

**Are Seasonal Interactions Mediated by Stress Responses in a Short-Distance
Migratory Bird?**

Honors Undergraduate Thesis

Valerie A. Gaulke

Advisor: Dr. Christopher Tonra

School of Environment and Natural Resources

College of Food, Agriculture, and Environmental Sciences, The Ohio State University

Kottman Hall, 2021 Coffee Road, Columbus, OH 43210



Abstract

Various stages within animals' annual cycle can affect one another and, thus, are not discrete events in time. What occurs during one period of the annual cycle (e.g. non-breeding) can alter the success or survival of animals in another period (e.g. breeding) of their annual cycle through non-lethal factors. These effects are termed "seasonal interactions" and are fueling a rapidly growing body of knowledge advancing our understanding of how populations are limited across the full annual-cycle. In order to examine these seasonal interactions, this study aims to determine if they occur across nonbreeding stages in a short-distance migratory bird, the white-throated sparrow (*Zonotrichia albicollis*). These sparrows are quite abundant throughout the eastern U.S. and have well defined annual cycles. Nearly all studies examining seasonal interactions have focused on neotropical migrants and effects on the breeding season. I measured physiological stress during nonbreeding stage to determine if seasonal interactions exist between the stages of molt, wintering, and spring migration. I found that stress levels (measured by corticosterone in feathers) varied by stage and sex and higher stress in molt correlated with decreasing fat reserves during winter. However, higher stress in winter correlated with increasing fat reserves during winter, and later departure for spring migration. Thus, it appears stress hormones and fat interact in complex ways across the annual cycle. A complete grasp of the full annual cycle, and not just the breeding season, is critical for conservation as the world is experiencing a drastic decline in "common" migratory birds, like the white-throated sparrow.



Table of Contents

Abstract.....1

Table of Contents..... 2

Introduction.....3

Methodology.....9

Results.....12

Discussion.....14

Acknowledgements.....19

References.....20

Figures.....26

Tables.....28



Introduction

Recent evidence has shown that many common and widespread bird species in North America are in decline (Rosenberg et al. 2016). Native migratory avifauna have declined by 28.3% from 1970-2017, representing a net loss of almost 2.5 billion birds and a staggering loss to biodiversity. Additionally, of 419 native migratory avian species, 58.2% are in population decline (Rosenberg et al. 2019). In order to prevent further losses, conservation professionals must take management actions to counteract negative impacts on these declining migratory populations. One factor limiting the ability to achieve this goal is a lack of information on all parts of migratory birds' annual cycles identifying when and where populations are limited.

Migratory birds, like most other animals, transition between different stages of their life history (e.g. breeding, migration, overwintering) in response to changes in the environment (Wingfield 2007). However, it has been shown that many animals can exhibit “seasonal interactions” in which they experience effects of one stage on a subsequent stage (Marra et al. 1998). In other words, these stages are not discrete events and in fact conditions in one stage can alter what may happen in subsequent stages, both at population and individual levels (Marra et al. 2015). For example, in several species of migratory birds evidence has been found for carry-over effects between overwintering and breeding, such that conditions experienced in winter influence productivity in the breeding season (e.g. Marra et al. 1998; Gunnarsson et al. 2005). Unfortunately, most of the research on vertebrate wildlife has focused on the breeding stage, because of logistics and it has historically been viewed as the most important stage to ensuring the long-term survival of species (Marra et al. 2015). Thus, for most species, little is known about nonbreeding stages (e.g. migration, feather molt) or how these different stages interact with one another. Acquiring this type of information has proven to be difficult in migratory

species since different stages happen in different parts of the world, sometimes thousands of kilometers apart. This knowledge is critical as, if effects exist from one stage on survival and/or reproduction in another, the environmental conditions important for limiting population growth may occur in disparate geographic areas (Webster et al. 2002; Marra et al. 2015).

There is strong evidence of individual level seasonal interactions (carry-over effects) in migratory bird annual cycles and their effects on fitness (i.e. survival and reproduction). A series of studies in the American redstart (*Setophaga ruticilla*) were able to identify winter conditions driving breeding success. Researchers determined that the type of wintering habitat occupied (wet vs. dry) affects timing of departure from nonbreeding sites and arrival at breeding grounds, which in turn influences breeding success (e.g. Marra et al. 1998; Reudink et al. 2009). Further, in years with more rainfall, individuals are in better energetic condition during winter and depart for spring migration earlier (Studds & Marra 2007; 2011). These types of studies are increasing the understanding of seasonal interactions. Information in this field is critical because seasonal interactions like these have been shown to be widespread and linked to a multitude of factors that can cause variation in fitness for animals (Harrison et al., 2011).

Important to understanding the nature of seasonal interactions is elucidating how they are mediated by physiological mechanisms, as physiology is the means by which individuals respond to the environment (Ricklefs & Wikielski 2002). Physiological responses by animals can be critical indicators of environmental stressors and can be used to identify conditions within different annual cycle stages. Corticosterone (hereafter: CORT) is a hormone found in avian species that falls into the class of hormones known as glucocorticosteroids (Siegel 1980; Sapolsky et al. 2000). It is produced by the hypothalamic-pituitary-adrenal axis which elicits a stress response by the animal, including behaviors that promote self-preservation (e.g. foraging,

finding shelter; Cannon 1915; Siegel 1980). Because of this, CORT levels in animal tissues can be used as a measure of the amount of both acute (e.g. storm events) and chronic (e.g. drought) stress that birds experience.

It is possible to use CORT as a measure of a bird's response to environmental changes because hormones within the body are released in response to extrinsic (e.g. the environment) or intrinsic (e.g. energetic condition) factors. The hormones then signal cells within the body to produce results specific to those hormones (Jacobs & Wingfield 2000). CORT can be released in increasing concentrations several minutes after a stress signal is received from the environment, but it can take up to hours for the hormone to affect various tissues within the body. Additionally, the effects of CORT can last from days up to weeks following the decline of the hormone (Sapolsky et al. 2000). While the effects of CORT can often be adaptive (e.g. facilitating pre-migratory fattening; Holberton 2007), it often is thought to be a "stress" hormone because it can have negative effects on the body (e.g. muscle catabolism). These responses inhibit normal bodily functions observed in homeostasis due to changing environmental conditions. Responses can include the depression of immune function, increased metabolism of fat reserves, increased appetite, and can inhibit reproduction (Sapolsky et al. 2000). For example, it was shown that in white-throated sparrow (*Zonotrichia albicollis*) that birds with higher levels of CORT during the breeding season have decreased parental behavior (e.g. lack of feeding visits to nestlings) and increased self-preservation behaviors (Horton & Holberton 2009). Thus, different levels of CORT can elicit different behaviors within birds.

Measuring stress quantitatively using CORT can prove to be quite useful. Specifically, CORT can be measured using feathers collected from birds. This method has proven useful, as

unlike blood samples, it minimizes stress to the animal during collection (Bortolotti et al. 2009). CORT concentration also remains stable in a feather over time and does not significantly decrease in concentration. Additionally, CORT in feathers can be used to track the levels of stress experienced by the bird over weeks (i.e. the period of feather growth) and not just a singular stressful event (Bortolotti et al. 2009). Thus, by collecting feather samples it is possible to assess how much stress is experienced during different parts of the annual cycle for a bird, provided the period of feather growth is known.

There are multiple life stages that occur during an annual cycle for migratory birds, occurring in different parts of their distribution. These stages are distinguished from one another due to occurring during specific times of the year having correlated morphological, physiological and behavioral traits within individuals. For migratory birds, these stages include (in order of occurrence): stationary non-breeding (i.e. winter), spring migration breeding, molt (the annual replacement of feathers), and fall migration (Wingfield 2007). For example, white-throated sparrows are a common, short-distance migratory songbird found in North America. They exhibit annual cycle stages where they breed from June to August in the boreal forests of Canada, then molt and migrate south to the Eastern U.S. from August to November and overwinter there from November through March. Following this, they then migrate back North to Canada from March to May to begin breeding again. Thus, there are multiple instances where seasonal interactions between different stages in this species, such as from molt to winter or from winter to spring migration (Falls & Kopachena 2010).

The organization of annual cycle stages is strongly controlled by the changing of the seasons, in accordance with the earth's rotation around the sun (Wingfield 2007). Birds will receive signals from their environment which can cause physiological and morphological

changes that will then cause changes in their behavior in order to transition from one stage to another (Jacobs & Wingfield 2000). On a larger scale the timing of stages, such as migration, are controlled by photoperiods, or the length of the day, but they are also controlled at a finer scale through endogenous means such as accumulation of fat reserves which respond to food availability in the environment (Gwinner 2003; 2008). By the bird perceiving these signals, they are able to time their actions in accordance with seasonal changes (Visser et al. 2010). This becomes increasingly evident as the consequences of climate change continue being observed around the world. It was shown that for multiple bird species in sub-Saharan Africa, departure for migration was delayed in correlation to increasing temperatures and decreased precipitation (Gordo et al. 2005). As climate change continues to alter environmental conditions, the processes driving migratory timing of birds could be altered (e.g. Both & Visser 2001). This could be detrimental because migration allows birds to travel to more suitable habitats for certain parts of the year, so if timing is not adjusted in step with environmental conditions, they could arrive in a habitat before it is suitable for that species of bird (Berthold 1996). Thus, identifying seasonal interactions (such as the influence of migration timing on reproductive success, e.g. Reudink et al. 2009) is critical to understanding the potential impacts of environmental change on migrants.

Seasonal feather molt (hereafter: molt) is an annual cycle stage that has received relatively little attention in studies of seasonal interactions (Tonra & Reudink 2018). This stage can be fundamental to the annual cycle of birds. Molt is the process by which birds lose their feathers to make way for the growth of new feathers (Howell et al. , 2003). Molt is critical to the life cycle as a whole due to its ability to affect flight performance (Swaddle et al. 1996), resistance to bacterial parasites (Gunderson et al. 2008), the ability to thermoregulate (Vézina et al. 2009) and feather coloration for breeding communication (Hill & McGraw 2006).

Importantly, molt is also the most energetically expensive stage of the annual cycle (Dietz et al. 1992, Vézina et al. 2009). Because of these critical factors, molting is therefore linked to the other stages of the annual cycle and the degree of optimal molting can then affect subsequent stages (Howell et al. 2003).

Nonbreeding stages (molt, migration, and wintering) are less understood compared to the breeding stage in birds, and specifically how events during these stages may carry-over and affect subsequent stages (Marra et. al. 2015). Therefore, this study seeks to determine how measurement of stress responses experienced by a short-distance migratory bird, white-throated sparrow, can be used to examine potential seasonal interactions between post-breeding molt, winter, and spring migration. If a stress response can serve as a mediator for seasonal interactions, then varying levels of stress during one stage should produce varying levels of performance of birds in subsequent stages. Specifically, the objectives of this study were to:

1. Establish if there is a difference in stress levels from the molt to winter period.
2. Determine how stress during post-breeding molt may affect body condition of birds during winter.
3. Determine how stress during winter may affect body condition of birds during winter.
4. Examine how stress during winter may affect timing of spring migration.

For the first objective, I predicted that white-throated sparrows would have higher CORT during molt as compared to winter due to the high energetic demands in replacing feathers. For the second objective, I predicted that white-throated sparrows experiencing higher CORT during post-breeding molt would exhibit poor winter body condition due to higher stress causing responses such as decreased immune function and metabolism of fat reserves. Accordingly, for the third objective it would also be predicted that white-throated sparrows experiencing higher

CORT during winter would exhibit poor body condition for the same reason. For the fourth objective, I predicted that sparrows experiencing higher CORT during winter would depart for spring migration later than sparrows experiencing lower CORT. Again, this would be due to responses such as metabolism of fat reserves or potential muscle catabolism, both of which are needed for migration. To test these predictions, I measured the concentration of CORT accumulated in feathers during the various stages in order to obtain a quantitative measure of stress responses and correlated this to a measure body condition (mass, fat stores) and migration timing (spring departure date) in the subsequent stage. Through both of these means, I am determining how one stage may affect the survival of these birds in the following stages using stress as a mediator.

Methodology

Field Site

I conducted this study at The Wilma H. Schiermeier Olentangy River Wetland Research Park (40°01'14.0"N 83°01'11.2"W; hereafter: wetlands). This is a 52-acre, urban site that features two experimental wetland basins, a bottomland hardwood forest as well as an oxbow wetland. It is bordered by the Olentangy River to the north and east (<https://u.osu.edu/orwrpramsar/>). There is a Motus Wildlife Tracking System (www.motus.org) automated telemetry tower operated at a central point of the site.

Field Data Collection

I conducted this study from Oct – May over two study-years (2018-19 and 2019-20). Members of my Tonra Lab of Avian Ecology and I set nylon mesh mist nets and baited cage traps in multiple locations at the wetlands to capture the sparrows. We fitted captured birds with a U.S. Geological Survey aluminum band and three plastic, colored bands, for individual

identification in the field. Morphometric data (mass, wing length, etc.) was collected along with the outermost tail feather from the right side of each individual, which was grown during post-breeding molt near the breeding grounds (Falls & Kopachena 2020), prior to fall migration and arrival at the study site (i.e. CORT represents stress levels during molt). Birds were recaptured throughout the banding season to collect the re-growing feather, induced from the previous collection, which is being grown at the wetlands (i.e. CORT represents stress during winter).

For individuals that were captured twice (i.e. have both CORT levels for molt and winter), a digital vhf radio transmitter (nanotag model NTQB2-3-2; Lotek, Inc.) was fitted and attached to the bird. In some years, not enough birds were caught twice so transmitters were attached to birds caught for their first time. These tags transmit an individually identifiable signal that can be detected by automated telemetry towers, operated by Dr. Tonra, and by a wider collaborative international network known as Motus (<https://motus.org>). A tower located at the study site was used to determine when birds leave, which can be validated by migratory movements via subsequent detection by other receiving stations to the north (e.g. Columbus Zoo, stations in northern Ohio and southern Ontario). Thus, these transmitters provided data on when these individuals departed for spring migration. Tags were placed on birds using a leg-loop harness (Rappole & Tipton 1991) and weigh <3% of body mass.

Following the collection of feathers, I extracted CORT in order to determine the amount of accumulated CORT for each bird at the time of feather growth (feather CORT; hereafter: fCORT). The procedure for this assay has been validated by Dr. Tonra following Bortolotti et al. (2008), as modified by Carbajal et al. (2014) using a commercial ELISA kit (CORT ELISA kit; Neogen Corporation, Ayr, UK). I minced feathers minced and incubated in HPLC methanol overnight while in a shaking water bath. To remove solids, I vacuum filtrated the extracts,

evaporated under nitrogen gas and reconstituted in the Neogen ELISA extraction buffer. I then ran the assay as per the kit's outlined ELISA procedure. I report fCORT in concentration values of pg/mg of feather. Assay recovery is assessed by adding 20 μ L of tritium-labeled CORT to each sample and is on average >93%.

From the morphometric data collected during banding, I also calculated a body condition index for each capture of a bird. I used a linear model with mass as the dependent variable and wing length as the predictor. Residual values were calculated for each capture based on this model and used as an index for body condition (i.e. negative residuals signified poor body condition). I calculated the mass change and fat change over winter for birds caught at least twice (2nd capture value – 1st capture value) to determine mass/fat gain or loss. As a possible covariate of these metrics of body condition change, I also calculated the number of days between captures. Additionally, I converted the departure dates from the transmitters to a be the nth day of the year (i.e. January 1st is day 1) so that the departure dates between study years were standardized. After the feathers had been used to determine fCORT, I sent the calamus' from a feather for each bird to IQ Bird Testing (<https://iqbirdtesting.com>) where the sex was determined by genetic analysis. The age of birds was determined during banding using Pyle (1997).

Data Analysis

To test the prediction that white-throated sparrows should experience higher levels of fCORT in molt as compared to winter, I ran linear mixed models in a repeated measures format (i.e. including birds for which both a molt and winter feather were collected). I included fCORT as the dependent variable and stage, age, and sex as fixed effects, and individual as a random effect. Additionally, I included interactions between stage and age as well as stage and sex. To test for each fixed effect significance, I used likelihood ratio tests of full and reduced models. I

first examined if any variables came out as uninformative ($P < 0.15$) and removed those for the final analysis. Larger P-values were considered in all of the models run due to the small sample size used.

To test the predictions that white-throated sparrows should show poor body condition in winter when they have high fCORT in molt, and poor body condition in winter when they have high fCORT in winter, I used generalized linear models. Either body condition index, mass change or fat change were the dependent variables, and fCORT from molt, sex and age as the predictors. I also included interactions between fCORT and sex as well as fCORT and age. As above, to increase statistical power, uninformative interactions or predictor variables ($P < 0.15$) were removed from the final model.

To test the prediction that white-throated sparrows should depart later for spring migration when they have high fCORT in winter, I ran a generalized linear model with departure date as the dependent variable and fCORT from winter, age, sex, fat, and body condition as the predictors. I also included interactions between fCORT and age, fCORT and sex, sex and body condition, age and body condition, sex and fat, and age and fat. Any uninformative interactions or variables ($P < 0.15$) were removed from the final model, as above.

Results

Over 2018-2020, a total of 28 white-throated sparrows were sampled for fCORT at the wetlands (16 from the 2018-19 season and 12 from the 2019-20 season). From this sample, there was a total of 14 female birds and 14 male birds, 24 birds were in their hatch-year and four were after-hatch-year. A total of 20 transmitters were attached to white-throated sparrows from this sample and 16 birds were sampled twice, once for molt and once for winter.

The final model examining the difference in fCORT over the two stages, molt and winter, included fCORT as the dependent variable and stage and sex as the predictors, after the noninformative parameter of age and its interaction were removed (both $P < 0.15$). fCORT varied based on sex ($\chi^2 = 7.55$, $df = 1$, $P = 0.006$), where males overall had lower fCORT compared to females ($\beta = -0.14$, $SE = 0.049$; Figure 1). Additionally, fCORT varied marginally by stage ($\chi^2 = 2.66$, $df = 1$, $P = 0.10$) and was lower for birds in winter as compared to those in molt ($\beta = -0.085$, $SE = 0.051$). The mean of logfCORT in molt was 1.63 whereas in winter it was 1.53. Females had an mean logfCORT of 1.73 in molt and 1.58 in winter while males had an mean logfCORT of 1.54 in molt and 1.52 in winter (Figure 1).

The final model predicting fat change over winter included fCORT from molt, age, the time interval and the interaction between fCORT and age as the predictors. The observed effect of fCORT on fat change depended upon age. Overall, hatch-year birds had lower fCORT but after-hatch-year birds had a stronger relationship with fCORT compared to hatch-years (Table 1). Fat change over winter was also positively related to the time interval. Fitted values were created for fat change to account for significant relationships with age, the time interval, and the interaction between fCORT and age to be plotted against fCORT from molt, which showed a negative relationship (Figure 2). Sex did not have any significant relationship with fat change in this model.

The final model used for objective three included fat change over winter as the dependent variable and fCORT from winter, age, sex, the time interval, and the interaction between fCORT and age. The effect of winter fCORT on fat change was dependent upon age. Overall, hatch-year birds had higher fCORT and after-hatch-year bird had a stronger relationship with fCORT compared to hatch-years. Fat change over winter was also positively related to sex and the time

interval (Table 2). Fitted values were created for fat change to account for significant relationships with age, sex, the time interval, and the interaction between fCORT and age to be plotted against fCORT from winter, which showed a positive linear trend (Figure 3).

The final model for objective four included departure date as the dependent variable and fCORT from winter as the predictor. In this model, departure date showed a positive relationship with fCORT from winter ($\beta=47.69$, $t_{df=12}=1.92$, $P=0.081$; Figure 4). Winter body condition, fat, sex and age did not have any relationship with departure date in this model.

Discussion

The goal of this study was to test for seasonal interactions among nonbreeding stages in a short-distance migratory bird, the white-throated sparrow, through the measurement of stress levels as a mediator for these interactions. This was accomplished by first showing that white-throated sparrows' level of stress varied between molt and winter, where CORT was higher in molt. A potential seasonal interaction between molt and winter was observed as white-throated sparrows with higher stress in molt corresponded to loss of fat over winter. In contrast, there was gain of fat over winter when birds had higher fCORT levels in winter. This higher stress in winter appears to carry-over to cause delayed departure for spring migration. Through these findings, several potential seasonal interactions were documented in this species by means of examining their stress levels during multiple stages of their annual cycle.

In examining objective one, where the goal was to determine if levels of fCORT were different between molt and winter, my prediction that white-throated sparrows would experience higher fCORT during molt as compared to winter was supported. It was also seen that females experienced higher fCORT compared to males in both molt and winter (Figure 1). Based upon this, there may be some condition(s) present during molt that are inducing higher levels of stress

as compared to winter. This might be due to the high energetic costs associated with feather replacement during molt (Dietz et al. 1992, Vézina et al. 2009). This finding is contradictory to previous studies which found suppression of CORT levels during molt (Echeverria et al. 2018, Romero et al. 2005). Additionally, in comparison of CORT levels throughout the annual cycle in white-crowned sparrows (*Zonotrichia leucophrys*), it was found that levels during molt were the lowest (Romero & Wingfield 1999). A point of difference though is that these studies measured CORT from plasma instead of feathers, which represents stress at the time of the sampling event as compared to a long-term variation in stress captured in feathers. Further research would be needed to examine the reason behind higher levels of fCORT seen during molt in this scenario.

In examining objective two, where the goal was to determine the relationship between fCORT in molt and body conditions during winter, my prediction was supported. White-throated sparrows experiencing higher fCORT in molt showed declined body condition in winter, as measured by fat load. Higher levels of fCORT corresponded to larger decreases in fat over winter (Figure 2). Thus, white-throated sparrows that experienced more stress during molt showed decreases in fat over winter. This is consistent with a seasonal interaction between molt and winter stages. High stress during molt can cause formation of lower quality feathers due to corticosterone inhibiting protein deposition necessary for feather development (Romero et al. 2005). Lower quality feathers can then cause reduced ability to thermoregulate (Vézina et al. 2009) and could result in birds needing to use more fat reserves during winter. Fat is a key attribute needed for survival of birds living in colder regions during the winter (i.e. areas that experience temperatures below freezing) as fat serves as a reserve of energy when birds need increased thermoregulation or have a lack of food (Blem 1990). This type of interaction could be key in examining the full annual cycle of birds as stressors during molt could cause decreased

survival/fitness during the winter when those stressors are no longer present. Further research should investigate what factors may be causing increased stress during molt that is driving this type of seasonal interaction. Perhaps high energetic costs present during molt (Dietz et al. 1992, Vézina et al. 2009) or overlapping molt with breeding (Echeverry-Galvis & Hau 2012) may drive this physiological response. Contrastingly, it was seen that higher fCORT in winter led to increased fat, suggesting there may be opposing mechanisms in CORT utilization during different stages.

In examining objective three, where the goal was to determine the relationship between fCORT in winter and body condition during winter, my prediction was not supported. I had predicted that higher fCORT in winter would also be correlated to poor body condition during winter. The opposite was seen as white-throated sparrows that experienced higher fCORT in winter had better body conditions. Higher levels of fCORT were correlated with increases in fat reserves over winter (Figure 3). This perhaps demonstrates an important physiological mechanism in maintaining body condition over winter using CORT. Although it is usually thought that increased CORT would cause metabolism of fat for self-preservation (Sapolsky et al. 2000), this finding may show that birds may experience higher stress in response to unfavorable weather events that would induce fat storing (Holberton et al. 2007). Further research could examine the opposing mechanisms used to alter body conditions during molt and winter via stress responses.

In examining objective four, where the goal was to determine the relationship between fCORT in winter and departure date for spring migration, my prediction was supported. White-throated sparrows experiencing higher fCORT in winter left for spring migration later as compared to birds with lower fCORT (Figure 4). Therefore, white-throated sparrows that

experienced more stress in winter showed delayed timing in departing for migration in the spring. This type of seasonal interaction shows the effect of winter condition altering phenology, as stress during winter appears to cause delays in migration timing (Marra & Holberton 1998). Changes in phenology via seasonal interactions have the potential to result in temporal mismatches if birds need to reach their breeding grounds during a specific time for optimal resources or for timing of breeding (Reudink et al. 2009). Thus, it could be seen that if events or factors caused increased stress during one stage, it may result in birds departing later for migration and having reduced fitness on their breeding grounds if it causes them to miss a critical time for resources/breeding. Taking into account seasonal interactions could be critical for examining altered phenology in migratory birds as shown here.

As various stages of the annual cycle occur during different times and in different places, particularly for migratory avian species, it is important for avian managers and researchers to recognize the importance of seasonal interactions. As particular observations, for example reduced body condition, may be seen during a particular stage of the annual cycle, it would be necessary to consider that the cause of that observation could be the result of events during a previous stage of the annual cycle. Using fCORT could prove to be a viable method to monitor these seasonal interactions and may be an important tool used for managers or researchers to coordinate actions across various stages and places for a species. Altered phenology may also be monitored through the use of fCORT as this becomes a more prevalent issue with climate change (Wingfield 2007).

Human-induced climate change continues to be an challenge for conservation. A pressing consequence of climate change is the extreme loss of biodiversity due to mass extinctions. Currently, the world is experiencing its sixth mass extinction. As climate change is projected to

continue to affect the planet going into the future, it can be expected then that extinctions will continue to occur. Even if anthropogenic emissions causing climate change were to be significantly reduced right now, climate change would not immediately disappear, and extinctions would still continue for some time (Carter 2019). Due to this, conservationists must be prepared to deal with species experiencing great losses. The information gained from this study demonstrates a method that could be employed to deal with this issue. Climate change could cause animals to receive altered signals from the environment, and thus the timing of various stages could be altered (Wingfield 2007) or extreme environmental variation due to climate change may cause greater physiological stress responses by animals (Deschner & Behringer 2019). Thus, it is important for the scientific community to be equipped with methods to study seasonal interactions that may be affected by consequences of climate change. Using CORT to measure seasonal interactions could be one of the ways this could be accomplished. Therefore, the knowledge gained from this study may contribute to methodology used to assess how species could be affected by consequences of climate change.

Acknowledgements

First and foremost, I would like to thank Dr. Christopher Tonra for his patience and help whilst I began to delve into the world of research and avian ecology. His knowledge and skills surrounding many avian species greatly helped this project progress. I would also like to thank all members and volunteers in the Tonra Lab of Avian Ecology for their help in banding white-throated sparrows, collecting morphometric data, and attaching transmitters. This project was a collective effort from everyone involved in the lab and I greatly appreciate everyone's contribution. In particular, I would like to express my gratitude to Elizabeth Ames who was an exceptional resource throughout my project. Lastly, I want to thank the faculty in the School of Environment and Natural Resources for providing a well-rounded and informative curriculum to help my understanding and application of wildlife ecology in this project. Funding for this project was provided by CFAES SEEDS: The OARDC Director's Undergraduate Research Program, American Ornithological Society: Hesse Award, and Ohio EPA: OEEF Scholarship.

References

- Berthold, P. (1996). *Control of Bird Migration*. London: Chapman & Hall.
- Blem, C. R. (1990). Avian energy storage. *Current Ornithology*, 7, 59 – 113.
- Bortolotti, G. R., Marchant, T., Blas, J., & Cabezas, S. (2009). Tracking stress: localisation, deposition and stability of corticosterone in feathers. *The Journal of Experimental Biology*, 212, 1477–1482.
- Both, C. & Visser, M.E., 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, 411(6835), 296-298.
- Cannon, W. (1915). *Bodily Changes in Pain, Hunger, Fear and Rage*. New York and London D. Appleton and Company.
- Carbajal, A., Tallo-Parra, O., Sabes-Alsina, M., Mular, I., & Lopez-Bejar, M. (2014). Feather corticosterone evaluated by ELISA in broilers: A potential tool to evaluate broiler welfare. *Poultry science*, 93(11), 2884-2886.
- Carter, P.D. (2019). Implications for Biodiversity of Potentially Committed Global Climate Change (from Science and Policy). In: Leal Filho W., Barbir J., Preziosi R. (eds) *Handbook of Climate Change and Biodiversity*. Climate Change Management. Springer, Cham. https://doi.org/10.1007/978-3-319-98681-4_8.
- Deschner, T., & Behringer, V. (2019). Endocrinological Analyses at Tai. In Boesch, C., & Wittig, R. (Eds.), *The Chimpanzees of the Tai Forest: 40 Years of Research* (pp. 78-86). United Kingdom: Cambridge University Press.
- Dietz, M.W., Daan, S. & Masman D. (1992). Energy Requirements for Molt in the Kestrel *Falco tinnunculus*. *Physiological Zoology* 65, 1217-1235.



- Echeverria, V., Estades, C. F., Botero, D. E., Wingfield, J. C., & González, G. P. L. (2018). Pre-basic molt, feather quality, and modulation of the adrenocortical response to stress in two populations of rufous-collared sparrows *Zonotrichia capensis*. *Journal of Avian Biology*, 49(11).
- Echeverry-Galvis, M.A., & Hau, M. (2012). Molt–breeding overlap alters molt dynamics and behavior in zebra finches, *Taeniopygia guttata castanotis*. *Journal of Experimental Biology*, 215(11), 1957-1964.
- Falls, J. B., & Kopachena, J. G. (2010). White-throated Sparrow (*Zonotrichia albicollis*), version 2.0. In *The Birds of North America* (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <http://doi.org/10.2173/bna.128>
- Gordo, O., Brotons, L., Ferrer, X., & Comas, P. (2005). Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Global Change Biology*, 11(1), 12–21. <https://doi.org/10.1111/j.1365-2486.2004.00875.x>
- Gunderson, A. R., Frame, A. M., Swaddle, J. P., & Forsyth, M. H. (2008). Resistance of melanized feathers to bacterial degradation: is it really so black and white? *Journal of Avian Biology*, 39(5), 539–545. <https://doi.org/10.1111/j.0908-8857.2008.04413.x>
- Gwinner, E. (2003). Circannual rhythms in birds. *Current Opinion in Neurobiology*, 13(6), 770–778. <https://doi.org/10.1016/j.conb.2003.10.010>
- Gunnarsson, T.G., Gill, J.A., Newton, J., Potts, P.M., & Sutherland, W.J. (2005). Seasonal matching of habitat quality and fitness in a migratory bird. *Proc. Roy. Soc. London B* 272, 2319–2323.



- Gwinner, E. (2008). Circannual clocks in avian reproduction and migration. *Ibis*, 138(1), 47–63. <https://doi.org/10.1111/j.1474-919X.1996.tb04312.x>
- Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R., & Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals: Carry-over effects in animal populations. *Journal of Animal Ecology*, 80(1), 4–18. <https://doi.org/10.1111/j.1365-2656.2010.01740.x>
- Hill, G. E., and K. J. McGraw (Editors) (2006a). *Bird Coloration, Volume II: Function and Evolution*. Harvard University Press, Cambridge, MA, USA.
- Holberton, R. L., Wilson, C. M., Hunter, M. J., Cash, W. B. & Sims, C. G. (2007). The role of corticosterone in supporting migratory lipogenesis in the dark-eyed junco, *Junco hyemalis*: a model for central and peripheral regulation. *Physiological and Biochemical Zoology*, 80(1), 125-137.
- Howell, S. N. G., Corben, C., Pyle, P., & Rogers, D. (2003). The First Basic Problem: A Review of Molt and Plumage Homologies. *The Condor*, 105(4), 635–653.
- Jacobs, J. D., & Wingfield, J. C. (2000). Endocrine Control of Life-Cycle Stages: A Constraint on Response to the Environment? *Ornithological Applications*, 102(1), 35–51. <https://doi.org/10.2307/1370406>
- Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E., & Tonra, C. M. (2015). A call for full annual cycle research in animal ecology. *Biology Letters*, 11(20150552). <https://doi.org/10.1098/rsbl.2015.0552>
- Marra, P.P. and Holberton, R.L. (1998). Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia*, 116(1), 284-292.



- Marra, P. P., Hobson, K. A., & Holmes, R. T. (1998). Linking Winter and Summer Events in a Migratory Bird by Using Stable-Carbon Isotopes. *Science*, 282(5395), 1884–1886. <https://doi.org/10.1126/science.282.5395.1884>
- Pyle, P. (1997). Identification Guide to North American Birds, Part I. Slate Creek Press, Bolinas, CA, USA.
- Rappole, J. H., & A. R. Tipton. (1991). New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology*, 62(3), 335–337.
- Reudink, M. W., Marra, P. P., Kyser, T. K., Boag, P. T., Langin, K. M., & Ratcliffe, L. (2009). Non-breeding season events influence sexual selection in a long-distance migratory bird. *Proc. R. Soc. B*, 276(1662), 1619-1626. [10.1098/rspb.2008.1452](https://doi.org/10.1098/rspb.2008.1452)
- Ricklefs, R.E., & Wikelski, M. (2002). The physiology/life-history nexus. *Trends Ecol. Evol.*, 17(10), 462–468.
- Romero, L. M., Storchlic D., & Wingfield J. C. (2005). Corticosterone inhibits feather growth: Potential mechanism explaining seasonal down regulation of corticosterone during molt. *Comp. Biochem. Physiol. A*, 142, 65 – 73.
- Romero, L. M., & Wingfield, J. C. (1999). Alterations in hypothalamic–pituitary–adrenal function associated with captivity in Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*). *Comp. Biochem, Physiol. B*, 122(1), 13-20. [https://doi.org/10.1016/S0305-0491\(98\)10161-X](https://doi.org/10.1016/S0305-0491(98)10161-X).
- Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Ford, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, et al. (2016). Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States.



- Partners in Flight Science Committee 199. <https://partnersinflight.org/wp-content/uploads/2016/08/pif-continental-plan-final-spread-single.pdf>
- Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., ... Marra, P. P. (2019). Decline of the North American avifauna. *Science*, *366*(6461), 120–124. <https://doi.org/10.1126/science.aaw1313>
- Sapolsky, R. M., Romero, L. M., & Munck, A. U. (2000). How Do Glucocorticoids Influence Stress Responses? Integrating Permissive, Suppressive, Stimulatory, and Preparative Actions. *Endocrine Reviews*, *21*(1), 55–89.
- Siegel, H. S. (1980). Physiological Stress in Birds. *BioScience*, *30*(8), 529–534. <https://doi.org/10.2307/1307973>
- Swaddle, J. P., Witter, M. S., Cuthill, I. C., Budden, A., & McCowen, P. (1996). Plumage Condition Affects Flight Performance in Common Starlings: Implications for Developmental Homeostasis, Abrasion and Moult. *Journal of Avian Biology*, *27*(2), 103–111. <https://doi.org/10.2307/3677139>
- Studds, C.E., & Marra, P.P. (2007). Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. *Climate Research*, *35*, 115–122. <https://doi.org/10.3354/cr00718>
- Studds, C.E., Marra, P.P. (2011). Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proc. Roy. Soc. London B*, *278*(1723), 3437–3443.
- Tonra, C.M. & Reudink, M.W. (2018). Expanding the traditional definition of molt-migration. *The Auk: Ornithological Advances*, *135*(4), 1123–1132.



- Vézina, F., Gustowska, A., Jalvingh, K. M., Chastel, O., & Piersma, T. (2009). Hormonal Correlates and Thermoregulatory Consequences of Molting on Metabolic Rate in a Northerly Wintering Shorebird. *Physiological and Biochemical Zoology*, 82(2), 129–142. <https://doi.org/10.1086/596512>
- Visser, M. E., Caro, S. P., van Oers, K., Schaper, S. V., & Helm, B. (2010). Phenology, seasonal timing and circannual rhythms: towards a unified framework. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555), 3113–3127. <https://doi.org/10.1098/rstb.2010.0111>
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes (2002). Links between worlds: Unraveling migratory connectivity. *Trends in Ecology & Evolution*, 17,76–83.
- Wingfield, J. C. (2007). Organization of vertebrate annual cycles: implications for control mechanisms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1490), 425–441. <https://doi.org/10.1098/rstb.2007.2149>
- Wingfield, J. C., & Silverin, B. (2002). Ecophysiological Studies of Hormone-Behavior Relations in Birds. *Hormones, Brain, and Behavior*, 2, 587–647.



Figures

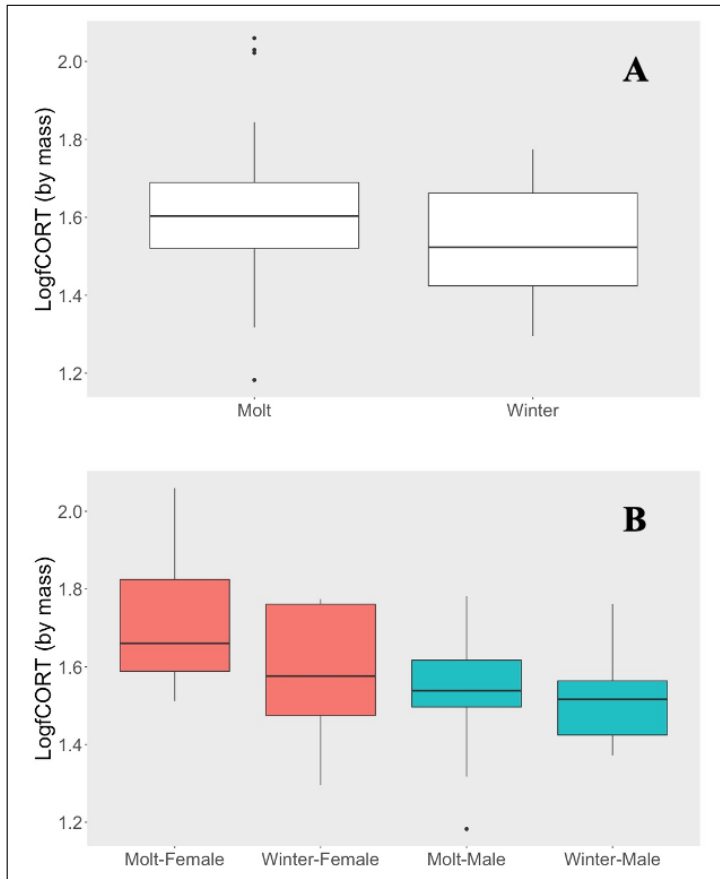


Figure 1. White-throated sparrows at the Olentangy Wetlands from 2018-2020. Plot showing difference between fCORT in molt and winter (A) and difference between molt and winter fCORT by sex (B).

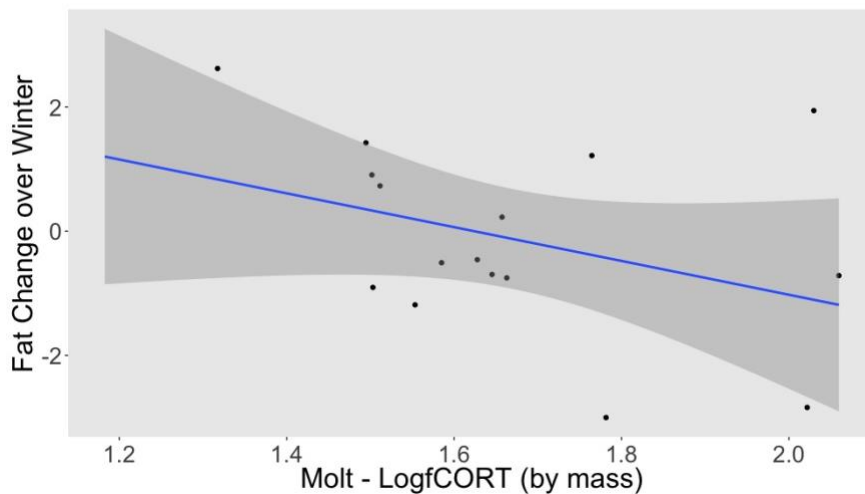


Figure 2. White-throated sparrows at the Olentangy Wetlands from 2018-2020. Fitted plot showing the relationship between fCORT from molt and fat change over winter corresponding to objective two. Fat change values have been fitted to account for significant predictors of age, time interval, and the interaction between LogfCORT and age. See Table 1.

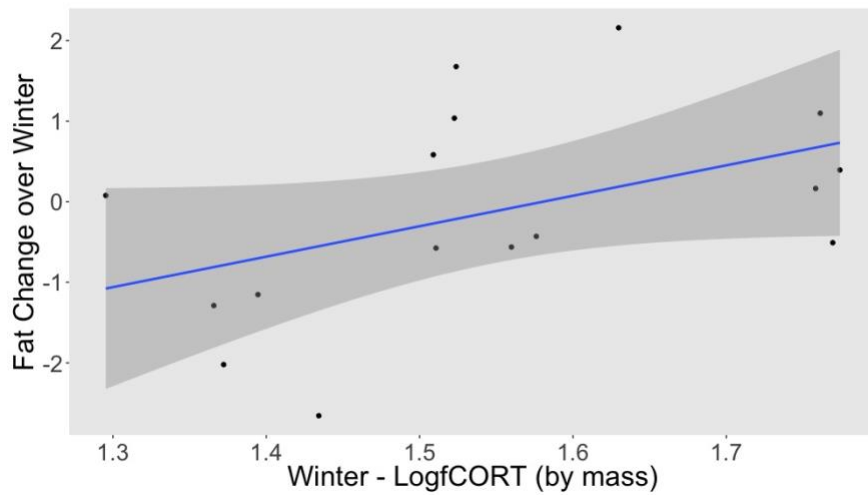


Figure 3. White-throated sparrows at the Olentangy Wetlands from 2018-2020. Fitted plot showing the relationship between fCORT from winter and fat change over winter corresponding to objective three. Fat change values have been fitted to account for significant predictors of age, time interval, sex and the interaction between LogfCORT and age. See Table 2.

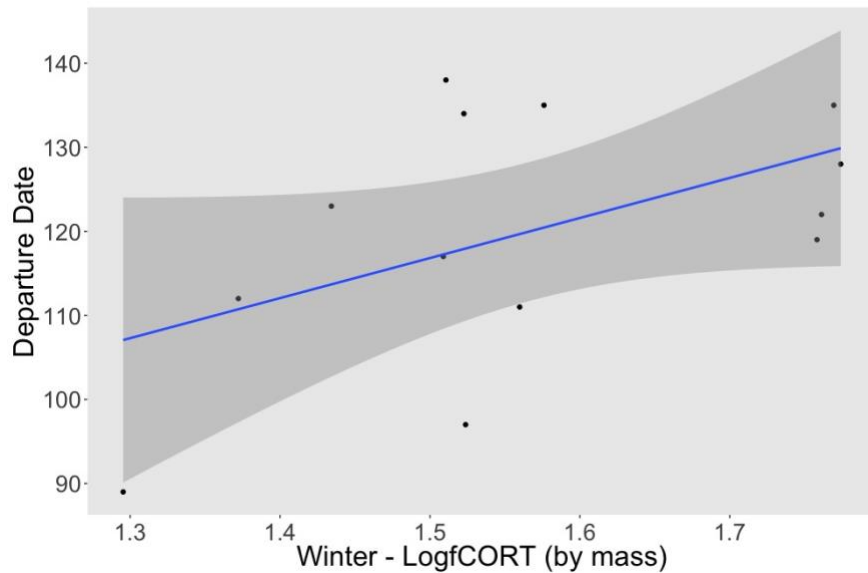


Figure 4. White-throated sparrows at the Olentangy Wetlands from 2018-2020. Plot showing the relationship between fCORT from winter and departure date corresponding to objective four. Departure date is represented as the day of the year (i.e. January 1st is day one).

Tables

Table 1. Statistics from generalized linear model testing the prediction from objective two. Fat change run as the dependent variable and LogfCORT from molt, age, time interval, and the interaction between LogfCORT and age. Fat change is measured over the winter period. "HY" represents birds in their hatch year. Time interval is measured as the number of days between two captures of a bird. Data for white-throated sparrows at the Olentangy Wetlands from 2018-2020.

	Estimate	t_{df=15}	P
LogfCORT (molt)	-21.6482	-3.032	0.01140
Age (HY)	-28.13145	-2.402	0.03511
Time Interval	0.04575	3.365	0.00631
LogfCORT*Age	18.51343	2.537	0.02763

Table 2. Statistics from a generalized linear model testing the prediction from objective three. Fat change run as the dependent variable and LogfCORT from molt, age, time interval, and the interaction between LogfCORT and age. Fat change is measured over the winter period. "HY" represents birds in their hatch year. Time interval is measured as the number of days between two captures of a bird. Data for white-throated sparrows at the Olentangy Wetlands from 2018-2020.

	Estimate	t_{df=15}	P
LogfCORT (molt)	35.22838	2.346	0.0409
Age (HY)	-52.49557	2.328	0.0422
Sex (Male)	1.80435	2.000	0.0733
Time Interval	0.03545	2.490	0.0320
LogfCORT*Age	-34.86393	-2.246	0.0485

