost of infection and migration, and thus they were not culled during migration (Bartel et al. 2011). We also found an interaction effect of infection intensity and species on body condition. As *Eimeria* and coccidia intensity increased in the fall, we observed a decrease in the body condition of CA Towhees, but an increase in the body condition of WCSPs. These results suggest the increased importance of good body condition for infected WCSPs to migrate, and may explain the enhanced body condition found in infected birds (Peacock et al. 2020). The high body condition in these WCSPs is also indicative of the potential for these individuals to have for robust immune systems, allowing them to tolerate high parasite loads without impacting body condition. Past studies of Bewick swans (*Cygnus columbianus bewickii*) support this idea, as they found no change in body condition as a result of infection in those with

strong immunity, but decreased body condition in those without strong immune defenses (Hoye et al. 2016). Our study can be enhanced in the future by specifically studying the role of immunity in WCSPs.

Our covariate, age, may be contributing to these relationships. Prior research has found that as age increases, so does infection and (Pigeault et al. 2020) and body condition (Siefferman et al. 2005). We also found that adult WCSPs had better body condition, but we did not consider the role of age in infection. We did not have any age or sex data on CA Towhees and this would be helpful to future studies to better understand the relationships between infection and body condition.

Although we see positive correlations between body condition and infection, it is only marginally significant and it is possible there is no cost of coccidia infection on body condition. Coccidiosis is the disease caused by coccidia infection, and it has been found to impact the health of the host, even if the individual does not exhibit symptoms (Lu et al. 2021). Coccidia is known to interact with the host's immune system, but the specifics regarding the cost of coccidia infection on body condition is relatively unknown (Lu et al. 2021). Therefore, the increased condition found in infected individuals may be due to the fact that coccidia infection is not very costly on body condition and we should better understand the specific costs for future analyses.

There are many other ways to advance our study in the future. It is important to assess the differences in the composition of the two data sets to better understand how representative the combination data set is of the capture data set. This can help explain the statistical differences. Fecal samples were not collected or analyzed in any systematic way that would generate bias within the combination data, but a greater emphasis in the future should be placed on considering ways researchers may inadvertently contribute to the difference effects observed.

Secondly, fecal weights were absent for many samples and thus the parasite eggs per gram could not be calculated for these observations, minimizing the sample sizes of the parasite intensity analyses. For example, we had no parasite eggs per gram data for WCSPs infected in the spring, and this is likely the reason for the interaction of intensity and season on body condition we observed. Without this group included in our models of infection intensity, we are unable to truly understand the effect of parasite intensity, season, and species on body condition. Prior research indicates the need to take both infection prevalence and intensity into account in a singular study to ensure the most accurate results, therefore it is specifically important to improve our infection intensity data (Shaw et al. 2018). Gathering the missing data and running the appropriate analyses will provide greater insight on infection and body condition for these two species. Additionally, we should continue bird capturing and analyzing parasites in order to increase the amount of data available. A larger sample size will increase the power of the statistical tests and our conclusions.

Despite the majority of birds in our data sets being first time captures, the complexities underlying infection, body condition, and migration dynamics can be simplified by measuring differential host responses to infection at different time periods for individual recaptures. Determining how an individual's parasite infection and body condition change over the course of time can help explain migration's role in the significant season by species interaction observed in this study, which is our primary future direction. This study did not do separate analyses between recaptured and newly captured birds, but it could be helpful to study a WCSP in the spring before migration and study the same individual in the fall after migration. We could then measure differences in parasite infection and body condition in this bird, which will likely be due to migration. Studying individual birds will also help us determine the direction of the

relationships, both potential causal and positive/negative associations, between infection, migration, and body condition, untangling many of the overlaps and uncertainties in current research.

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Appendix A: Photos of Parasites



Figure 21. *Eimeria* oocysts found in a chicken
(Zajac and Conboy 2012).



Figure 22. Unsporulated *isospora* oocysts
(Western College of Veterinary Medicine 2021)

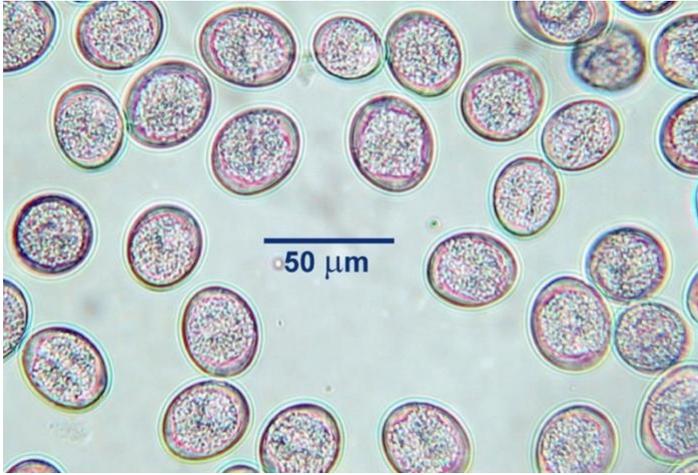


Figure 23. Sporulated *isospora* oocytes
(Western College of Veterinary Medicine 2021).

*Both unsporulated and sporulated *isospora* were included in our *isospora* analyses.

Appendix B: Does this effect of infection on body condition vary by season or species?

Table 18. The relationship between coccidia presence, season, species, the interaction of season and species, the interaction of coccidia presence and season, presence and species, and the interaction between the three on body condition (139 observations for 115 individuals).

	Estimate ± SE	df	t-value	p-value
Coccidia presence	0.0149±0.010 7	107	1.39	0.168
Season	- 0.0499±0.013 9	118	-3.59	<0.001
Species	- 0.158±0.0112	131	-14.1	<0.001
Coccidia presence:Season	0.0287±0.020 4	99.0	1.41	0.161
Coccidia presence:Species	- 0.0115±0.014 1	114	-0.812	0.418
Species:Season	0.0726±0.017 5	105	4.16	<0.001
Coccidia presence:Season:Species	- 0.0306±0.025 0	102	-1.23	0.223

Table 19. The relationship between *Eimeria* presence, season, species, the interaction of *Eimeria* presence and season, the interaction of *Eimeria* presence and species, the interaction of season and species, and the interaction of the three on body condition (139 observations for 115 individuals).

	Estimate ± SE	df	t-value	p-value
<i>Eimeria</i> presence	0.0160±0.0129	124	1.24	0.219
Season	-0.0407±0.0131	129	-3.11	0.00228
Species	-0.158±0.00989	122	-16.0	<0.001
<i>Eimeria</i> presence:Season	0.0302±0.0250	90.6	1.21	0.228
<i>Eimeria</i> presence:Species	-0.0137±0.0153	130	-0.890	0.375
Season:Species	0.0655±0.0158	129	4.15	<0.001
<i>Eimeria</i> presence:Season:Species	-0.0401±0.0289	97.9	-1.39	0.168

Table 20. The relationship between *Isoospora* presence, season, species, the interaction of *Isoospora* presence and season, the interaction of *Isoospora* presence and species, and the interaction of season and species on body condition (139 observations for 115 individuals).

	Estimate ± SE	df	t-value	p-value
<i>Isoospora</i> presence	- 0.00450±0.01 11	78.3	-0.404	0.687
Season	- 0.0500±0.012 7	119	-3.94	<0.001
Species	- 0.170±0.0094 6	131	-18.0	<0.001
<i>Isoospora</i> presence:Season	0.0315±0.025 5	132	1.23	0.220
<i>Isoospora</i> presence:Species	0.0146± 0.0138	90.8	1.06	0.293
Season:Species	0.0757±0.014 9	109	5.08	<0.001