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Weathering the Storm: Physiological and Behavioural Responses of White-Throated Sparrows to Inclement Weather Cues

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Abstract

Changes in weather patterns and extreme weather events are becoming more common with the onset of climate change. This predicted increase in severe weather globally is alarming and it draws concern for the adaptability and ultimate survival of many species. It is clear that birds are able to cope with and respond to inclement weather with physiological and behavioural responses in many circumstances, but as environmental conditions become more severe, the adaptive coping responses of many species may be pushed to their limit. As such, it is important to understand the effects that such changes in environmental conditions will have on birds. Most of our current understanding of how birds respond to inclement weather relies on observational field studies, but these types of studies are unable to draw conclusions about which specific weather variables, or the changes in such variables, are mainly responsible for physiological and behavioural responses. Through experimental studies simulating inclement weather cues, my doctoral research investigated a general question: how do white-throated sparrows (*Zonotrichia ablicollis*) respond to exposure of inclement weather cues? Within this thesis, I examined the effects of recurrent inclement weather cues (Chapter 2), and also acute exposure to inclement weather cues (Chapter 5) in a controlled setting to investigate the responses of birds to individual weather cues. I also investigated how temperature alone can influence migratory behaviour (Chapter 3). To complement these experimental studies, I also examined the effects that natural storm systems had on birds in a controlled setting (Chapter 4). I found interesting effects that were sex- and season-specific throughout. White-throated sparrows are able to detect changes in both temperature and barometric pressure, and respond to each cue differently depending on the season. For example, exposure to acute changes in temperature alone influenced behavioural responses in spring, but acute exposure to both temperature and barometric pressure elicited a stronger response of both physiological and behavioural measures in the winter. Food availability had limited effects throughout, suggesting that a variety of alternative external and endogenous factors influence the response of birds to storm exposure. Combined, these projects provide further evidence of the complexity of responses of birds to inclement weather, but these responses are dependent upon a variety of factors. Thus, it is difficult to draw a linear conclusion from these studies. This thesis reflects other multi-directional findings within the published literature, highlighting that white-throated sparrows must use a variety of cues to respond to inclement weather, and that multiple other factors including season, sex and food availability can influence this response. However, further research is needed to understand how external and endogenous factors interact to modify birds' responses to inclement weather.

Keywords

Inclement weather, environmental cues, white-throated sparrow, corticosterone, feeding behaviour, stress.

Co-Authorship Statement

All chapters presented within this thesis were completed under the supervision and in collaboration with S.A. MacDougall-Shackleton at the University of Western Ontario. Funding for this research was received from S.A. MacDougall-Shackleton and supported by a research grant from the Animal Behavior Society.

A version of Chapter 1 was written as a review paper with S.A. MacDougall-Shackleton, but not yet published.

A version of Chapter 2 will be combined with a prior study I completed during my MSc and submitted for publication with S.A. MacDougall-Shackleton and K. Munoz-Ramos as co-authors. S.A. MacDougall-Shackleton contributed to experimental design and K. Munoz-Ramos analyzed Noldus behavioural videos. I contributed to overall design, obtained subject species, and acquired and analyzed data. I also thank T. Kelly, K. Erhard, S. Mischler, T. Farrell, and E. Lovett for their assistance.

A version of Chapter 3 will be submitted for publication and co-authored with S.A. MacDougall-Shackleton and T. Kelly. S.A. MacDougall-Shackleton provided logistical support and experimental design input. T. Kelly provided design and data acquisition input, as well as statistical support. I contributed to overall design, obtained subject species, and acquired and analyzed data. I also thank K. Munoz-Ramos and B. Azad for their assistance.

Versions of Chapters 4 & 5 will be combined and submitted for publication and co-authored with S.A. MacDougall-Shackleton. S.A. MacDougall-Shackleton contributed to experimental design. I contributed to overall design, obtained subject species, and acquired and analyzed data. I also thank K. Munoz-Ramos for video analysis, and T. Kelly, B. Azad, M. Brodbeck, C. Bottini, C. Carter, and A. Beauchamp for assistance with blood sampling and animal care. I also thank L. Grieves for assistance with genetic sex and morph determination.

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Chapter 1

1 General Introduction

Virtually all organisms on earth are subject to seasonal and short-term variations in abiotic conditions. Abiotic factors such as temperature, precipitation and solar radiation can shape ecosystems. Abnormal fluctuations in these abiotic factors, including weather patterns, can shift ecosystem dynamics. All species have a specific tolerance range and limit to such factors that dictates dispersal and colonization, geographic distribution, reproductive success, population dynamics, and overall survival (Parmesan 2006). Species thrive in specific geographic locations when they are well matched to the local abiotic factors; however, species' abilities to tolerate such factors are now being compromised as a result of climate change. Rapid, but transient, changes in the abiotic environment, especially inclement weather events, are common in most terrestrial habitats and species have evolved adaptations to cope with such events. However, climate change may be pushing some species to their tolerance limit with respect to rapid fluctuations in climatic abiotic factors (Freeman and Class Freeman 2014), depending on the degree of variation in adaptive traits that currently exist in the population (Charmantier and Gienapp 2014). As climate change advances, rapid fluctuations in abiotic factors such as temperature, precipitation, wind, and storms in general are increasing in severity and frequency; that is, there is increased frequency and severity of extreme weather events occurring across the globe (IPCC 2014). Even short-term changes in environmental conditions can cause direct threats to reproductive success and overall survival of species. As such, species must now adapt their tolerance limits in order to thrive in their current geographical ranges, shift their range for survival, or ultimately go extinct.

Many studies are currently focused on the influence of climate change on physiological and behavioural responses of species (Easterling et al. 2000, Walther et al. 2002, Davis et al. 2005, Parmesan 2006). However, responses to short-term inclement weather exposure remain equally important to understand how species will respond. Changing weather patterns can affect most terrestrial animals, including birds, making it an increasingly important topic to study with the onset of climate change. Throughout this chapter, I will discuss birds' responses to inclement weather and changing weather patterns, including the environmental factors that change during inclement weather with the seasons, the effects that inclement weather has on the physiology, morphology and behaviour of birds, the mechanisms that drive such changes, and the cues used to detect oncoming inclement weather. Continuing research on birds' responses to inclement weather is critical to understand how bird populations may respond to increased frequency of inclement weather associated with climate change, which is the overall goal of my thesis research.

1.1 Inclement weather and climate change

Inclement weather is defined as stormy, severe or tempestuous outdoor conditions. In most cases, inclement cloudy, wet weather is associated with a low pressure system, and fair weather is accompanied by a high pressure system (Ahrens 2012). There are several different classes of inclement weather events across the globe, most of which are becoming more frequent and severe under global climate change (IPCC 2014). Most inclement weather events form as a result of changing atmospheric conditions and moving pressure systems over an area (Ahrens 2012). In the northern hemisphere, winter storms can pose significant challenges with respect to survival in many species. During winter in the northern hemisphere, some of the most severe storms are associated with a low pressure system and an accompanying cold front. A front is a boundary separating two different air masses; during severe winter storms in North America, a cold front typically forces a frigid continental arctic air mass to displace a less cold continental air mass, creating extremely cold temperatures. These systems cause changes in the air's moisture content (relative humidity, dew point) due to new air masses passing over the area, shifts in wind speed and direction, decreasing barometric pressure, and significant snowfall and resultant ice cover (Ahrens 2012).

Weather and climate differ in respect to the time period of reference. Weather refers to the current outdoor conditions and state of the atmosphere on a daily time scale, and climate refers to the atmospheric conditions across a longer time scale, usually 30 years. Climate change is typically characterized by long-term changes in air and ocean temperatures, shifts in average precipitation amounts and patterns, and changes in the prevalence of severe weather events over an extended period of time. In North America, increased air temperatures and shifts in precipitation patterns have already led to a higher frequency of extreme weather events than recorded in previous years, including heat waves, heavy precipitation and flooding, a sharp increase in thunderstorms and unstable air, and diminishing ice cover (Environment Canada 2017). Globally, climate change is affecting natural systems and animal populations through changes in global temperatures and annual precipitation levels (Easterling et al. 2000, Parmesan and Yohe 2003). Even fifteen years ago, forty-one percent of plants and animals sampled had already been affected by an increase in average global temperature of just 0.6 °C (Parmesan and Yohe 2003). This number of affected species has increased since 2002, as a further increase of global land temperatures rose to 1.42 °C above average in 2018 (NOAA 2018). Since records began in 1880, 2016 was the warmest year ever recorded (NOAA 2018), even though the central and eastern United States and Canada have experienced record-breaking low temperatures throughout the past few winter seasons. Nine of the ten warmest years on record have occurred since 2005, with the last five years, including 2014-2018, comprising the five hottest (NOAA 2018). Average global temperatures are expected to increase further in coming decades (IPCC 2014, NOAA 2018), leading to further unanswered fundamental questions as to how species can respond to these changes (Sutherland et al. 2013).

Climate change has also been linked to an increase in the frequency and severity of violent, unpredictable storms and other extreme weather events at nearly all latitudes (Easterling et al. 2000, Meehl et al. 2000, Beniston and Stephenson 2004, IPCC 2014), which may be a result of an altered jet stream (Francis and Vavrus 2015), although this remains inconclusive. Jet streams are fast moving currents of air located between the troposphere and stratosphere that typically flow from west to east. They are the result of a combination of the earth’s rotation and solar radiation and can aid with enhancing the predictability of meteorological forecasts depending on their location (Saucier 2003). Jet stream patterns are now weakening due to a greater proportion of warming temperatures at higher latitudes and unequal warming patterns across the globe. This increases the likelihood of slower moving, high amplitude jet stream patterns that ultimately increases the likelihood and duration of extreme weather events occurring (Francis and Vavrus 2015). In 2019, a weakening of the polar jet stream caused a polar vortex event to break record daily cold temperatures in southern Canada and throughout the United States (NOAA 2019). These extreme conditions can be difficult for even humans to appropriately respond, and many plants and animals will likely also have difficulty adapting to these transient extreme conditions.

Changes in global climate patterns, including increasing temperature, precipitation, and frequency of extreme weather events are having profound effects on many species of birds and other taxa. As a result of global change, we are now observing changes in migration and behavioural patterns, delays or advances in the onset of life history events, diminishing home ranges, and an increase in species extinctions (Walther et al. 2002). In many cases, inclement weather alone is directly linked to higher mortality (Newton 2007). Since the classic reports by Bumpus (1898), severe storms have often been observed to result in bird mortality. However, even if inclement weather does not directly cause mortality, it can act indirectly by negatively affecting reproduction (Wingfield 1985a), food availability (Boyle et al. 2010), and/or suitability of habitats, leading to further population declines. In the following sections I further describe the effects that inclement weather events have on birds.

1.2 Impacts of inclement weather on birds

Studies of the effects of inclement weather on wild animals are becoming more widespread as climate change accelerates and inclement weather events become more common. Poor weather conditions can have adverse effects on individuals, populations and species, and entire avian assemblages. Inclement weather may account for several billion mortalities among many different bird species in just the past 100 years (Newton 2007). Storms can have direct and/or indirect effects on all birds; juvenile and adult, terrestrial and marine, migrating and non-migrating, large, small, granivores, insectivores, and frugivores (Newton 2007). Almost all documented large-scale bird mortalities, up to several thousand birds at a time, are a result of inclement weather either during migration, shortly after arrival at breeding territories, or just prior to departure for their wintering territories (Newton 2007). Many of the environmental factors associated with winter storms can pose challenges with respect to regulating body temperature, locating food sources, maintaining territories, and ultimately survival (Carey and Dawson 1999; Parmesan and Yohe 2003). These conditions can create life threatening conditions, and may continue to cause lasting problems that persist after the storm. Birds can have different responses to inclement weather depending on the annual life history stage during which the event occurs. Storms can cause individuals to delay or abort life history phases, including migration, reproduction, and moult, as will be discussed in upcoming sections.

1.2.1 Impacts on migration

Inclement weather can affect the ability of birds to successfully migrate from breeding grounds to wintering grounds, and vice versa (Richardson 1978). Birds exhibit two main migration strategies: facultative and obligate. Facultative migration is influenced by proximal cues, such as a lack of available food or inclement weather, forcing an individual to flee their current home to escape poor conditions in the immediate future, regardless of season (Gill 2007). As a result of diminished food supply, high-elevation white-ruffed manakin (*Corapipo altera*) residents in Costa Rica were more strongly affected by inclement weather than their lower-elevation conspecifics. More frequent inclement weather occurring at high altitudes impacts the availability of food to manakins, which caused increased corticosterone levels and initiated an altitudinal facultative migration among these birds (Boyle et al. 2010). Obligate migration is more dependent on endogenous timing mechanisms and occurs at a similar time each calendar year in the spring and autumn with less influence of proximal cues (Newton 2012). When weather conditions are severe enough, birds undergoing obligate migrations can additionally undergo facultative migrations to escape inclement conditions (Streby et al. 2015). For example, golden-winged warblers (*Vermivora chrysoptera*) escaped a severe tornadic storm less than 24 h after returning to their breeding grounds, facultatively migrating an additional 1500 km (Streby et al. 2015).

Severe weather along obligate migratory paths can create obstacles for birds, especially those travelling over water with nowhere to stop and take shelter (Richardson 1978). As a result of poor weather conditions, long-distance obligate migrants can undertake facultative migrations during or after their current obligate migration (Streby et al. 2015). Strong winds and heavy precipitation may push obligate migrants off their path, or force them to land, resulting in fatal collisions, drowning if over water, or freezing. Severe storms during autumn migration and increased precipitation on their wintering grounds reduced overall survival of adult burrowing owls (*Athene cunicularia*) over a 15-16 year period (Wellicome et al. 2014). A comparative study between eastern and western migratory North American songbirds showed the former suffered higher mortalities when migrating to their wintering destinations (Butler 2000), possibly due to the higher-than-average number of storms along the eastern migrants’ path compared to those migrating from the west (Butler 2000). During fall migration, atmospheric humidity levels affected flight take-offs over water in Swainson's thrushes (*Catharus ustulatus*) and wood thrushes (*Hylocichla mustelina*). Only thrushes with maximum fat reserves departed during high atmospheric humidity, as higher humidity levels correspond to more tempestuous weather conditions (Deppe et al. 2015). Radar data recording migratory flight in southern Italy determined fog directly limited migratory flight intensity among many species, including European honey buzzards (*Pernus aviporus*), common/pallid swift species (*Apus sp*.), bee-eaters (*Merops apiaster*), house martins (*Delichon urbica*), and barn swallows (*Hirundo rustica*; Panuccio et al. 2019). Additionally, significant decreases in the abundance of mourning warblers (*Oporornis philadelphia*), blackpoll warblers (*Dendroica striata*), and rose-breasted grosbeaks (*Pheucticus ludovicianus*) arriving at their wintering grounds was also directly related to a higher frequency of severe storms occurring in the Atlantic Ocean and Gulf of Mexico throughout these species' fall migrations (Butler 2000). Temperature directly influenced the intensity of migratory restlessness behaviour in captive white-throated sparrows (*Zonotrichia albicollis*), suggesting that birds can respond to temperature directly independently of other weather cues (Metcalfe et al. 2013, Berchtold et al. 2017). These observations support the notion that successful migrations could be reduced by an increase in frequency and severity of storms. Clear evidence supports that inclement weather cues can influence the timing of migration and the duration spent at stopovers, but there is limited research determining which individual weather factors influence migration.

Although inclement weather conditions can negatively affect migration, other weather conditions may actually improve conditions for some migrants, allowing them to travel further with less energy use (Richardson 1978). Soaring or flying along favourable tail winds can increase the travelling speed and also reduce energy expenditure (Shamoun-Baranes and van Gasteren 2011), however, if winds become too strong and tempestuous conditions persist, fatal accidents may occur. As storms become more frequent and severe, the likelihood of sustained favourable conditions aiding migrants may be reduced.

1.2.2 Impacts on reproduction

Inclement weather can delay or terminate reproduction prior to or during the breeding season. Poor weather can also delay or reduce reproductive hormone concentrations and result in total abandonment of the breeding territory. For example, male song sparrows (*Melospiza melodia*) in New York state had a delay in testicular development and decreased levels of circulating testosterone after a particularly harsh winter season and severe early-spring storms (Wingfield 1985a). In addition to a disruption of the reproductive cycle, these birds also exhibited an increased overall body mass and total fat mass compared to the previous spring under more typical weather conditions. Such changes did not impact corticosterone levels, indicating that although changes occurred, it was not necessarily perceived as “stressful” to male song sparrows (Wingfield 1985a). The same severe winter differentially affected female song sparrows. Females, like the males, experienced a delay in gonadal development. However, overall body mass and fat mass decreased and females experienced an increase in corticosterone levels (Wingfield 1985b), indicating the severe winter storm was stressful to females. This indicates that depending on the sex, reproduction may be influenced differently as a result of inclement weather. In Lapland longspurs (*Calcarius lapponicus*), corticosterone levels nearly doubled in years with higher-than-average severe weather events compared to less severe years during the breeding season, influencing reproductive output (Krause et al. 2018). An additional study on Puget Sound white-crowned sparrows (*Zonotrichia leucophrys pugetensis*) found inclement early spring weather caused a delay in breeding by one month and a delay of the vernal increase of circulating reproductive hormones (luteinizing hormone and testosterone; Wingfield et al. 1983), providing further evidence that inclement weather can delay or interrupt breeding. In the Sierra Nevada, white-crowned sparrows (*Z. l. oriantha*) temporarily abandoned high elevation breeding grounds during inclement weather and exhibited facultative altitudinal migration to lower elevations. Exogenous corticosterone treatment caused a delay in the return to their breeding sites during poor weather conditions, providing additional evidence of reproduction being affected by inclement weather patterns (Breuner and Hahn 2003). Thus, inclement weather can delay successful breeding and reproduction and associated hormones.

1.2.2.1 Impacts on rearing young

Inclement weather can pose several challenges when birds are trying to successfully incubate eggs and raise nestlings, and thus directly reduce fitness. Snow cover can create obstacles for rearing young by reducing the ability of ground-feeding species to collect food for young. Severe winds can create treacherous conditions for parents to navigate and locate food sources, and heavy rain can flood areas and destroy nests (Carey and Dawson 1999). Often these effects are sex-specific (Wingfield 1985a, b; Wingfield and Ramenofsky 2011a, Krause et al. 2018), and they may involve a response of the adrenal stress response and increased levels of circulating corticosterone. Low food availability and unfavourable weather conditions can therefore affect whether parents continue to raise their offspring or abandon a nest an await better conditions (Wingfield et al. 2016).

Several studies have documented inclement weather disrupting egg and nestling care in birds. Adélie penguins (*Pygoscelis adeliae*) with experimentally increased baseline corticosterone levels were more likely to have incubation failure or an increase in the overall incubation period in response to inclement weather (Thierry et al. 2013). Treating black-legged kittiwakes (*Rissa tridactyla*) with corticosterone for just two days reduced prolactin levels by 30% and impaired parental care (Angelier et al. 2009). Song sparrows that experienced an early-summer storm had a reduced ability to successfully feed young: a severe storm that depleted food resources resulted in a significant decline in body condition and an increase in corticosterone levels in males (Wingfield 1985a), opposite of the effects observed after the severe winter storm noted above. The same early-summer storm affected females differently; corticosterone levels were not affected by the early-summer storm (Wingfield 1985b). This difference was likely due to males being the main provider of food at the time of the early-summer storm. Bull-headed shrikes (*Lanius bucephalus*) showed a positive correlation between nestling deaths and total precipitation per day (Takagi 2001), indicating further that rearing young becomes more difficult under inclement conditions. In addition to affecting sexes differently during the rearing stage, inclement weather can affect individuals differently depending on the time of year and reproductive state (Wingfield et al. 1983, Romero et al. 2000, Romero 2002). Among Lapland longspurs, hypothalamic pituitary adrenal axis (HPA; discussed further in section 1.4.1) activity was up-regulated in response to winter storms, however once birds entered the parental stage, HPA axis activity was not affected by similar winter storms (Krause et al. 2016a). In the pre-breeding season, inclement weather had no effect on corticosterone levels in three Arctic passerines, however, once nestlings were present, corticosterone levels increased, possibly corresponding to the inability of the parents to properly feed young (Romero et al. 2000). Thus, once young are in the nest, inclement weather appears to induce a stress response and impair reproduction in many songbird species. In white-crowned sparrows, corticosterone levels rose in response to storms when adults were feeding young, but not after the young had fledged the nest (Wingfield et al. 1983). Increases in corticosterone during feeding periods also led to an increase in the amount of abandoned nests during this time (Wingfield et al. 1983). Many of these findings suggest that the suppressive effects of stress on reproductive success may operate via corticosterone.

1.3 Responses of birds to inclement weather

With global change contributing to higher frequencies of storms and inclement weather, birds must cope with short-term changes, adapt to changing environmental conditions in both the short- and long-term, or go extinct. Such adaptations to environmental changes are key for positive fitness and survival in the face of climate change (Newman et al. 2011). There are several different responses to inclement weather, and further, to climate change. The severity and duration of the altered environmental state will likely determine which type of response occurs – an adaptation, range shift, or extinction. The probability that birds can cope with an increased frequency of inclement conditions will depend on the degree of plasticity of different adaptive traits that currently exist in the population and the degree to which there will be active selection relative to the speed at which climate change alters natural conditions.

For temperate-zone birds, surviving winter months is challenging if temperatures drop too low or there is a severe shortage of food. It becomes critical to survival for birds to make behavioural, physiological, and morphological adjustments when they experience severe winter weather (Carey and Dawson 1999). Birds can respond to climate change and changing weather patterns through adaptive evolution and/or phenotypic plasticity. Evolutionary adaptations will take place over a longer time frame, and are likely not appropriate for short-term changes in weather. Phenotypic plasticity involves the ability of organisms to change their behaviour, morphology, and/or physiology in response to changing environmental conditions on a shorter time scale (Bradshaw and Holzapfel 2006). Below I review phenotypic plasticity as a mechanism to respond to inclement weather conditions.

1.3.1 Phenotypic plasticity

Phenotypic plasticity involves the alteration of behaviour, morphology, and/or physiology within an individual’s lifetime to adjust to environmental conditions. Phenotypic plasticity can occur on various time scales including developmental plasticity and seasonal plasticity, as well as more rapid responses (phenotypic flexibility) to short-term environmental changes. For example, during winter, birds are able to increase their external cold resistance through acclimatizing (Carey and Dawson 1999). Acclimatized birds can maintain a stable internal temperature in cold conditions approximately 6-7 hours longer than they can during summer months (Carey et al. 1989). This results in wintering birds being able to withstand colder temperatures without needing to expend extra energy for thermoregulation. During this time, birds also increase their fat stores and lower their metabolic rates (Carey and Dawson 1999). Birds are also plastic in the sense that their neural and endocrine systems are altered depending on the stage of the annual cycle, availability of food, sex, and reproductive state (e.g., Wingfield 1985a, b). Below I survey some of the plasticity birds exhibit in response to changes in weather and climate, including morphological and physiological adjustments.

1.3.1.1 Plumage adjustments

Morphological adaptations are an important group of phenotypic responses that affect body temperature regulation. The most important physical attribute for insulation is a full coat of down feathers. Down feathers are the main insulating feathers, however exterior contour feathers do provide a level of insulation to birds as well (Gill 2007). Preen oil applied to contour feathers creates a waterproof coating that is resistant to precipitation. By keeping the skin dry, birds can conserve additional energy from having to further regulate thermogenesis. Prior to each winter season, birds living in temperate/arctic climates complete a prebasic moult in part to enhance insulation and decrease the lower critical temperature (Jenni and Winkler 1994). During mid-moult when feathers have been shed but not yet regrown, insulation is compromised and if temperatures drop to abnormal levels, or if species live in Arctic regions, energy must be rerouted to heat production rather than feather regeneration (Romero et al. 2000). Thus, the timing of moult in relation to relation to changes in weather is critical for survival. If optimal timing of moulting is limited due to harsh environmental conditions, moulting may have to occur in stages, which takes a longer period of time and a higher expenditure of energy. The high energy expenditure required for moulting makes avoiding stressors throughout this time important (de Bruijn and Romero 2013). Corticosterone increased during moult under cold conditions in three Arctic bird species: Lapland longspurs, snow buntings (*Plectrophenax nivalis*), and redpolls (*Carduelis flammea*). All three species had increased plasma levels of corticosterone during moult due to frigid temperatures and the high amount of expended energy (Romero et al. 2000). Although the timing of moult in temperate-zone birds is now shifting as winter and spring seasons are shifting in time (Ambrosini et al. 2011, Barshep et al. 2013), it is still critical for birds to be able to undergo morphological adjustments at appropriate times.

1.3.1.2 Physiological and body composition adjustments

Birds adjust their body mass in response to ambient conditions both on daily and seasonal time scales. In autumn and winter, acquired fat stores diminish earlier and more quickly in the evening than in the spring as a result of seasonal changes in temperature and day-length (Lehikoinen 1987). Fat stores continue to be depleted until morning when foraging activities can resume. Birds residing in colder geographic regions are fatter during the winter than during summer or autumn. This seasonal variation of weight is referred to as ‘adaptive winter fattening’ due to the need for higher energy stores in winter (Lehikoinen 1987). In most small passerines, the fat stores created are only large enough to sustain them for up to two days of no food during winter (Carey and Dawson 1999), which is why they are sometimes referred to as emergency fat reserves. Increased fat stores and higher foraging rates have several accompanying potential costs, including increased expenditure of energy to forage and search for food, increased risk of predation by increased exposure, and higher costs of flight due to increased mass (Carey and Dawson 1999). Optimal fat stores therefore involve a trade-off between maintaining sufficient energy stores and these costs. Thus, minimum daily fat stores decrease slowly in spring as the benefits of higher energy stores decrease with the onset of more benign weather (Lehikoinen 1987, Bednekoff and Houston 1994).

One of the primary means birds use to stay warm in winter is heat generation by shivering (Marsh and Dawson 1989). In birds, shivering occurs through the rapid contraction of the opposing pair of flight muscles, pectoralis and supracoracoideus, to create heat (Marsh and

Dawson 1989, Eduardo et al. 2001). Other strategies birds employ to keep warm include huddling together, residing in microclimates such as hiding under dense foliage or in cavities, increasing exposure to incoming solar radiation, or, in migrating birds, fleeing the area when possible (Carey and Dawson 1999). It is important to note that climates in many regions, including those to which many migratory birds move, are being altered as a result of recent climate change. Some regions are seeing warmer, wetter climates, while others are seeing abnormally frigid, snowy conditions. Temperate North American species will need to shift their physiological adjustments to compensate for the severe winter weather seasons now occurring. For example, white-throated sparrows that migrate to the southeastern United States are now more commonly experiencing severe winter storms on their wintering grounds, regardless of being a migratory species. The southeast United States has experienced record-breaking low temperatures and snowfall amounts in the past several years (NOAA 2018).

Body composition changes are also required during migration. Prior to beginning migratory flight, birds must put on a significant amount of weight, mostly in the form of fat. Some birds can nearly double their pre-migratory mass to prepare for their long distance flights (Lindström and Piersma 1993). The accumulation of fat stored in adipose tissue, liver and muscle cells are used throughout the migratory route so birds can continue flying without needing to stop and use additional energy searching for food. Creating fat reserves for migratory flights can also become important if inclement weather is experienced along the route and birds are forced to undergo facultative migrations along obligate migratory paths. The conditions experienced along stopover sites can influence the ability of birds to refuel and thus affect the timing of the migration (Goymann et al. 2010, Seewagen and Guglielmo 2010).

1.4 Inclement weather and the stress response

Rapid changes in environmental conditions can be a source of stress to birds. Although definitions of stress are often vague, one common definition of a stressor is anything that is perceived as a threat to the well-being or survival of an organism (Wingfield and Ramenofsky 1997). A single storm may act as an acute stressor to birds and thus an increased frequency of storms may act cumulatively as a chronic stressor and induce a longer-term endocrine stress response. Prior work has shown that frequent, repeated acute stressors can cumulatively create a condition of chronic stress (Busch et al. 2008). Thus, more frequent recurrences of inclement weather have the potential to act as a chronic stressor, impacting the individual's overall health and fitness. However, extreme conditions may not necessarily act as stressors in and of themselves if they are predictable. There are two general responses of birds to an environmental disruption: anticipatory changes or changes during or after the disruption (Wingfield and Ramenofsky 2011a). Many species are able to prepare for extreme conditions if there are cues that reliably predict such conditions. For example, migration may be energetically demanding but not a stressor per se. In contrast, more rapid fluctuations in the environment that are more difficult to predict (e.g., storms) may be perceived as a stressor and activate neural and endocrine stress responses.

There is relatively little known about the hormonal responses of birds to inclement weather events, however, it is known that the emergency life-history stage is activated when vertebrates encounter environmental perturbations. This can activate a fight-or-flight response, facultative behavioural and physiological responses via the hypothalamic pituitary adrenal (HPA) axis (i.e., temporarily abandon territory, mobilize energy stores, seek refuge), and multiple other coping strategies (i.e., abandon life history stages; Wingfield and Ramenofsky 2011a).

1.4.1 HPA axis

When birds encounter a stressor, physiological and behavioural responses are activated, including hormone secretion, reallocation of energy, and increased feeding behaviour. Once a stressor is encountered and the emergency life-history stage is induced, the hypothalamic pituitary adrenal (HPA) axis is activated and energy resources are allocated towards self-maintenance (Wingfield et al. 1998, Reneerkens et al. 2002). To activate the HPA axis, a stressor is first perceived and processed in the hypothalamus. The hypothalamus then stimulates secretion of corticotropin-releasing hormone (CRH). CRH travels to the anterior pituitary gland where it then stimulates the secretion of adrenocorticotropic hormone (ACTH). ACTH then enters the bloodstream and provokes the adrenal cortex to produce and secrete glucocorticoid hormones (Rivier and Vale 1983). Glucocorticoids are mainly responsible for the overall health of an individual, including regulating energy, immune reactions and stress responses. Glucocorticoids also mobilize energy stores and suppress non-essential physiological and behavioural pathways and responses until the perturbation has recessed. Hormones play a large role in the ability of birds to modify physiology and behaviour in response to environmental factors (Wingfield et al. 1995). In birds, the primary glucocorticoid secreted through the HPA axis is corticosterone (Holmes and Phillips 1976), thus measuring corticosterone levels under potentially stressful situations may provide a good indicator of the stress response of the individual.

Following elevated corticosterone secretion, energy stores and other resources are diverted from growth and maintenance of the individual to facilitate immediate survival. Continuing non-essential processes are energetically expensive and could negatively affect fitness (Wingfield et al. 2017). Concentrations of corticosterone are dependent on the age and sex of the individual and the time of year (Wingfield et al. 1983; Wingfield 1985b, a; Romero et al. 2000). Corticosterone levels are usually highest during the breeding season when resource allocation must be focused on reproduction (Romero 2002). The severity of the stressor can also influence the secretion of glucocorticoids. As expected, more stressful events induce higher levels of glucocorticoids (Romero 2002), however, the relationship between increases in corticosterone and increased feeding rates remains poorly understood (Krause et al. 2017).

Stressors are often assessed by measuring glucocorticoid levels in individuals. Corticosterone levels can fluctuate depending on the age and sex of the individual, the severity of the stressor, and the time of year (Wingfield et al. 1983; Wingfield 1985a, b; Romero et al. 2000). The response or sensitivity of birds to a severe weather stressor can also depend on the current level of circulating glucocorticoids at the time of the event. Birds with elevated glucocorticoid levels prior to a severe storm delayed their return to the breeding site, whereas birds with low glucocorticoid levels prior to the storm were not as affected (Breuner and Hahn 2003). Glucocorticoids thus appear to interact with reproductive physiology in determining how birds delay or terminate reproduction in response to inclement weather. However, it is much less clear to what extent glucocorticoids and the stress response modify responses to storms during the non-breeding season. Much further work is required to characterize how seasonal changes in the stress response interacts with birds' responses to changes in weather and climate, and to determine whether higher baseline corticosterone levels will impact bird populations via weakened immunity, organ damage, or mortality. The specific coping strategies employed during natural storms at different points along the life history stage remains relatively unexplored

(Wingfield and Ramenofsky 2011a). The strategy employed likely depends on the current life history stage, and the facultative physiological and behavioural responses may differ due to current body condition, trade offs of employing a certain strategy, costs and benefits of fleeing, energy expenditure, and available resources (Carey and Dawson 1999, Wingfield and Ramenofsky 2011a).

1.4.2 Allostasis

The ability of birds to deal with the energetic demands of life-history stages in addition to the demands of unpredictable perturbations is termed allostasis. The concept of allostasis states organisms can adjust physiologically to both predictable and unpredictable events to remain in a stable state, or maintaining stability through change (Wingfield, 2003; Korte et al., 2005). Life-history stages during the annual life cycle (e.g., breeding and migration) are energetically demanding for birds, but vary seasonally. Allostasis distinguishes the demands and mechanisms between predictable events (e.g., seasonal changes in temperature) from unpredictable events (e.g., inclement weather; McEwen 2002). Allostasis differs from homeostasis in the sense that homeostasis is the process whereby variables are maintained at a specific state, whereas allostasis is the process of adjustments of internal variables among different physiological states to allow stability through change (Landys et al. 2006). Allostatic load thus includes all experiences of an individual during the predictable life cycle and also the unpredictable events creating potential stress, instead of considering each as separate issues (Wingfield and Ramenofsky 2011a).

The physiological and behavioural states achieved through allostasis are achieved through primary mediators, such as hormones, the immune system, neural pathways and other responses (McEwen 2002). Allostatic load represents the cumulative cost of demands relating to predictable and unpredictable events in an organism’s environment, which also holds a threshold for the organism. Inclement weather may act as a stressor and therefore increase allostatic load. For example, birds may prepare for winter weather in response to changes in photoperiod, but rapid, short term fluctuations such as storms are less predictable and may act as a stressor and increase an individual’s overall allostatic load (de Bruijn and Romero 2011).

Allostatic overload may be reached when an increased frequency and/or intensity of a perturbation, such as inclement weather, occurs and the allostatic pathways and mechanisms are no longer able to keep the body in a stable state (McEwen and Wingfield 2003), which can happen particularly often during the winter season with limited food supply. More recently, the perturbation resistance potential has been added to the allostatic model, incorporating the resources available to an individual to compare to costs associated with daily routines and additional stress (Wingfield et al. 2017). When the perturbation resistance potential reaches critically low levels, an emergency life-history stage is activated to enhance survival. This often includes temporary disruption of the current life-history stage, such as migration or reproduction (Wingfield et al. 1998, 2017).

Stressors may be real or perceived. If an organism is adapted to or has abundant available resources, extreme conditions may not perceived or responded to as stressful. An increase in allostatic load occurs in response to unpredictable events, however, this still may not be perceived as stressful. If the allostatic load increases to allostatic overload (can also be referred to as the emergency life-history stage), then the organism is in danger if the stressor is not under control.

1.4.3 Behavioural responses and cues influencing them

Birds must be able to respond to environmental perturbations not only through changes in physiology and glucocorticoid secretion, but additionally through behavioural changes to enhance survival. The behavioural strategies employed by birds also varies on a seasonal and daily basis (Carey and Dawson 1999). These adaptive behaviours may include redirecting activity to increasing foraging, facultative migrations, temporarily abandoning territories or nests, or ceasing normal life-history stages altogether (Wingfield et al. 1998). Birds can facultatively adjust their rate of movement during migration depending on different environmental factors, including inclement weather (Boyle et al. 2010). A key factor that plays into how a bird will respond behaviourally, particularly relating to energetically demanding life-history stages or perturbations, is food availability (Carey and Dawson 1999). Food availability, which can be directly influenced by inclement weather, can dictate whether a bird continues with or ceases a life-history stage. When birds are presented with limited food supply, energy reserves can also be reallocated and used as fuel, which contributes to an overall decline in body condition (Wingfield and Ramenofsky 2011a). For some mountain birds, inclement weather during the breeding season can cause temporary abandonment of the breeding territory by facultative altitudinal migration to lower elevations where birds can access more food (Breuner et al. 2013). Food availability can also impact the behavioural strategies of birds during migration. With ample food and energy reserves, birds may decrease the stopover time along the migratory route (Gwinner et al. 1990), therefore altering their normal behavioural strategies. There is also considerable individual variation in physiology and behaviour that depends on prior stressors encountered, social status, and early life experience (Romero et al. 2009). Integrating seasonal differences in glucocorticoid concentrations with different physiological states or different life history stages allows a new understanding of how glucocorticoids help aid in survival during stress (Romero 2002).

The responses or coping mechanisms of birds to inclement weather cues has only recently been studied in controlled settings (e.g., Breuner et al. 2013, Metcalfe et al. 2013, Berchtold et al. 2017), and there are fewer experimental studies investigating these effects over different periods of the annual cycle and with different food availabilities. The current literature therefore lacks information on the effects of inclement weather cues during different periods of the annual cycle of birds and how allostatic load is impacted.

1.5 Predicting inclement weather

The occurrence of inclement weather is often unavoidable, and can affect nearly every animal, either directly or indirectly, by impacting foraging behaviour (Boyle et al. 2010, Breuner et al. 2013), migratory movement (Newton 2007, James and Abbott 2014), territorial defense (Carey and Dawson 1999), mate acquisition (Wingfield 1985a, b; Vitousek and Romero 2013), and survival (Romero et al. 2000, Takagi 2001, Walther et al. 2002, Parmesan 2006). Thus, detecting and responding appropriately to inclement weather is important to overall fitness. The fact that inclement weather has occurred throughout the history of the evolution of life on earth would suggest that many species will have adaptations to detect and respond or cope with storms or notable weather events. There are a number of cues that many animals can potentially use to detect an impending storm, including cloud cover, barometric pressure, temperature, wind, precipitation, and infrasound (Richardson 1990; Carey and Dawson 1999; Streby et al. 2015). Different cues emerge depending on the timeline of the storm's arrival. Obvious cues that a storm has already arrived are cloud cover, heavy winds, and precipitation. If these three cues were the only cues detected, there would be little benefit to the observer, as they typically indicate that a storm is already present and there would be little-to-no time to prepare. However, prior to the approach of a storm, there is also typically a decrease in barometric pressure and a change in temperature; an increase or decrease depending on the season and the geographic location of the storm.

As extreme weather can pose several challenges to birds, it is important that they are able to detect the onset of storms in order to properly prepare themselves. Typical responses to severe storm cues include increasing food intake and creating emergency fat stores to ride out the storm, abandoning territories and home ranges for areas of shelter such as underbrush or cavities, or fleeing the entire storm region and relocating to an area of calm weather (Carey and Dawson 1999). Predicting weather patterns is not only beneficial for survival, but also to aid birds along their migratory path (Newton 2007). For example, some birds may adjust their migratory path or departure date depending on the current or predicted weather conditions to save energy along their route (Richardson 1990). The following are several cues that birds may use to predict inclement weather and aid them in enhancing survival.

1.5.1 Barometric pressure

As noted previously, severe winter storms can be accompanied with decreasing barometric pressure. The most reliable cue used by vertebrates to detect an incoming storm is barometric pressure (Heupel et al. 2003, Breuner et al. 2013, Metcalfe et al. 2013). Prior to an incoming storm, barometric pressure can decrease on average anywhere between 2-12 kPa over just 24 h (Ahrens 2012).

Among birds, a main factor in responding to decreasing barometric pressure, and thus a storm, is the availability of food for survival (Breuner and Hahn 2003). Captive sparrow species increased their overall feeding and decreased their feeding latency when exposed to decreases in barometric pressure (Breuner et al. 2013, Metcalfe et al. 2013). Sparrows are typically ground-feeding species, so storms, particularly those with significant precipitation, can deplete food sources leading to an increase in feeding prior to storms. These studies suggest that birds are able to sense changes in barometric pressure and alter their behaviours to maximize survival. Birds can be impacted differently depending on their geographic location and their foraging abilities, but storms can have negative impacts on all birds, making it essential for them to be able to accurately detect the onset of inclement weather.

The mechanism surrounding how birds can detect oncoming storms through changes in barometric pressure, however, still remains unknown. It is suggested that the paratympanic organ (PO), a sensory organ in the middle ear, likely plays a role (Breuner et al. 2013, Metcalfe et al. 2013). The PO was discovered over 100 years ago in birds (Vitali 1911), but its function and origin are still largely unknown. Although lesion studies in pigeons indicate that the PO may not function as an barometer (Giannessi et al. 1996), the possibility remains that birds may still use this organ as a barometer. Further study of the paratympanic organ is required to determine if it is responsible for the detection of fluctuating barometric pressure, and if so, how.

1.5.2 Temperature

Temperature can impact the timing of many life-history stages in birds, including reproduction, moulting, and migration (Heard et al. 2012, Tomotani et al. 2016). Delays or advances in plant or insect phenology as a result of temperature can strongly affect food availability, habitat availability, and migratory successes. Thus, using temperature as a cue to predict the direct and indirect impacts of inclement weather could benefit an animal. Birds clearly possess the ability to perceive and respond to temperature, for example by regulating their internal body temperatures depending on ambient conditions (Randall 1943). However, the neural pathways and sensory mechanisms involved in how temperature is perceived remain unknown (Caro et al. 2013).

Although reliable cues that a winter storm is approaching may be a change in both temperature and barometric pressure, findings suggest that birds respond more strongly to changes in barometric pressure than they do to temperature when adjusting feeding rates (Metcalfe et al. 2013). In contrast, adjustments of migratory restlessness appear to be affected by temperature more than barometric pressure (Metcalfe et al. 2013, Berchtold et al. 2017), though the data are limited. Further research is still required to confirm the importance of temperature relative to other cues as a predictor of inclement weather.

1.5.3 Infrasound

Infrasound is very low frequency sound (0.01 to 10 Hz) that is below the range of human hearing. It can travel far distances (>1000 km) due to very little attenuation of the sound. Infrasound is generated from many natural sources, including tornadoes, volcanoes, earthquakes, and avalanches. The most well-known use of infrasound in birds is to aid in navigation. Homing pigeons (*Columba livia domestica)* use acoustical maps that are created by infrasonic cues which are emitted from certain topographic features (Hagstrum 2000, 2013).

It has also recently been suggested that birds may also have the ability to detect infrasound from storms (Streby et al. 2015). As noted above, breeding golden-winged warblers made a facultative migratory trip away from their breeding sites >24 h before the arrival of a severe tornadic storm, and well in advance of any other environmental cues appearing (i.e., prior to changes in barometric pressure, temperature, cloud cover). The hypothesized cue that birds used from the tornadic storm was infrasound, which would have radiated from over 1000 km away (Streby et al. 2015). However, the current literature does not have strong enough evidence to confirm this, and future studies should examine if and how birds may use infrasound to avoid storms.

1.5.4 Other cues

Birds can visually detect cloud cover and precipitation through visual, auditory, and tactile cues (Carey and Dawson 1999). However, once these cues are detected, the storm is likely already present in the area, allowing limited time, if any, to prepare. During severe precipitation, significantly fewer migrating birds take flight (Richardson 1990). A study of white-ruffed manakins showed that birds residing in higher elevations were more likely to migrate down the mountain when exposed to heavy precipitation, as the availability or accessibility of food is greater and more predictable at lower elevation. Birds of the same species that resided further down the mountain were seemingly unaffected by approaching storms, since food abundance is plentiful in their home ranges (Boyle et al. 2010). Thus, although precipitation cues provide more information that inclement weather is present, rather than approaching, birds may respond to cues of precipitation directly to avoid costs of exposure.

1.6 Impacts of inclement weather on other wildlife

In addition to having an impact on birds, inclement weather can affect nearly all wild animals: terrestrial, freshwater, and marine, both directly or indirectly (Walther et al. 2002, Parmesan 2006). Like birds, many other animals can sense and detect the onset of inclement weather through changes in barometric pressure and temperature and attempt to respond accordingly (Lederhouse et al. 1987, Heupel et al. 2003, Pellegrino et al. 2013).

In a controlled laboratory setting, decreasing barometric pressure affected pheromone emission and mating in both true armyworm moth (*Pseudaletia unipuncta*) and potato aphid (*Macrosiphum euphorbiae*) females (Pellegrino et al. 2013). Inclement weather can be a significant source of mortality to small insects, therefore, avoiding certain behaviours during poor weather is advantageous. In some anuran species, calling behaviour in prolonged breeders ceases due to weather conditions (i.e. decreasing barometric pressure, low temperature, and low relative humidity) than compared to short-breeding species (Oseen and Wassersug 2002).

Inclement weather can also affect many marine animals, particularly those residing in shallow waters (Heupel et al. 2003, Crinall and Hindell 2004). Some Australian fishes move into shallow salt marshes as barometric pressure starts to decline, likely to feed prior to the incoming storm (Crinall and Hindell 2004). Prior to severe tropical storms, juvenile blacktip sharks (*Carcharhinus limbatus*) leave the shallow waters of their nursery area into deeper open water (Heupel et al. 2003). The retreat to open water occurs as barometric pressure begins to decline to abnormally low levels but prior to severe rainfall, changing tidal level or tidal flow, and heavy winds, suggesting elasmobranch species can also detect changes in barometric pressure and respond accordingly.

The mortality incidence of black swallowtail butterflies (*Papilo polyxenes*) are indirectly affected by inclement weather, due to an increased likelihood of predation (Lederhouse et al. 1987). As noted above, inclement weather increases the need for foraging in vertebrates, and butterflies are a source of food among many vertebrates, including birds. During inclement weather, mortality rates of black swallowtails increased by 25% due to an increased rate of predation (Lederhouse et al. 1987). Thus, evidence shows that inclement weather can affect many animals both directly and indirectly. However, the focus of this thesis are the effects of inclement weather on birds.

1.7 Future directions to understand responses to inclement weather

As the presence of climate change and the new realm of extreme weather is being observed across the globe, novel experiments are required to understand how birds are responding at ecological, behavioral, and physiological levels. The study of the effects that individual weather variables such as barometric pressure, temperature, and humidity have on birds is not attainable through field observations alone. Several studies have looked at the effects that natural storms have on populations and individuals overall (e.g., Romero et al. 2000, Wingfield 1985a), however, there have been limited experiments on birds that have directly manipulated barometric pressure, temperature, or humidity in a controlled setting to recreate natural storm conditions. Manipulation studies in controlled settings allow for further insight into how species respond to storms, as the researchers are in control of changing environmental conditions and are able to keep track of all subjects, which is a highly unlikely scenario in the field. Such studies have only emerged from 2013 onward, but advancing technologies offer the likelihood of an increase among controlled manipulation studies. For example, Breuner et al. (2013) manipulated barometric pressure experienced by captive white-crowned sparrows to identify the effects it had on physiology and behaviour over a short-term period. They measured activity, food intake, metabolic rates and corticosterone levels. As barometric pressure was experimentally decreased, there was no effect on metabolic rate or in the level of glucocorticoid hormones, however, there was an increase in feeding behaviour and overall activity. The presence of low pressure systems typically brings precipitation and since these birds are ground feeding species, the probability of unpredictable foraging conditions are increased. Increased feeding prior to storms further supports that birds are able to detect changes in barometric pressure (Breuner et al. 2013). A second study that looked at white-throated sparrows had similar findings (Metcalfe et al. 2013). Experimentally decreasing barometric pressure led to a decrease in feeding latency providing further evidence that birds detect and respond to incoming low pressure systems. Similar to white-crowned sparrows, white-throated sparrows are also ground-feeding birds affected by precipitation during inclement weather.

Prior research has focused on how birds cope with cold winter weather (e.g., Lehikoinen 1987) and their ability to predict oncoming inclement weather (Breuner et al. 2013, Metcalfe et al. 2013), but little to no research has expanded upon how birds respond, both physiologically and behaviourally, to higher frequencies of recurrent inclement winter storms over a long-term period. Of the limited short-term manipulation experiments described above, none have examined the long-term effects that continuous inclement weather cues have on physiological or behavioural responses. Previous studies have focused on a drastic decline in barometric pressure which occurred between 30 minutes to 3 hours (Breuner et al. 2013, Metcalfe et al. 2013), and both studies spanned a short-term timeline. Although these novel studies supported the ability of birds to respond directly to changing barometric pressure, further long-term manipulation studies of inclement weather are becoming increasingly important.

Birds can use changes in barometric pressure and temperature as reliable cues that inclement winter weather is approaching. Previous findings indicate that a change in barometric pressure is the most influential and reliable cue that indicates the presence of a storm (Ahrens 2012, Metcalfe et al. 2013), allowing the changes observed in a laboratory to accurately represent responses that would also occur in the wild. The use of technologies such as hypobaric chambers or climatic wind tunnels should encourage experimental studies on the effects of inclement weather on birds. Controlled studies on weather patterns are important as extreme weather events are forecasted to increase in frequency and severity across time. Understanding the physiological and behavioural changes observed in individual species as a result of changing weather patterns will ultimately enhance the ability to more accurately predict the long-term survival of species and create future conservation plans. To create and implement such strategies, we must first understand the mechanisms behind how species are coping and, ultimately, responding to changing weather conditions. This will require data from several layers of interactions among species, as the complexity of relationships and interactions is highly intertwined.

The impacts of climate change are likely pushing some species to an abiotic tolerance threshold, depending on the degree of variation in adaptive traits that currently exist in the population. As climate change advances, changes in abiotic factors such as temperature and storm activity are increasing, which may shift behavioral and physiological mechanisms to the limits of existing phenotypic plasticity. While long-term changes in climate may impact species' foraging behavior and/or the timing of life history events, the most intense responses are to likely be attributed to the increased frequency and intensity of inclement weather. The response of birds to more intense environmental perturbations still remain largely unknown, however, short-term acute changes can initiate an endocrine response and are perceived as stressful events (de Bruijn and Romero 2013). Further work is needed to determine the limits to which birds can cope with extreme weather events (resulting in allostatic overload) and how these limits vary between food availability and season. These are the overall research goals of this thesis.

1.8 Study species used in this thesis

White-throated sparrows are short-distance migrants residing throughout Canada and the United States. Their mass varies between 22-32 g. White-throated sparrows breed in the boreal forest and winter throughout the eastern United States, from southern Ontario to the Gulf of Mexico (Falls and Kopachena 1994). In most of their wintering range, individuals still experience inclement cold winter weather conditions, however, less harsh than if they remained on their breeding grounds. With advancing climate change, much of the wintering grounds of white-throated sparrows are being impacted with more frequent and severe winter weather conditions. For example, a 2016 winter storm brought heavy snowfall to North Carolina and Tennessee, a region of high density of wintering white-throated sparrows. During the 2017-2018 winter season, extremely cold temperature conditions reached from southern Ontario to the northern range of Florida. Regions in Louisiana, Florida and Texas experienced record low temperatures and received notable amounts of snow, which is an anomaly in these southern regions (NOAA 2018). As such, migratory species wintering in these regions, including white-throated sparrows, must respond to such changing weather conditions. Thus, the presence of inclement winter weather conditions on their wintering and breeding grounds, and their ability to adjust particularly well to captivity, make white-throated sparrows an ideal species to study the effects of inclement weather cues.

White-throated sparrows have two genetically distinct morphs: white-striped individuals and tan-striped individuals. The two morphs are visibly distinguishable in the breeding plumage, but are more difficult to distinguish in basic (winter) plumage (Piper and Wiley 1989, Falls and Kopachena 1994). Plumage differences occur in the colouration of the median crown stripe, the lateral and superciliary crown stipes, and the amount of streaking on the breast (Lowther 1961). These morphs arise due to a chromosomal inversion polymorphism ($ZAL2_m$). White-striped individuals are heterozygous ($ZAL2_m$/ *ZAL2*) and tan-striped individuals are homozygous (*ZAL2/ ZAL2*; Thorneycroft 1966). White-striped and tan-striped birds differ in numerous behavioural traits (Kopachena and Falls 1993, Falls and Kopachena 1994). Although differences in morphs was not a primary research goal, I used genetic markers to determine the morph of birds in these experiments in order to account for any variation in my studies.

1.9 Environmental control systems used in this thesis

For much of the work within this thesis, I used a hypobaric climatic wind tunnel at the Advanced Facility of Avian Research to mimic inclement weather conditions. Although the wind tunnel is normally used to study flight under different environmental conditions, I used the tunnel to experimentally simulate weather events since it can control temperature, barometric pressure, humidity and wind speed (Metcalfe et al. 2013).

Temperature can be controlled anywhere between -15 °C to 30 °C within the tunnel. This control capability is based on two interconnected systems that both chill and heat incoming air in order to maintain control. The first system is a condensing unit on the roof of the building that maintains a refrigerant at ~ -24 °C. The second system is a recirculating brine loop system which uses ethylene glycol as a heat transfer medium to alter air temperature. The researcher has control over the ratio of chilled brine being mixed with brine returning from the heat exchanger that enters the tunnel.

Relative humidity is controllable between ~5 to 95% within the tunnel. A constant air flow system dehumidifies incoming air to a -30 °C dew point temperature. The air handling systems described above include a condensing surface and steam injectors to control the moisture content within the air before it enters the tunnel, allowing alteration of the relative humidity within the unit.

Barometric pressure can be maintained at ambient down to ~37 kPa (equivalent to ~7000 m altitude) through the use of powerful vacuum pumps that can extract air from within the tunnel air space more rapidly than fresh air enters the tunnel through air handling systems described above. In order for control of barometric pressure to be accurately maintained, two airlocks (heavy steel doors with gaskets) can be sealed to create an airtight space within the wind tunnel and workroom surrounding the tunnel's working section (plenum). Importantly for weather manipulation studies, air pressure can only be decreased below ambient, not increased. Thus, the highest barometric pressure depends on ambient outdoor pressure conditions. The system cannot maintain high pressure if ambient conditions are low, as associated with inclement weather. For the purpose of this thesis, maintaining high pressure conditions was not an issue.

1.10 Thesis objectives and hypotheses

Poor weather conditions can have negative effects on birds, but they must somehow cope with such conditions by attempting to maintain a stable physiological state. My overall goal for this thesis was to study the facultative physiological and behavioural adjustments of birds when coping with or responding to inclement weather cues in a controlled setting. I focused mainly on the cumulative effects of repeated exposure to storm cues, however, I also examined acute effects of abrupt changes in weather. Another main objective of my thesis research was to investigate how food availability influences responses to both chronic and acute exposure to storm cues.

We cannot have a full understanding of how birds cope with inclement weather events, and thus, how they will cope with advancing climate change in the future, based solely on observations in the field. Field studies may reveal correlations of behavioural responses to weather, but this does not provide information on causal mechanisms. Thus, I analyzed the responses of birds to experimentally simulated inclement weather cues and also monitored responses to natural storm exposure in a controlled setting. I explored which physiological and behavioural traits were altered when birds were exposed to: recurrent simulated inclement weather cues over a long-term period (Chapter 2), and abrupt, acute changes in weather cues at different life-history stages (Chapter 5). I also examined the effect of temperature on the migratory restlessness behaviour of white-throated sparrows (Chapter 3), and which specific weather cues in an outdoor setting influenced physiological responses of sparrows in outdoor aviaries (Chapter 4). Many of these responses should differ depending on energy balance and food availability, as energy reserves can elicit changes in the response of birds. Thus, I also assessed how food availability influenced these responses within each of these studies.

Birds should exhibit distinct changes in physiological and behavioural pathways when exposed to inclement weather cues, especially depending on the available energy of an individual. Birds are predicted to increase their foraging activity, fat reserves, and corticosterone levels. When storms are approaching or are present in an area, foraging behaviour in birds should increase to ensure sufficient energy reserves are available for that individual, which will therefore alter birds' fat reserves. As birds are repeatedly exposed to winter storm cues, these acute stressors may act chronically and increase corticosterone levels. I tested these predictions throughout the studies in this thesis.

1.10.1 Exposure to simulated storm cues

Chapter 2 evaluates how repeated exposure to simulated storm cues over a period of weeks influences physiological and behavioural traits in white-throated sparrows. This is a follow-up study to Boyer (2015), wherein I increased the frequency and duration of storm exposure to determine any cumulative effects. I exposed white-throated sparrows to decreases in temperature and barometric pressure twice per week for 12 weeks. I predicted that increased exposure to inclement weather cues should increase corticosterone levels, fat mass content, and feeding activity as these cumulative cues should be perceived as stressful and thus cause the individual to enter an emergency life-history stage.

In contrast, Chapter 5 identifies how white-throated sparrows respond to acute exposure to simulated storm cues in both winter and spring. This study determined how abrupt changes in weather differ across seasons and also among different food availability. Exposure to acute stressors can have varied responses in birds (e.g., Jeronen et al. 1976, de Bruijn and Romero 2013, Abolins-Abols et al. 2016), but we do not know the seasonal or resource-dependent responses. I predicted that birds would detect these abrupt changes and increase corticosterone levels, glucose levels, and overall feeding behaviour to prepare for anticipated environmental changes.

Chapter 3 examined how temperature influences the migratory restlessness behaviour of white-throated sparrows in both autumn and spring migratory seasons. I predicted that cold treatments in autumn should increase nocturnal migratory restlessness behaviour in birds, as cold temperatures indicate that winter is approaching and fleeing to the wintering grounds is necessary. I predicted that warm temperatures in spring should increase nocturnal migratory restlessness behaviour, as warm temperatures indicate that birds should return to their breeding grounds to prepare for reproduction.

1.10.2 Natural exposure to storms

In Chapter 4, I held white-throated sparrows in outdoor aviaries in early winter and monitored corticosterone levels and body composition. Much of the published literature focuses on observational field studies to determine how birds respond to changes in weather, but it is difficult to acquire physiological and behavioural measurements in natural settings. This study allowed me to keep birds exposed to natural outdoor settings and closely monitor changes. I predicted that corticosterone levels and fat mass should increase when storms are approaching or are already present in the area, but food availability should influence these responses. Birds receiving limited food amounts should perceive approaching inclement weather as more stressful, since they may be unable to adequately prepare for the storm.

Combined, these studies (Chapters 2-5) provide insight to how birds respond to cumulative and acute weather cues during different phases of the life-history stage, and how food availability can influence these overall responses. As weather is predicted to reach new extremes in coming years, understanding these relationships and potential thresholds of inclement weather exposure in songbirds remains especially important.

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Chapter 2

2 Responses to recurrent simulated winter storm cues of white-throated sparrows

2.1 Introduction

Birds are exposed to seasonal and daily fluctuations within their environment that can influence survival. These fluctuations include resource availability, disease exposure, predator interactions and inclement weather, and all can vary across temporal and spatial scales. Weather conditions, specifically, can be a major factor affecting individual survival and reproductive success, both directly and indirectly (Newton 1998). Inclement weather can impact foraging behaviour (Boyle et al. 2010, Breuner et al. 2013), migration (Newton 2007, James and Abbott 2014), territorial defence (Breuner and Hahn 2003) and mate acquisition (Wingfield 1985a, Vitousek and Romero 2013). In addition to external fluctuations varying across seasonal and daily scales, endogenous factors also vary across such temporal scales. For most northern hemisphere songbirds, fat stores in winter are much higher than compared to reserves in summer (Carey and Dawson 1999), as there are different pressures presented during these times. Behavioural responses to certain environmental perturbations can also differ across time (Carey and Dawson 1999). Glucocorticoid concentrations vary across such seasonal and daily scales and can influence responses to environmental disturbances (Remage-Healey and Romero 2000, Romero 2002). Thus, understanding how birds respond to inclement weather requires an understanding of how external and endogenous factors change across different time scales.

Birds can respond to variation in weather depending on the predictability of the event and the availability of resources available at that time. For example, seasonal changes in temperature or precipitation across an annual scale are predictable over longer time scales for birds because they use consistent cues such as photoperiod to predictably adjust to seasons. Food availability is also somewhat predictable along a seasonal scale, with food resources being most abundant in spring and summer and more sparse in winter in temperate zones. A storm occurring at any time across this annual seasonal scale is unpredictable as birds may only have hours or even minutes to prepare to changing environmental conditions (Wingfield 2003). In addition, unpredictable weather events can indirectly influence other factors, such as food availability. Severe storms can diminish food availability for several days through excess precipitation washing away or covering resources, and strong winds blowing away resources or making it difficult for individuals to access them (Carey and Dawson 1999). Depending on the availability of food and energy reserves, birds may perceive the risk of, or respond differently to, storms. Thus, birds must be able to survive in these unpredictable instances where food availability is sparse or unavailable for extended periods of time for survival.

Although there are no universally accepted definitions of stress, many define a stressor, in part, as an unpredictable challenge (Romero 2012). However, unpredictability alone may not induce a stress response if it does not pose a threat to an organism. For example, if an unpredictable severe weather event occurs, it may not be perceived as a stressor to birds if there are ample food resources and energy reserves. Alternatively, it may be perceived as a stressor if food availability and energy reserves are low. This may result in the animal entering an emergency life-history stage since the current metabolic demands of the birds cannot be met (Wingfield et al. 1998). When birds encounter a stressor and the emergency life-history stage is induced, physiological and behavioural responses are activated, including corticosterone secretion, reallocation of energy towards self-maintenance, and increased feeding behaviour (Wingfield et al. 1998, Reneerkens et al. 2002). Different factors, including food availability and severity of the storm, can therefore influence whether a storm will be perceived as a stressor or not, and will affect responses such as hormone secretion, metabolism and behaviour accordingly.

Birds must be able to respond physiologically to environmental perturbations through changes including glucocorticoid secretion and behavioural changes to enhance survival. The behavioural responses employed by birds also varies on a seasonal and daily basis (Carey and Dawson 1999). This adaptive behaviour may include redirecting behaviour to increasing foraging activity (Metcalfe et al. 2013), facultative migrations (Boyle et al. 2010), temporarily abandoning territories (Streby et al. 2015) or nests (Thierry et al. 2013), or ceasing normal life-history stages altogether (Wingfield et al. 1998). Food availability plays into how a bird will behaviourally respond, particularly during energetically demanding life-history stages or in response to energetically demanding perturbations (Carey and Dawson 1999). Food availability can also dictate whether a bird continues with or ceases a life-history stage. When birds are presented with limited food supply, energy reserves can also be reallocated and used as fuel, which contributes to an overall decline in body condition (Wingfield and Ramenofsky 2011a). There is also considerable individual variation in behaviour and physiology that depends on prior stressors encountered, social status, and early life experience (Romero et al. 2009).

If we want to understand the responses of birds to inclement weather cues, we cannot solely rely on correlational field observations. A full understanding of the responses to storms requires experimental studies where researchers can have some form of control over environmental conditions. The responses or coping mechanisms of birds to inclement weather have only recently been studied in controlled settings (Breuner et al. 2013, Metcalfe et al. 2013). My objective for this project was to build on a previous controlled study that found that weekly exposure to winter storm cues led to increased fat and lean mass in sparrows (Boyer 2015). I wanted to determine how birds respond to an increased frequency of repeated inclement winter weather cues and whether increased frequency of exposure would cause cumulative effects. Thus, this study tested the hypothesis that an increased rate of exposure to inclement weather cues will elicit greater physiological and behavioural responses.

When storms are approaching or are present in an area, foraging behaviour in birds should increase to ensure sufficient energy reserves are available for that individual. Storms should therefore alter body composition. As birds are repeatedly exposed to winter storm cues, these acute stressors may act chronically and increase baseline corticosterone levels. Some of these responses should differ depending on energy balance and food availability, as energy reserves can elicit changes in the response of birds. I thus predicted that exposed birds should increase fat and overall body mass, as accumulating fat reserves is a main coping technique employed by wintering birds (Carey and Dawson 1999). Birds receiving unlimited food should have higher fat mass than birds with limited diets. Birds in both food treatments should increase their feeding duration and overall movement as they are exposed to additional inclement weather cues. Repeated exposure to simulated storm cues may not be stressful to a bird if there are excess food and energy reserves available, but if a storm occurs when food availability and energy reserves are low (i.e., birds receiving limited food access), there may be a higher perceived threat to survival. It will likely act as a stressor and result in the bird entering an emergency life-history stage and increasing corticosterone levels. I predict that birds receiving limited food amounts should increase their corticosterone levels. Integrating seasonal differences in glucocorticoid concentrations with different physiological states or different life history stages allows a new understanding of how glucocorticoids help aid in survival during a stressful experience (Romero 2002). By comparing these results to a previous study (Boyer 2015), I will determine whether an increased frequency in simulated storms will cumulatively increase physiological and behavioural responses. To test these predictions, I exposed birds receiving either unlimited or limited food to two simulated winter storms per week in a hypobaric climatic wind tunnel, and measured corticosterone levels, body composition, and feeding behaviour.

2.2 Methodology

2.2.1 Study species

White-throated sparrows (*Zonotrichia albicollis*) naturally experience winter and spring storms in their native habitat and home ranges, thus making them an ideal species to study responses to inclement weather cues in captivity. White-throated sparrows winter throughout the eastern United States, from southern Ontario to the Gulf of Mexico (Falls and Kopachena 1994). In most of their wintering range, individuals still experience inclement cold winter weather conditions, however, less harsh than if they remained on their breeding grounds in the Canadian boreal forest. See section 1.8 for more detail on white-throated sparrows.

2.2.2 Capture and housing conditions

Fifty-two white-throated sparrows were caught during autumn migration in London, Ontario and near Long Point, Ontario between 13 October 2015 and 19 October 2015. Seven individuals were caught using seed-baited Potter traps in London, and forty-five individuals were caught near Long Point using mist nets. All birds were brought to the Advanced Facility for Avian Research at the University of Western Ontario in London, Ontario. Upon arrival, I measured weight, wing length and tarsus length. Definitive identification of sex, morph and age was not possible given the difficulty when birds are in winter plumage. Sex was later determined using genetic markers using a small blood sample collected from each bird, described in more detail in section 2.2.7. I randomly selected twenty-four birds for the experiment and immediately placed birds in environmental chambers held at 11 °C in individual cages (33 cm x 36 cm x 38 cm) under natural outdoor photoperiods (~10L:14D). 11 °C is a temperature that white-throated sparrows would naturally experience on their wintering grounds as a daily high (NOAA 2018), however, temperature can fluctuate widely depending on the time of year and the passing of a storm system or abnormal conditions. I changed photoperiods once per week to mimic natural outdoor sunrise/sunset times throughout eastern United States. The environmental chambers were placed under quarantine for 2 weeks until all birds were deemed healthy. For the initial two weeks of captivity, birds received an unlimited amount of 50:50 mixture of ground Mazuri Small Bird Maintenance Diet (catalogue number 56A6, Brentwood, MO, USA) and Premium Budgie Seed (Hagen), a commercial seed mix. This has previously been proven to provide sufficient nutrients and to maintain stable body condition of captive white-throated sparrows (Boyer 2015). Following this two weeks, I randomly assigned birds into either control group (n=12) or experimental group (n=12). Within each group of 12, birds were also randomly assigned either unlimited food access (n=6) or a limited amount of 8 g of food per day (n=6). Limited food amounts of 8 g were previously determined in another study (Boyer 2015) as sufficient to maintain stable body condition. This amount was chosen so birds did not experience food shortages that negatively affected body condition or survival, but they would not perceive food availability as continuously unlimited.

This experiment was approved by the Animal Care Committee of the University of Western Ontario. An Environment Canada scientific permit (CA 0244) for collecting birds under S.A. MacDougall-Shackleton was also obtained.

2.2.3 Procedure

This project was a follow-up study to a previous project completed in 2015 (Boyer 2015). The goal of the present study was to determine the effects that recurrent inclement winter weather cues had on physiological and behavioural responses in white-throated sparrows. In the original study (Boyer 2015), I moved birds into the hypobaric climatic wind tunnel once per week for 9 weeks and they experienced one environmental manipulation for one 24 hour period each week. In this follow-up study, I moved birds into the hypobaric climatic wind tunnel twice per week for 24 hours each for 12 weeks and they thus experienced two environmental manipulations per week, increasing both the frequency of manipulations and the overall duration of the study.

The hypobaric climatic wind tunnel at the Advanced Facility of Avian Research can control temperature, barometric pressure, humidity and wind speed. The tunnel can control temperature values from -15 °C to 30 °C and barometric pressure from ambient down to ~37 kPa (equivalent to ~7000 m altitude). Relative humidity can be controlled from nearly 0 to 100%. Although it is normally used to study flight, I used the hypobaric climatic wind tunnel to experimentally simulate weather events (Metcalfe et al. 2013). For example, when a low pressure system passes through an area, barometric pressure decreases and temperature can drastically change. I simulated those changes in the wind tunnel to mimic a weather event passing through the area. To expose birds to simulated weather changes I housed them in a hypobaric room (hereafter *plenum*) within the wind tunnel structure, but birds did not fly in the working section (Figure 2.1).

Each week, I moved both control and experimental groups into the wind tunnel plenum twice for 24 hours each. For example, on Day 1, I moved the experimental group into the plenum at noon and took them out at noon on Day 2. I then immediately moved the control group into the plenum following the removal of experimental birds on Day 2. Control birds were removed at noon on Day 3. This cycle repeated itself again until each group was housed in the tunnel for two 24 h periods and resumed the following week (Figure 2.2). Each time birds moved into the wind tunnel, environmental conditions reflected those in the environmental chambers at 11 °C, ambient barometric pressure, and ~60% humidity. Throughout the 24 h period in the tunnel, experimental birds received a rapid yet realistic decrease in temperature and barometric pressure simulating a winter storm (i.e., a low pressure system with an associated cold front). Control birds remained in the tunnel with no changes to environmental conditions to account for any potential stressors birds may experience while entering the tunnel. Experimental birds endured a change in temperature from 11 °C to 1 °C over 6 hours, at an average rate of decreasing 1.9 °C per hour, consistent with the original study (Boyer 2015). This rapid change in temperature reflected realistic changes in temperature that could be experienced naturally on their wintering grounds during significant inclement weather. Birds also experienced a decrease in barometric pressure from ambient to 96 kPa (Figure 2.3) and a consistent shift in air water content to maintain approximately 60% relative humidity. These values are also realistic for a decrease in pressure during a severe winter weather event on the wintering grounds (NOAA 2018). The decrease in barometric pressure was dependent upon ambient barometric pressure on that day, but on average decreased 1 kPa per hour. Following this manipulation, I maintained temperature and barometric pressure at 1 °C and 96 kPa for approximately 13 h overnight, and then the next day returned these variables to resting conditions of 11 °C and ambient barometric pressure over approximately 5 hours. Following this, experimental birds would return to the environmental chambers.

I divided the experimental and control groups in half for physiological measurement purposes. One week, half of the experimental birds had a blood sample taken to measure corticosterone levels, and the remaining birds received a Quantitative Magnetic Resonance (QMR) scan to measure body composition (Guglielmo et al. 2011). The following week, birds would undergo the alternate physiological measurement (i.e., week 1 blood sample birds would undergo QMR scans on week 2, and return to blood samples on week 3). Control birds were also on the same bi-weekly schedule. This bi-weekly schedule was to ensure birds were not experiencing additional handling stress and potentially increasing baseline corticosterone levels as a result of continuous handling. This also ensured birds were not losing higher blood volumes than necessary.

Figure 2.1 Cages set up in the plenum of the hypobaric climatic wind tunnel. Lights were added to provide additional lighting to bottom cages. Each cage on the rack housed an individual bird during the experimental manipulations, and identical cages and racks housed individual birds in their home rooms.

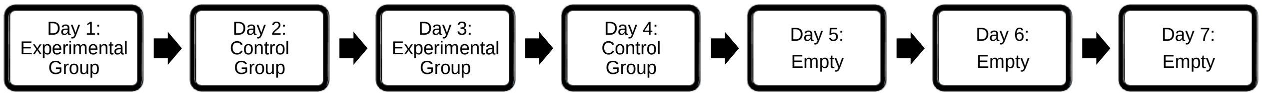

Figure 2.2 A timeline of weekly events in the hypobaric climatic wind tunnel.

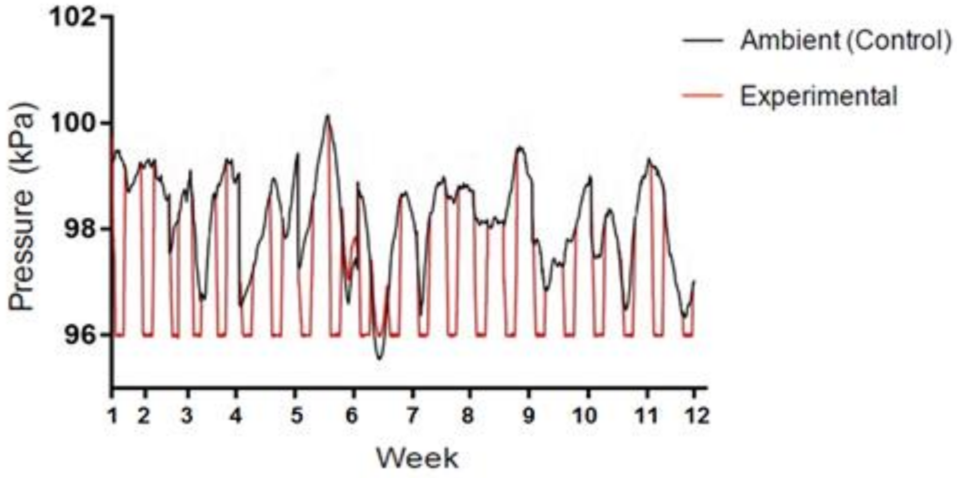

Figure 2.3 Pressure manipulations occurred twice per week for 12 weeks in experimental birds. The black line indicates natural changes in ambient barometric pressure during the study, to which control birds were exposed while held at 11 °C. The red line indicates the experimental manipulations of barometric pressure to which experimental birds were exposed while also being exposed to a drop in temperature to 1 °C.

2.2.4 Body composition

I used QMR scans to non-invasively obtain body composition data, including fat mass and lean mass content from each bird every second week. Before the scan, I weighed each bird with a spring scale. Birds were placed in a small plastic tube specially designed to hold sparrow-sized birds. I then carefully inserted the tube into the QMR instrument for approximately 3 minutes to obtain body composition results. The QMR instrument uses nuclear magnetic resonance relaxometry in different tissues to determine the spin relaxation rates. Lean tissue has the largest spin relaxation rate, followed by water, fat, and free water (Seewagen and Guglielmo 2010). During the scan, a magnetic field aligns the spins of hydrogen nuclei. The radio energy released differs between fat tissue and lean tissue, thus the two types of tissue can be differentiated (Guglielmo et al. 2011). Calibration of the instrument occurred each day of scans using 476.5

and 94 g standards of canola oil to ensure accurate readings to the nearest 0.001 g (Gerson and Guglielmo 2011, Guglielmo et al. 2011). Once each scan was completed, I immediately returned birds to their individual cages and left them undisturbed for the remainder of the day. I scanned half the birds on either odd weeks (i.e., week 1, 3, 5, 7, 9, 11) or even weeks (i.e., week 2, 4, 6, 8, 10, 12). Since I scanned each individual bird only once every other week, I condensed the results into fortnight (2 week period), rather than analyzing the data by week.

2.2.5 Corticosterone

Baseline corticosterone levels may reflect the relative condition or health of an individual over an extended period of time. Baseline levels usually increase when vertebrate animals are exposed to cumulative stressors (e.g., recurrent environmental perturbations) over a long-term period (Bonier et al. 2009; but see Dickens & Romero 2013). Blood samples were taken 2-3 days after birds had last been exposed to new housing conditions and environmental manipulations in the wind tunnel. This timing allowed birds to recover from potential acute stress experienced from being moved in and out of the wind tunnel that may influence baseline glucocorticoid levels.

All blood samples were obtained within 3 minutes of entering the birds' environmental chamber. In birds, baseline corticosterone levels take approximately 3 minutes to be influenced by an acute stressor and thus changing concentrations in the bloodstream (Romero and Romero 2002). To obtain samples, feathers were plucked along the wing to expose the alar vein, if necessary. Approximately 75 μL of blood was taken from the alar vein using a 26-gauge needle and collected in heparinized microhematocrit tubes. Cotton balls were applied with light pressure to the vein until bleeding stopped and birds were released back into their cage. Samples were immediately placed on ice and spun down within 30 minutes of collection. Plasma was separated from red blood cells by an IEC Micro-MB centrifuge for 11 minutes. Plasma was collected with a Hamilton syringe and stored in a -30 °C freezer until all samples were collected. Corticosterone levels were quantified using an enzymeimmunoassay (EIA) kit that has been previously validated in sparrows (Wada et al. 2007). I used Enzo kit ADI-901-097 and followed the manufacturers instructions, except that plasma was treated with 1% steroid displacement buffer and was diluted 1:40 with assay buffer prior to the assay. The intra-assay coefficient of variation was 8.6% for a low control and 3.3% for a high control. Any value outside of the standard curve (n=4) was set to the corrected sensitivity (1.37 ng/ml).

As is consistent with body composition, I also condensed the corticosterone data into fortnights, rather than analyzing the data by week. This was to ensure the changes in hormone levels were based on changes seen by each individual bird when it was sampled, rather than changes in hormone concentrations between two groups of birds (i.e., even or odd week sampled birds).

2.2.6 Behavioural analysis

High resolution microvideo cameras (Supercircuits, model PC182XS) were placed in the wind tunnel plenum to quantify feeding behaviour (feeding duration) and overall movement (total distance moved, time spent moving). Behaviour was recorded during the time birds were housed in the plenum, but not when birds were housed in their environmental chambers. Due to technical difficulties, video was not recorded for the first two weeks of the experiment. Six cameras were set up to record all 12 birds in the plenum. The Noldus EthoVision XT software used centre-point detection settings to track each individual with static subtraction. Static subtraction uses a static reference image to compare the video to which aides in detection movement within the video frame. The reference image was created by taking a screenshot of each cage arena and editing out the bird from the frame using Pixlr Photo Editor. This ensured the subject was always darker than the background image, allowing smooth tracking. The software analyzed total distance moved (cm) and cumulative duration of movement (s). The start velocity of movement was set to 3.01 cm/s which was independently verified for this project. I also analyzed cumulative duration spent in zone (s), and latency to first approach to zone (s), with the zone representing each individual food cup.

2.2.7 DNA extraction and genetic sexing

I obtained a blood sample from each bird from the alar vein to genetically determine sex. Blood was smeared on filter paper and left to dry. Filter paper was individually stored in plastic card holders and frozen until further use. DNA was extracted using an ammonium-based protocol to salt out proteins, modified from Griffiths et al. (1998). The DNA concentration was quantified using a NanoDrop 2000 Spectrophotometer (ThermoScientific) and diluted with 1 x TE to make a usable stock of 60 ng/ml and 30 ng/ml for subsequent polymerase chain reactions (PCRs). In birds, females are the heterogametic sex (ZW) and males are the homogametic sex (ZZ). Detection of the W sex chromosome will determine the sex of the individual, thus the DNA sexing technique among birds targets the chromobox-helicase-DNA binding gene (CHD-W). I used P2 and P8 primers to amplify portions of the CHD-W and CHD-Z genes. The PCR reaction mixture consisted of 3 µl of genomic DNA, 1x PCR buffer, 2 mM MgCl2, 0.2 mM dNTP, 0.2 µM P2 and P8 primers, and 1 unit of Taq DNA polymerase. PCR thermal cycle conditions were 94°C for 1 minute (initial denaturing), 40 cycles of 94 °C for 30s, 48 °C for 45s, and 72 °C for 45s, and 72 °C for 5 minutes (final extension). PCR products were separated on a 3% agarose gel pre-stained with Sybersafe (S33102 Thermofisher Scientific) in 1x TAE buffer. The final gel electrophoresis showed two bands for females and one band for males.

Twenty-two of 24 individuals were determined to be male, thus, sex was excluded from further statistical analysis.

2.2.8 Food consumption measurement

When the birds entered the plenum, I weighed each food cup for both unlimited and limited diet birds. After the birds were inside the wind tunnel for 24 hours, I immediately weighed each food cup to determine the amount of food ingested for each bird. I used a digital food scale that measured to the nearest 0.1 g. I assumed spillage of seed between each food cup would be relatively consistent among birds, thus I did not account for lost mass via spillage.

2.2.9 Statistical analysis

Data were analyzed using linear mixed models in SPSS (IBM, Version 25.0). Fortnight, food and experimental group, and their interactions were entered as fixed effects. To control for repeated measures, bird ID was entered as a random effect.

2.3 Results

2.3.1 Body composition

Control birds had higher fat mass content than birds that underwent inclement weather events (Figure 2.4a), but I detected no difference between experimental groups in lean mass content

(Figure 2.4b) or overall body mass (Figure 2.4c). I did not detect any differences between food groups. There were no significant interactions. A complete list of body composition results can be found in Table 2.1. Experimental birds ingested more food than control birds (Figure 2.5, Table 2.2) and increased food consumption across time (Table 2.2).

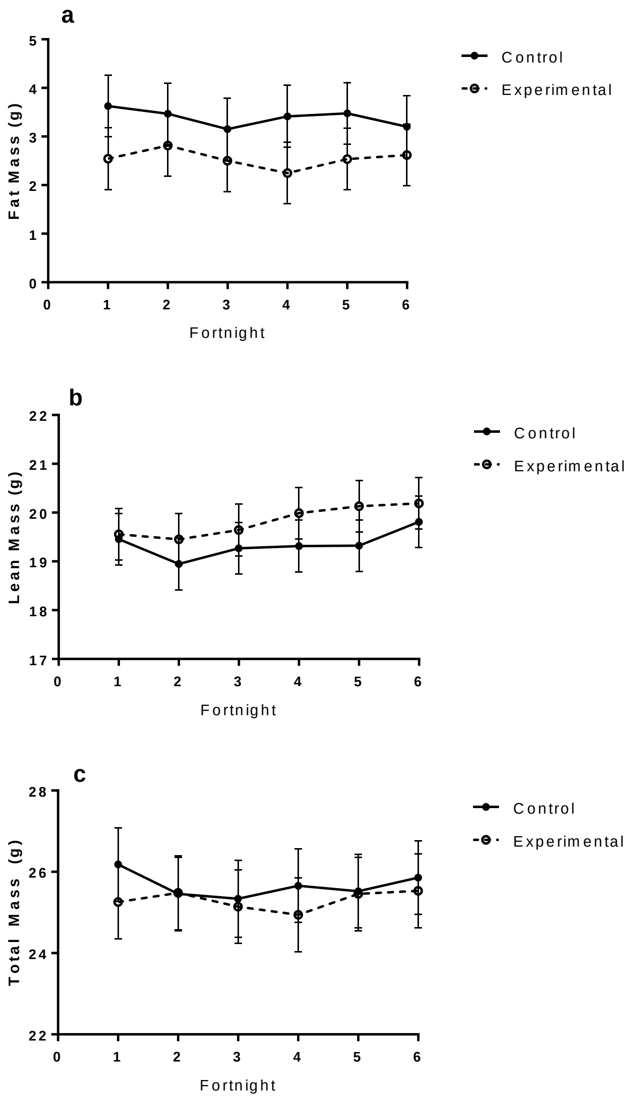

Figure 2.4 Body composition readings of white-throated sparrows exposed to inclement weather cues or control conditions, including a) fat mass, b) lean mass, and c) total body mass. a) Control birds have higher fat mass content than birds that underwent repeated simulated storm cue exposure in the wind tunnel. b) There was no difference in lean mass between experimental groups. c) There was no difference of overall body mass between control and experimental groups. Points indicate mean total mass values and error bars indicate SEM.

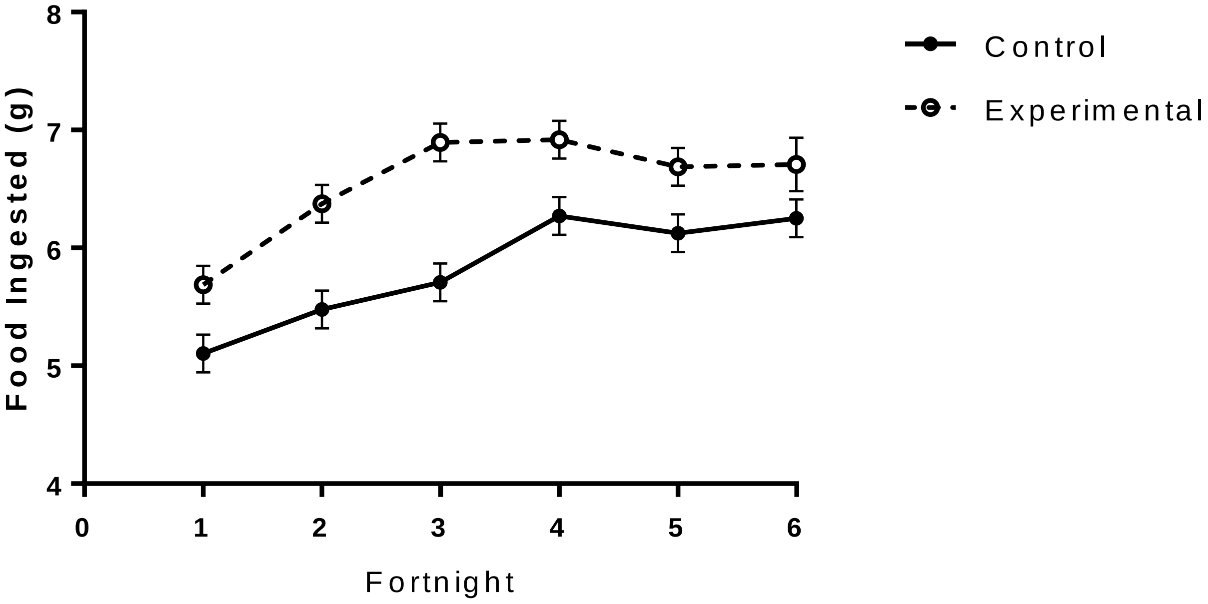

Figure 2.5 Food consumption of white-throated sparrows exposed to inclement weather cues or control conditions. Birds that were repeatedly exposed to simulated storm cues ingested more food than control birds. Points indicate mean food amounts ingested (g) and error bars indicate SEM.

Table 2.1 Parameter estimates from the linear mixed effects model of body composition (fat, lean, and overall body mass) between experimental (exp) groups, food groups and across time. Significant main effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Fat Mass: Exp Group	*1*	*25.62*	*1.746*	*0.023*
Fat Mass: Time	6	116.165	0.051	0.822
Fat Mass: Food Group	1	25.77	0.102	0.752
Lean Mass: Exp Group	1	22.085	0.029	0.866
Lean Mass: Time	6	116.114	2.702	0.757
Lean Mass: Food Group	1	22.18	0.516	0.480
Body Mass: Exp Group	1	131	0.490	0.485
Body Mass: Time	6	114.86	1.012	0.317
Body Mass: Food Group	1	23.14	0.43	0.838

Table 2.2 Parameter estimates of food ingested between experimental groups and across time. Significant main effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Food Ingested: Group	*1*	*504*	*45.917*	*<0.0001*
Food Ingested: Time	*6*	*504*	*14.715*	*<0.0001*

2.3.2 Corticosterone

Contrary to predictions, control birds had higher baseline corticosterone levels than experimental birds (Figure 2.6). Corticosterone levels also decreased across time, but there were no significant differences between food groups. There were no significant interactions. A complete list of parameter estimates is found in Table 2.3.

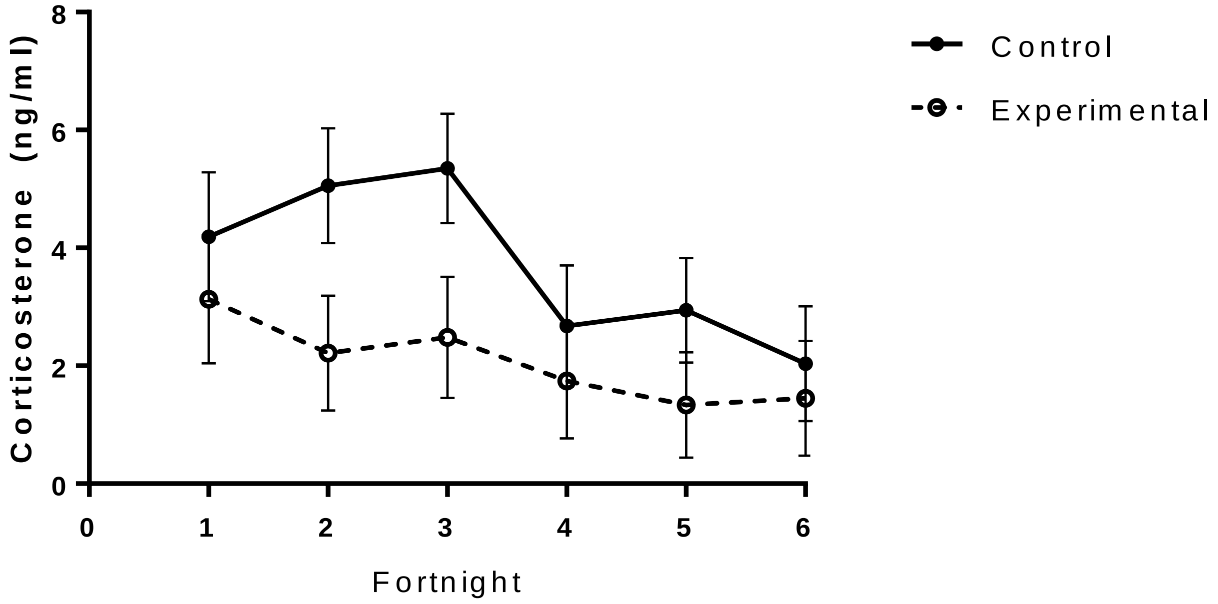

Figure 2.6 Total plasma corticosterone of white-throated sparrows exposed to inclement weather cues or control conditions. Control birds had higher corticosterone levels and decreased levels across time. Points indicate mean corticosterone levels (ng/ml) and error bars indicate SEM.

Table 2.3 A summary of parameter estimates of corticosterone levels (CORT) between experimental (exp) groups, food groups and across time in birds exposed, or not exposed, to inclement weather cues. Significant main effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
CORT: Exp Group	*1*	*55.575*	*4.098*	*0.048*
CORT: Food Group	1	56.248	0.391	0.534
CORT: Time	*6*	*88.313*	*12.575*	*0.001*

2.3.3 Behavioural response

2.3.3.1 Feeding duration

There was no difference in the total time spent feeding between birds receiving limited or unlimited food access (Table 2.4), but experimental birds spent more time feeding than control birds (Figure 2.7). Birds increased their feeding duration across time (Table 2.4).

Table 2.4 Behavioural statistical analysis of feeding duration in white-throated sparrows exposed or not exposed to recurrent simulated weather cues. Significant main effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Feeding Duration: Experimental Group	*1*	*57.840*	*12.948*	*0.001*
Feeding Duration: Food Group	1	58.440	0.617	0.435
Feeding Duration: Time	*6*	*353.364*	*8.699*	*0.003*

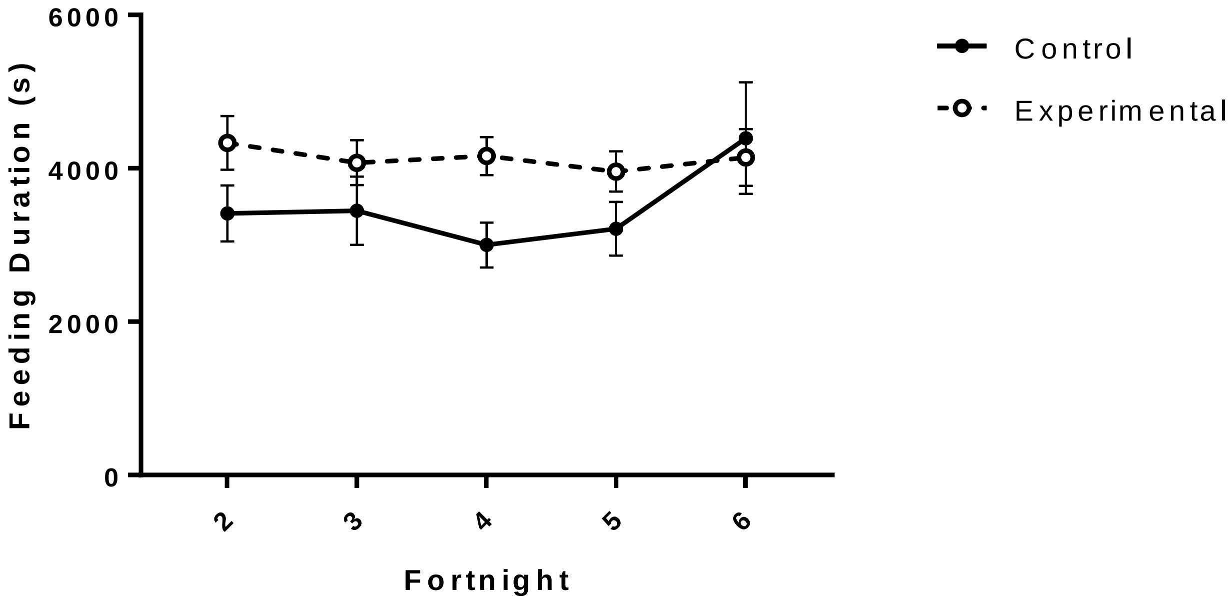

Figure 2.7 Feeding duration of white-throated sparrows exposed to inclement weather cues or control conditions. Experimental birds spent more time feeding than control birds. Points indicate mean feeding duration (s) and error bars indicate SEM.

2.3.3.2 Movement

There was no difference between food or experimental groups in the total duration or distance of movement, but both increased across time (Table 2.5).

Table 2.5 Fixed effects of movement responses, including total distance moved (cm) and total duration of movement (s). Significant effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Distance Moved: Experimental Group	1	39.275	0.665	0.420
Distance Moved: Food Group	1	39.569	0.094	0.761
Distance Moved: Time	*6*	*353.442*	*17.417*	*<0.0001*
Movement Duration: Experimental Group	1	38.293	1.206	0.279
Movement Duration: Food Group	1	38.571	0.010	0.921
Movement Duration: Time	*6*	*353.361*	*26.022*	*<0.0001*

2.4 Discussion

I analyzed physiological and behavioural responses, including corticosterone levels, body composition, feeding and overall behaviour in white-throated sparrows exposed, or not exposed, to recurrent inclement winter weather cues. Birds that were repeatedly exposed to storm cues responded both physiologically and behaviourally, however, most responses did not match predictions. Birds that did not experience repetitive storm simulations had higher baseline corticosterone levels and higher fat mass content compared to birds that did undergo simulated storm exposure. There was no difference in lean mass content or feeding duration between groups, however, experimental birds did ingest more food. Thus, this study provides further evidence that birds can sense changes in temperature and barometric pressure. However, the responses differed from predictions, and additionally from my prior study with only one experimental manipulation per week (Boyer 2015).

2.4.1 Body composition

Environmental manipulations did affect body composition, however, these changes did not match predictions. Fat mass content was higher in control birds that were not exposed to storm cues than in birds that were exposed to repeated storm cues. Increasing fat stores is a common wintertime response to the onset of inclement winter weather to prepare against unpredictable future foraging (Carey and Dawson 1999), thus, I predicted birds exposed to simulated storm cues should have higher fat, rather than control birds. Higher fat mass was observed in a previous study with individuals exposed to one simulated storm per week (Boyer 2015; Table 2.6), however, the opposite effect was observed with increased storm exposure in the present study. Interestingly, the amount of food ingested during the storm simulation was higher in experimental birds, but these birds still had lower levels of fat. This suggests that although birds exposed to inclement weather cues were ingesting more food during simulated storm exposure, they were unable to allocate energy to creating additional fat stores. Combined with the prior study, these results suggest that in response to inclement weather cues birds will eat more and store more fat, but if the energetic demands of storms are too high, fat stores may be reduced below control conditions.

Environmental manipulations did not affect lean mass content in neither birds exposed or not exposed to storm cues. Increased thermogenic demand can cause increased lean mass to enhance thermogenesis (Carey et al. 1989). In most birds, shivering is the primary means of thermogenesis (Carey and Dawson 1999), which involves the movement of the large supracoracoideus and pectoralis breast muscles. Through winter acclimatizing, the flight muscles are often enlarged to be able to more effectively carry out shivering responses (Swanson 2001), which would result in an increase in lean mass content. I thus predicted an increase in lean mass in birds exposed to storm cues, however, this relationship was not observed in the present study. In a previous study where the frequency and duration of simulated storm exposure was less (Boyer 2015), lean mass was higher in experimental birds (Table 2.6). No difference between birds exposed or not exposed to storm cues in the present study may show birds are not able to adapt as well to a higher exposure of inclement weather cues. Shivering is an energetically costly task, requiring an expenditure of additional energy while in the wind tunnel plenum. The main energy substrate for shivering, and thermogenesis in general, comes from fatty acids (Carey and Dawson 1999). Since there was low fat mass content, birds had limited energy availability to use. Energy that is required to build muscle to induce shivering activity may have been depleted to other factors contributing to survival.

The results in body composition and food consumption indicate that exposure to two simulated storms per week exceeds birds' ability to cope and may exceed a threshold for storm exposure in white-throated sparrows. Experimental birds in the present study used food energy differently than experimental birds in the original study (Boyer 2015). Birds were ingesting more food but were unable to maintain fat reserves or increase lean mass, indicating the energy was being used immediately to cope rather than being stored. A previous study found that red knots (*Calidris canutus*) exposed to cold conditions also increased their food ingestion, accompanied with increased body mass and lean muscle content to cope with cold conditions (Vézina et al. 2006), suggesting that food ingestion and lean muscle mass to enhance shivering is important to regulate thermogenesis. Undetectable differences in body mass or lean mass may mean there is a different metabolic response in songbirds depending on frequency of storm exposure. Future studies could compare metabolic rates of birds exposed to different frequencies of storm cues to confirm this effect.

2.4.2 Corticosterone

Birds not exposed to repeated weather cues had higher levels of corticosterone. As continuous acute exposures to inclement weather conditions should have acted cumulatively as a chronic stressor, this was unexpected. White-crowned sparrows with completely diminished food availability for just one hour showed an increase in baseline corticosterone levels, and a decrease in overall body mass, with no change in fat mass or lean mass (Krause et al. 2017). This suggests that reduced food availability can influence a rapid elevation in baseline corticosterone even under small time periods (Krause et al. 2017). In contrast, repeated acute exposure to simulated inclement weather cues in European starlings (*Sturnus vulgaris*) did not elicit a change in baseline corticosterone levels (de Bruijn et al. 2017). However, over longer timeframes I detected a different change, a decrease in corticosterone levels.

Boyer (2015) did not find differences in corticosterone levels between experimental groups (see Table 2.6), but the present study found lower corticosterone levels in birds exposed to simulated weather cues. Thus, there was a response of glucocorticoid secretion, however, the effect did not match predictions. Lower corticosterone levels in experimental birds in the present study may suggest that birds exposed to storm cues downregulated their responses to recurrent stressors. Prolonged elevations of baseline corticosterone can negatively influence a bird's overall health (Sapolsky et al. 2000), thus a reduced response in corticosterone may actually be beneficial to the individual. Birds exposed to two simulated storms per week may lower corticosterone levels to conserve energy. A lack of response to a repeated stressor, as indicated through experimental birds' body composition, may indicate a disruption in HPA axis function due to chronic stress (de Bruijn et al. 2017). As per the allostasis model, corticosterone may not increase until energetic stores are exhausted and food availability is completely unavailable to restore metabolism (McEwen 2013).

Simulated inclement weather events did elicit a change in body composition, but it did not cause an increase in corticosterone as predicted. This may represent a downregulation of the HPA axis under chronic stress conditions (de Bruijn et al. 2017). Indeed, the relationship between environmental stressors and baseline corticosterone levels is not as established as some studies suggest. HPA function, including the directional changes of glucocorticoid concentration, can differ widely across species exposed to repeated stressors and chronic stress (Dickens and Romero 2013). A response in HPA function itself is more informative than the actual direction of that change (e.g., increasing or decreasing glucocorticoid levels; Dickens & Romero 2013). Further work, perhaps using ACTH and dexamethasone challenges to characterize HPA function, would be required to better determine how birds are altering corticosterone regulation in response to storm cues.

2.4.3 Behavioural response

2.4.3.1 Feeding duration

In the winter, a low pressure cold front can bring precipitation in the form of snow through most of white-throated sparrows' wintering range, especially now with the onset of climate change. Since these birds are ground feeding species, they need to forage prior to the onset of the storm as food may become less available once the ground is covered in snow. I therefore predicted that foraging time should increase in birds exposed to simulated inclement weather, which was observed in this study. Birds exposed to recurrent simulated weather cues also increased the amount of food ingested during this time.

Previous studies that also experimentally decreased barometric pressure found that birds decreased their latency to feed and increased the feeding amount (Breuner et al. 2013, Metcalfe et al. 2013), which was partially found in the present study. The prior study the present study was based off found no difference in the total time spent feeding among white-throated sparrows exposed to recurrent inclement weather cues (Boyer 2015; Table 2.6), suggesting that more frequent exposure to storm cues will increase the feeding duration and ingestion of food to prepare for the approaching storm.

Increased levels of corticosterone can lead to an increased rate of foraging (Breuner and Hahn 2003), however, this direct relationship was not observed in this study. Experimental birds showed lower corticosterone levels but did increase their feeding duration and food ingestion, indicating that there was still a response as a result of repeated storm cues, but these repeated storm cue exposures did not act as a stressor to induce an HPA response. Interestingly, a limited or unlimited diet did not influence any behavioural or physiological responses. Captive white-crowned sparrows showed little activity around their food cups when food was unlimited, but activity at the food cup increased once food was removed (Astheimer et al. 1992). Whether birds in the present study had unlimited or limited food amounts, they were still consistently exposed to food, therefore there may not have been a strong response to immediately forage once environmental changes were detected due to the predictability of resources. In the present study, experimental birds ingested more food and spent more time feeding but had lower fat mass content and corticosterone levels. This indicates that the rate of feeding may have been higher and more intense when birds were at the food cups. Although feeding duration and ingestion increased in experimental birds, I did not detect more fat mass in these individuals, indicating the higher frequency of storm cues occurring did affect how food was stored and metabolized after ingested due to environmental manipulations.

Table 2.6 A comparison of results of birds exposed or not exposed to recurrent inclement winter weather cues in the present study and a previous study conducted in 2015. The present study had storm exposure twice per week and the original study had storm exposure once per week.

	One simulated storm per week (Boyer 2015)	**Two simulated storms per week (present study)**
Fat Mass	Experimental birds had higher fat mass.	Control birds had higher fat mass.
Lean Mass	Experimental birds had higher lean mass.	There was no difference in lean mass between groups.
Corticosterone	There was no difference in corticosterone between groups.	Control birds had higher corticosterone levels.
Feeding Duration	There was no difference in feeding duration between groups.	Experimental birds spent more time feeding.
Overall Movement	There was no difference in overall movement between groups.	There was no difference in overall movement between groups.

2.4.3.2 Overall movement

Experimental birds did not increase their overall movement and activity during environmental manipulations. A common response to small passerines to inclement winter weather involves hiding in microclimates and taking shelter where possible (Carey and Dawson 1999), assuming fat and energy stores are available. No detectable change in locomotor activity may be attributed to a strategy to take cover during the impending storm. Increased movement has been previously documented as a food seeking behaviour in birds (Astheimer et al. 1992, Lynn et al. 2003, Fokidis et al. 2011), but since the food was only located in one area of the cage, it is not surprising that overall movement was unaffected, even with an increase in feeding duration and ingestion. Metcalfe et al. (2013) found that white-throated sparrows moved more often as barometric pressure was decreasing, however, a similarly conducted study did not observe any differences in overall movement (Boyer 2015; Table 2.6), which is consistent in the present study.

Although white-throated sparrows migrate in the autumn to avoid severe winter weather, they are not long-distance migrants. Their wintering grounds still receive snow and inclement winter weather, even more so within the past few years as climate change is influencing the presence of severe winter weather across their wintering range. Unpredictable foraging conditions as a result of heavy precipitation can cause birds to increase overall activity and travel to areas that are unaffected by snow (Wingfield and Ramenofsky 1997). White-throated sparrows are likely prepared to respond to such inclement weather cues through increasing food seeking behaviour, and thus, overall activity (Lynn et al. 2003), but this relationship is difficult to observe in a captive setting.

2.4.4 Summary and conclusions

The responses of birds exposed to simulated storms twice per week for 12 weeks, compared to a previous study exposing birds once per week for 9 weeks (Boyer 2015), were remarkably different (Table 2.6). These results suggest birds can detect changes in temperature and barometric pressure and can respond accordingly, however, there may be a threshold of storm frequency to which birds are able to cope, both metabolically and physiologically. The present findings suggest that increasing the frequency of storm exposure from once per week to twice per week may exceed the physiological threshold for tolerance among these songbirds.

Previous findings suggest that a change in barometric pressure is the most influential and reliable cue that indicates the presence of a storm (Ahrens 2012; Metcalfe et al. 2013), allowing the changes observed in a laboratory to accurately represent responses that would also occur in the wild. This study further confirms that birds can use changes in temperature and barometric pressure as reliable cues that inclement winter weather is approaching. These findings also support that certain predictions regarding behaviour and stress levels may not apply under certain scenarios, either indicating a need for further manipulation studies or a different theoretical approach. Future research should continue to look at different severity and frequencies of inclement weather events, changing food restrictions, sex differences, and resident vs. nonresident species. This study, and continuing those like it, are important as extreme weather events, including winter storms, are predicted to increase in frequency and severity across time through climate modelling (NOAA 2018) . Understanding the physiological and behavioural changes observed in individual species as a result of changing weather patterns will ultimately enhance the ability to more accurately predict the long-term survival of songbird populations. Future studies could also take a deeper look into the metabolic differences observed between birds exposed or not exposed to inclement weather cues. Overall, this study has contributed to the limited body of work surrounding global change manipulation studies. I have documented physiological and behavioural responses that have not been previously observed under controlled inclement weather scenarios.

2.5 References

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Chapter 3

3 Spring and autumn temperature manipulations differentially affect nocturnal migratory restlessness in a migratory songbird

3.1 Introduction

Seasonal migration is the movement from one geographic area to another as weather and resource availability differ across the year. Many northern hemisphere songbirds migrate south to their wintering grounds in autumn, spend several months at their wintering grounds, and migrate north to their breeding grounds in the spring. The timing of this migratory phase is controlled by endogenous circannual rhythms that interact with external annual factors (Gwinner 1996). Spring and autumn migration, then, are influenced by both endogenous factors such as timing mechanisms and energy reserves, and external factors, such as seasonal changes in photoperiod and resource availability (Gupta and Das 2016), and weather cues including temperature, wind, and barometric pressure (Richardson 1978, Shamoun-Baranes and van Gasteren 2011). These factors may influence multiple aspects of birds' migratory phenotype including changes in body composition and migratory behaviour.

Beyond the long-term effects of climate change on the timing of migration departure in birds (Jenni and Kery 2003, Hedenström et al. 2007), it has long been observed that short term weather conditions affect the timing of bird migratory flights (Richardson 1978). Although there is clear evidence that inclement weather cues can influence the timing of migration and the duration spent at stopover sites (Smolinsky et al. 2013, Deppe et al. 2015), there is limited research determining which individual weather factors influence migration (Berchtold et al. 2017). It is difficult in observational field studies to determine which specific weather factor is causing a delay or advancement in migratory behaviour as weather variables are highly interconnected. For example, observed changes in temperature can also be associated with decreases or increases in barometric pressure, wind speed and direction, humidity levels and precipitation. This study sought to specifically determine how temperature would affect migratory restlessness during both autumn and spring seasons, and how temperature response may vary with food availability in captive migratory birds.

Temperature effects across seasons may depend on food availability and/or energy stores. As birds are preparing for migration, they induce hyperphagia through an increase in daily food intake to increase fat stores. Increases in feeding and decreases in metabolic rates allow migrating birds to maintain high levels of body fat to fuel migratory flight (Stuber and Bartell 2013). Limited resource availability can induce changes in migratory behaviour, including extending migratory stopovers and shifting departure and arrival times (Gwinner et al. 1990). Whether a bird migrates or not depends on its fat stores (Lindström and Piersma 1993, Boyle et al. 2010, Deppe et al. 2015), but the amount of a bird's fat stores can also depend on temperature. It is therefore also important to consider how food availability and body composition influence migration, alongside temperature cues. Thus, this interaction may increase or decrease migratory behaviour depending on whether there are adequate resources to fuel migration.

Captive nocturnally migrating songbirds exhibit migratory restlessness behaviour, or *zugunruhe*, at night (Gwinner 1996). In emberizid sparrows, migratory restlessness behaviour involves perch hopping, wing whirring, flying and beak-up activity in overnight hours (Agatsuma and Ramenofsky 2006). Previous studies that have measured migratory restlessness behaviour in response to experimental temperature manipulations have measured behaviour in only one migratory season and all birds received unlimited food (Metcalfe et al. 2013, Berchtold et al. 2017). To date, there has not been a study that has analyzed an entire evening of migratory restlessness as temperature conditions are changing across seasons, or with birds with different food availability. Therefore, my study analyzed migratory restlessness behaviour in white-throated sparrows (*Zonotrichia albicollis*) from lights off to lights on in both autumn and spring migratory conditions. I tested the hypothesis that adjustment of migratory behaviour in response to temperature will differ between autumn and spring migration. Temperature should have opposite effects in autumn and spring. I predicted that birds would increase nocturnal migratory restlessness in response to cooler temperature in autumn migration (Berchtold et al. 2017) and decrease nocturnal migratory restlessness in response to cooler temperature in spring migration (Metcalfe et al. 2013). I further predicted that the effects of food availability on migratory restlessness would vary seasonally. In autumn, the amount of migratory restlessness should increase with decreasing temperature as birds may be motivated to reach their wintering grounds to obtain food. Autumn birds receiving unlimited food should also exhibit less migratory restlessness than those with a limited food supply, even during colder temperatures, as decreased food availability in winter is an important factor driving migration. In spring, the amount of migratory restlessness should increase with warmer temperatures as birds, particularly males, may be motivated to reach their breeding grounds to initiate reproduction. Birds receiving a restricted amount of food in spring should exhibit an increased rate of migratory restlessness, even during warmer temperatures as adequate resource availability is important to enter the reproductive phase. To test these predictions, I experimentally manipulated temperature each evening to birds receiving unlimited food access or limited food amounts and analyzed behaviour during autumn and spring migration.

3.2 Methodology

3.2.1 Study species, housing, and procedure

I used white-throated sparrows because they routinely experience inclement weather conditions on both their wintering and breeding grounds (see section 2.2.1). Twenty-four white-throated sparrows were caught in mist-nets near Long Point, Ontario between 12-19 October 2016 and transported to London, Ontario the same day of capture (Environment Canada Permit CA 0244). Thus, birds were captured during the peak of their autumnal migration. I brought birds to the Advanced Facility for Avian Research and immediately weighed them. Birds were placed in individual cages (33 cm x 36 cm x 38 cm) in two environmental chambers with temperature and humidity control. Temperature was set to a constant 14 °C and humidity remained set to natural indoor conditions. 14 °C was used as a baseline, or neutral, temperature given that it reflects an average daily high temperature experienced during white-throated sparrows' fall migration (WeatherNetwork). Photoperiod was set to reflect natural outdoor sunrise/sunset conditions (~10L:14D) and changed once per week to reflect natural photoperiod changes. I randomly selected 12 birds to receive unlimited food amounts and the remaining 12 birds received 8 g of food per day. This amount was previously determined as a minimum amount required to sustain birds' body condition but not represent an unlimited supply of food (Boyer 2015). Birds were given a 50:50 mix of ground Mazuri Small Bird Maintenance Diet (catalogue number 56A6, Brentwood, MO, USA) and Premium Budgie Seed (Hagen), a commercial seed mix. White-throated sparrows have previously thrived in a laboratory setting on this mix of diet (Boyer 2015). A random mix of 12 unlimited and limited diet birds were housed in one environmental chamber and a random mix in a second environmental chamber. Both chambers were set to identical conditions prior to the beginning of the experiment.

I measured migratory restlessness in both autumn and spring. In autumn, recording of migratory restlessness began one day after birds entered the facility. Approximately two hours before sunset each night, temperature in each chamber would either shift from 14 °C to 4 °C to represent a cold evening, from 14 °C to 24 °C to represent a warm evening, or remain at 14 °C. Temperature would remain steady until approximately one hour after sunrise when it would slowly return to 14 °C for the remainder of the day. The night following any change to 4 °C or 24 °C temperature would remain at 14 °C so birds could adjust back to neutral temperature settings (Figure 3.1). Temperature manipulations occurred from 13 October 2016 to 15 November 2016, at which point birds no longer exhibited migratory restlessness. Each environmental chamber was on a different temperature manipulation schedule to ensure that ambient conditions (e.g., barometric pressure) were not confounded with my temperature manipulations.

Once birds stopped exhibiting migratory restlessness behaviour in autumn, they were housed in the same environmental chambers for the duration of the winter. Each bird was given unlimited food from mid-November until the end of March. They remained in their individual cages at 14 °C. Photoperiod was adjusted once per week to reflect the natural changes in photoperiod for London, Ontario. At the end of March, half of the 24 birds were randomly given the same food treatment they received in the autumn study. The remaining 12 birds had their food amounts switched (i.e., from unlimited to limited, or vice versa). Once birds started exhibiting signs of spring migratory restlessness in the evening, temperature manipulations resumed beginning 17 April 2017. Identical conditions resumed until birds no longer exhibited migratory restlessness on 20 May 2017. This experiment was approved by the Animal Care Committee of the University of Western Ontario.

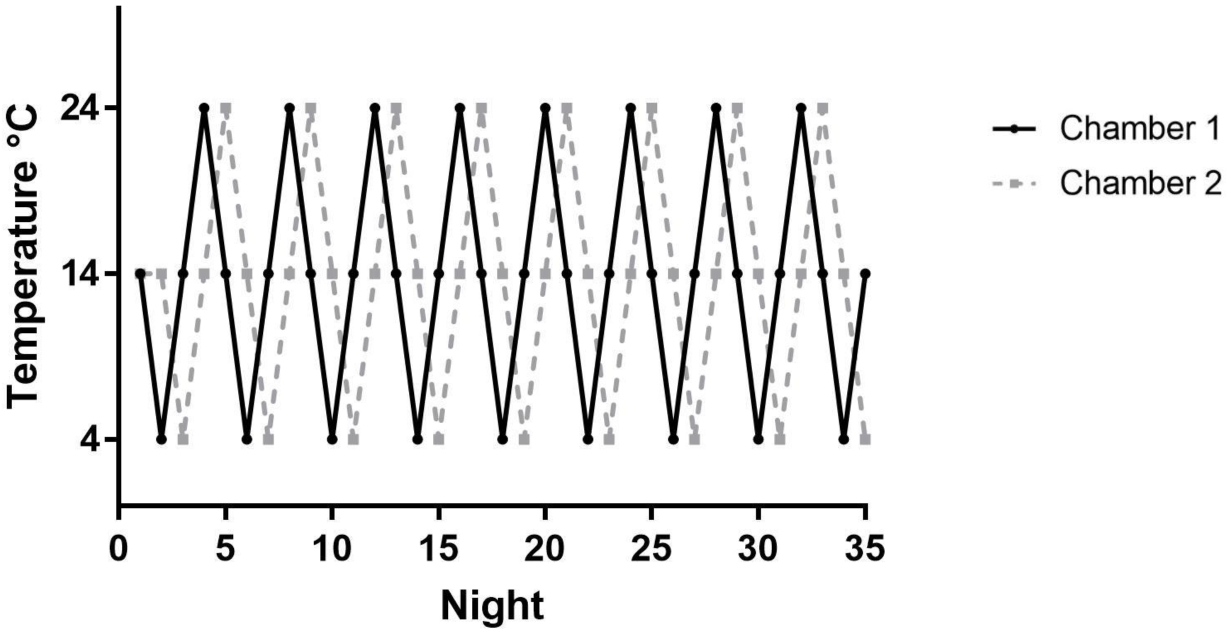

Figure 3.1: Autumn and spring nighttime temperature manipulations in two environmental chambers. Each night, temperature differed between two chambers. Environmental chambers were held at either 4 °C, 14 °C, or 24 °C. Each data point represents one night. The solid black line indicates temperature in one chamber and the grey black line the other.

3.2.2 Behavioural analysis

Each night during autumn and spring, birds were recorded using high resolution microvideo cameras (Supercircuits, model PC182XS) and infrared illuminators (850 nm Smart B-Series, model AT-35-B). Six cameras were set up in each environmental chamber to record two birds each. Recordings began 30 minutes before lights out and ceased 30 minutes after lights on the next morning. I used Noldus EthoVision XT software (version 10.0.826) to analyze total distance moved, cumulative duration of movement and mobility. Movement was quantified as movement of the bird's centre point from one location to another (Figure 3.2). Mobility was quantified as changes in the contour of the bird as a whole, including wing flapping and beak-up behaviour. The EthoVision software calculates the duration for which the complete area detected as the bird is moving, even if the center point remains the same. The mobility state was classified as either mobile or immobile. A bird was considered mobile at a threshold above 2%, and immobile was below 2%. The start velocity threshold for mobility was set to 1 cm/s. These thresholds were previously validated in white-throated sparrows (Kelly 2018).

Figure 3.2 A screenshot capture of the Noldus EthoVision software using centre-point detection. The yellow colouration captures the whole bird and the red dot indicates the centre of the bird. The red line shows the previous movement of the bird (1-2 seconds prior).

3.2.3 Body composition analysis

One day post capture, I measured body composition using a Quantitative Magnetic Resonance (QMR) scan to obtain a baseline body composition reading (Echo-Medical Systems, Houston, TX, Echo-MRI-B). QMR scans are a non-invasive way to accurately obtain fat and lean mass values (Guglielmo et al. 2011; see section 2.2.4). Scans were completed every other week for the duration of each experiment to assess and track changes in body composition, for a total of three body scans during each experiment.

3.2.4 DNA extraction, genetic sexing and morph determination

In between autumn and spring migratory seasons, I obtained a blood sample from each bird from the alar vein to genetically determine sex and morph. Blood was smeared on filter paper and left to dry. Filter paper was individually stored in plastic card holders and frozen until further use. For further information on the genetic sexing protocol, see section 2.2.7.

3.2.4.1 Genetic morph determination

The same DNA samples from the sexing procedure were used to determine genetic morph. Forward and reverse primers were used instead of P2 and P8 to generate genetic morph outcomes (Michopoulos et al. 2007). A 285 bp sequence was first amplified using the primer set described by Michopoulos et al. (2007). Ten µl of PCR product was then digested for 2 hours at 37 °C using 20 units of DraI in 1x of CutsmartTM buffer (New England Biolabs). PCR products were then run on 3% agarose gel. The sequence amplified by the primers contains the recognition sequence required for cleavage by DraI in white-striped birds only, resulting in bands at 200 bp and 85 bp. Tan- striped birds yield a single band at 285 bp, therefore white-striped individuals showed two bands and tan-striped individuals showed one band in the final gel.

3.2.5 Statistical analysis

Total distance moved (cm), cumulative duration of movement (seconds) and mobility state (seconds) were all highly correlated as migratory restlessness measures using Pearson’s correlation. These 3 measures were thus combined in a principal component analysis (PCA) by using the *prcomp* command in R (Version 3.5.1; Kelly 2018) for the purposes of statistical analyses. However, for clarity of presentation I used time mobile in figures.

I used a global linear mixed model to analyse nocturnal migratory restlessness behaviour. Global models included a combination of trial night, food group, treatment, sex, morph, and two-way interactions and included random intercept and slope terms for the effect of each individual bird to account for repeated measures. Mean barometric pressure each night was added as a main effect, but it reduced model efficiency and was thus removed from the model. Models were ranked based on AICc values. For the autumn analysis, six models were within two AICc units of each other, thus model averaging was implemented using conditional averaging through the model.avg function in MuMIn. For spring analysis, three models were within two AICc units of each other. Conditional averaging was also used.

Body composition was assessed with a linear mixed model in SPSS (IBM, version 25.0) by using fat mass and lean mass as dependent variables, respectively. Food group, sex, morph, week and their interactions were entered as fixed effects. To control for repeated measurements, bird ID was entered as a random effect.

3.3 Results

3.3.1 Autumn

3.3.1.1 Behavioural response

Principal component analysis was used to reduce dimensionality of the observed migratory restlessness behaviours. PC1 was the only principal component to have an eigenvalue greater than one and explained over 93% of the overall variance (Table 3.1). I thus used PC1 as an index of nocturnal migratory restlessness behaviour.

Table 3.1 A summary of principal component 1, including Eigenvalue, percent variance explained, and factor loadings for migratory restlessness models in Autumn and Spring.

	Eigenvalue	**% Variance explained**	**Factor loadings**	
PC1 – Autumn	1.67	93.69	Distance	0.57
			Movement	0.58
			Mobility	0.58
PC1 – Spring	1.71	97.86	Distance	0.57
			Movement	0.58
			Mobility	0.58

I used global linear mixed models to assess which factors influences migratory restlessness. There were six top models that were within two AICc units of each other, all of which included temperature treatment and night (Table 3.2). Other top models also included food group, sex, food group × treatment, and treatment × night. Birds significantly increased their restlessness behaviour across time (Table 3.3; Figure 3.3). Despite that all top models retained temperature treatment as an important parameter, none of the parameter estimates of temperature treatment, food group, morph or sex were significantly different from zero (Table 3.3). There was a significant interaction between unlimited food groups and warm nights, however, this relationship is likely to be a purely additive effect and is likely masked by strong trial night effects.

Table 3.2: Top six models of autumn migratory restlessness behaviour of white-throated sparrows. Second-order Akaike information criterion (AICc), the difference in AICc between candidate models (ΔAICc), number of parameters (K) and proportional weight of each model (w_i) are all reported.

ranked candidate models	**K**	**AICc**	**ΔAICc**	**w_i**
sex + treatment + trial	9	1731.7	0.00	0.209
sex + treatment + trial + treatment × trial	11	1732.0	0.32	0.178
food group + sex + treatment + trial + food group × treatment	12	1732.0	0.34	0.176
treatment + trial	8	1732.3	0.64	0.152
food group + sex + treatment + trial + food group × treatment + treatment × trial	14	1732.4	0.68	0.149
treatment + trial + treatment × trial	10	1732.6	0.86	0.136
null	5	1743.6	11.86	0.00

Table 3.3 Parameters of conditional averaging of top autumn migratory restlessness models with estimates, standard errors, and p values reported. Significant effects are italicized.

parameters of conditional averaging	**estimate**	**std. error**	**p**
intercept	0.21	0.13	0.102
sex: female	-0.29	0.17	0.091
treatment: cold	-0.10	0.13	0.416
treatment: warm	0.01	0.18	0.948
trial	*0.02*	*0.01*	*0.004*
treatment: cold × trial	-0.002	0.007	0.75
treatment: warm × trial	0.012	0.007	0.075
food group: unlimited	0.10	0.18	0.56
food group: unlimited × treatment: cold	-0.17	0.12	0.16
food group: unlimited × treatment: warm	*-0.28*	*0.12*	*0.023*
sex: female × treatment: cold	0.102	0.13	0.417
sex: female × treatment: warm	-0.15	0.13	0.24

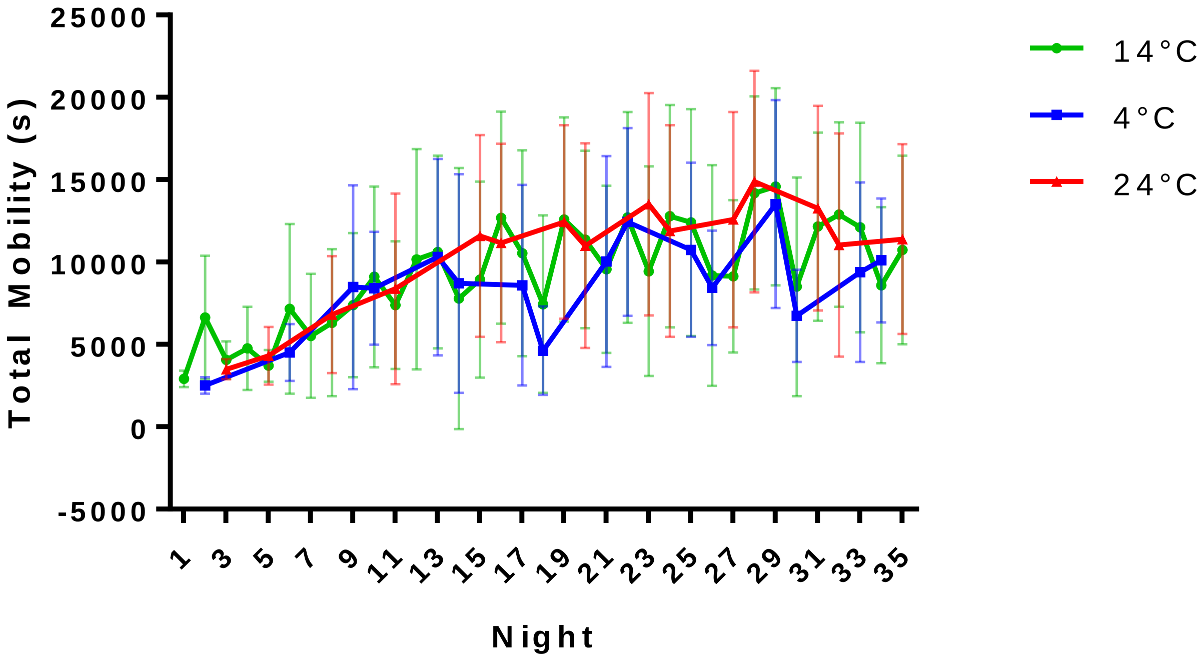

Figure 3.3 Autumn nocturnal migratory restlessness behaviour between 3 temperature treatments. Migratory restlessness behaviour is increasing across time. Since distance moved (cm), movement (s) and mobility (s) were all highly correlated (>93%), mobility is presented here to indicate overall restlessness behaviour. Points represent mean values and errors bars represent SEM.

3.3.1.2 Body composition

Fat mass did not differ between food groups ($F_{1,21}$=0.048, p=0.829), but did increase across time ($F_{2,32}$=48.283, p<0.0001). There were no differences in lean mass between food groups ($F_{1,21}$=0.056, p=0.815) or across time ($F_{2,32}$=2.703, p=0.078).

3.3.2 Spring

3.3.2.1 Behavioural response

As observed in autumn migratory restlessness, principal component analysis yielded one component, PC1, that had an eigenvalue greater than one and explained over 97% of the overall variance (Table 3.1). PC1 was used as an index of nocturnal migratory restlessness behaviour, consistent with the autumn data. Three top models were within two AICc values, thus conditional averaging was used. Temperature treatment, trial night and sex were all included (Table 3.4). Food group, morph, food group × sex, and treatment × night were also included in some top models. The effect of temperature varied across time: migratory restlessness behaviour increased across time in both cold and warm treatments. Overall, birds exhibited less restlessness on cold nights (Table 3.5) and increased restlessness across time (Table 3.5; Figure 3.4). Restlessness behaviour was lower in females compared to males (Table 3.5; Figure 3.5). Additionally, females receiving unlimited food supply were also less restless than food restricted females (Table 3.5; Figure 3.6).

Table 3.4: Top three models of spring migratory restlessness behaviour of white-throated sparrows. Second-order Akaike information criterion (AICc), the difference in AICc between candidate models (ΔAICc), number of parameters (K) and proportional weight of each model (w_i) are all reported.

ranked models	**K**	**AICc**	**ΔAICc**	**w_i**
sex + treatment + trial + treatment × trial	11	1351.5	0.00	0.305
food group + morph + sex + treatment + trial + food group × sex + treatment × trial	14	1352.3	0.76	0.209
morph + sex + treatment + trial + treatment × trial	12	1352.5	1.01	0.184
null	5	1411.9	60.34	0.00

Table 3.5 Parameters of conditional averaging of top spring migratory restlessness models with estimates, standard errors, and p values reported. Significant effects are italicized.

parameters of conditional averaging	**estimate**	**std. error**	***p***
intercept	*0.72*	*0.24*	*0.003*
sex: female	*-0.598*	*0.24*	*0.016*
treatment: cold	*-0.24*	*0.089*	*0.008*
treatment: warm	-0.036	0.089	0.68
trial	*0.045*	*0.007*	*<0.0001*
treatment: cold × trial	*0.013*	*0.004*	*0.004*
treatment: warm × trial	*0.013*	*0.004*	*0.003*
food group: unlimited	0.38	0.25	0.129
morph: tan-striped	0.31	0.22	0.157
food group: unlimited × sex: female	*-1.07*	*0.46*	*0.019*

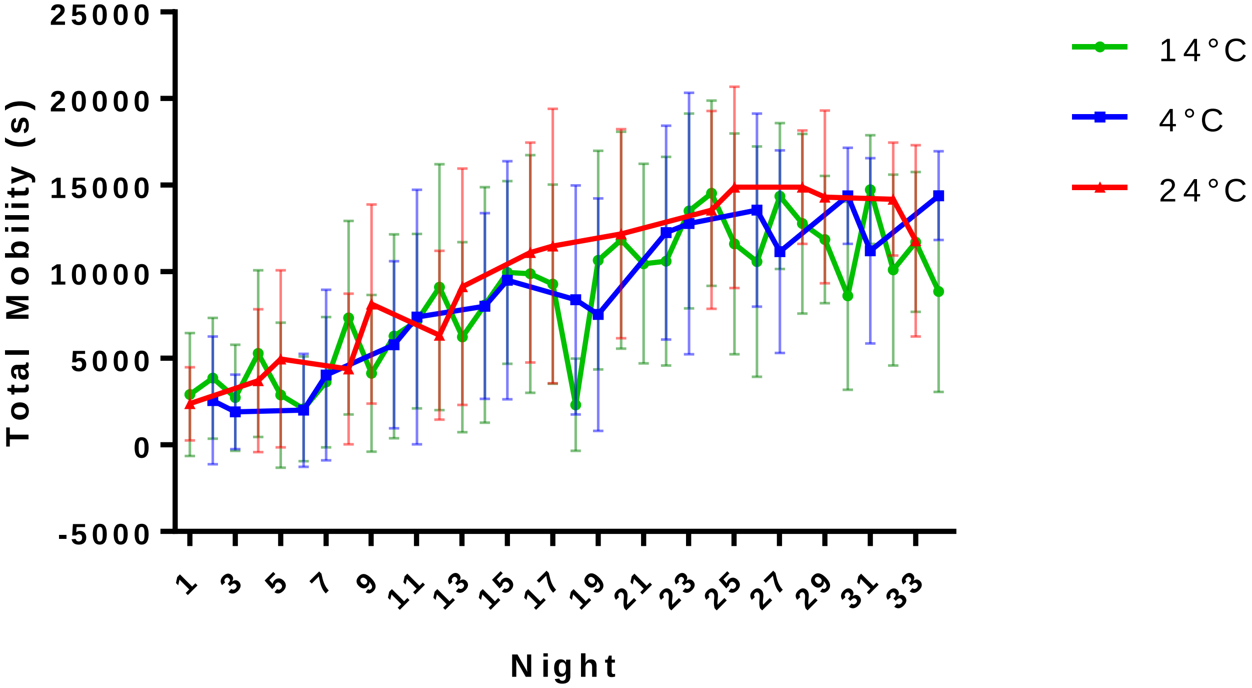

Figure 3.4 Spring nocturnal migratory restlessness behaviour between 3 temperature treatments in white-throated sparrows. Birds exhibited less restlessness on cold nights and an increase across nights. Since distance moved (cm), movement (s) and mobility (s) were all highly correlated, mobility is representing restlessness behaviour. Points represent mean values and errors bars represent SEM.

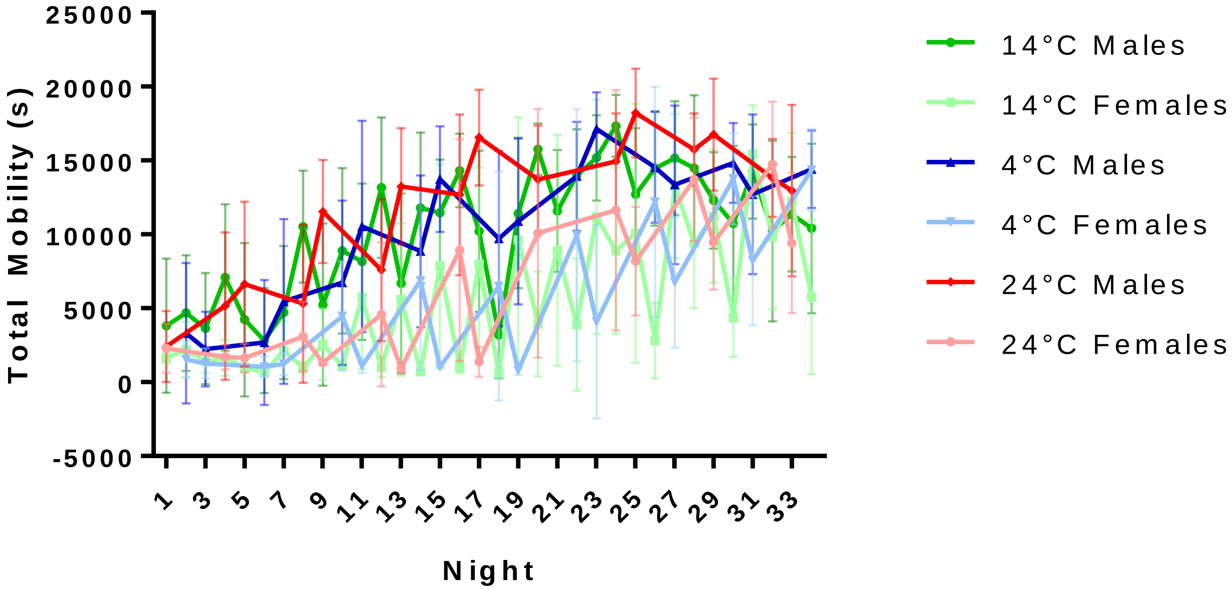

Figure 3.5 Spring nocturnal migratory restlessness behaviour between 3 temperature treatments across sexes. Females exhibited less migratory restlessness behaviour than males. Mobility is representing restlessness behaviour. Points represent mean values and errors bars represent SEM.

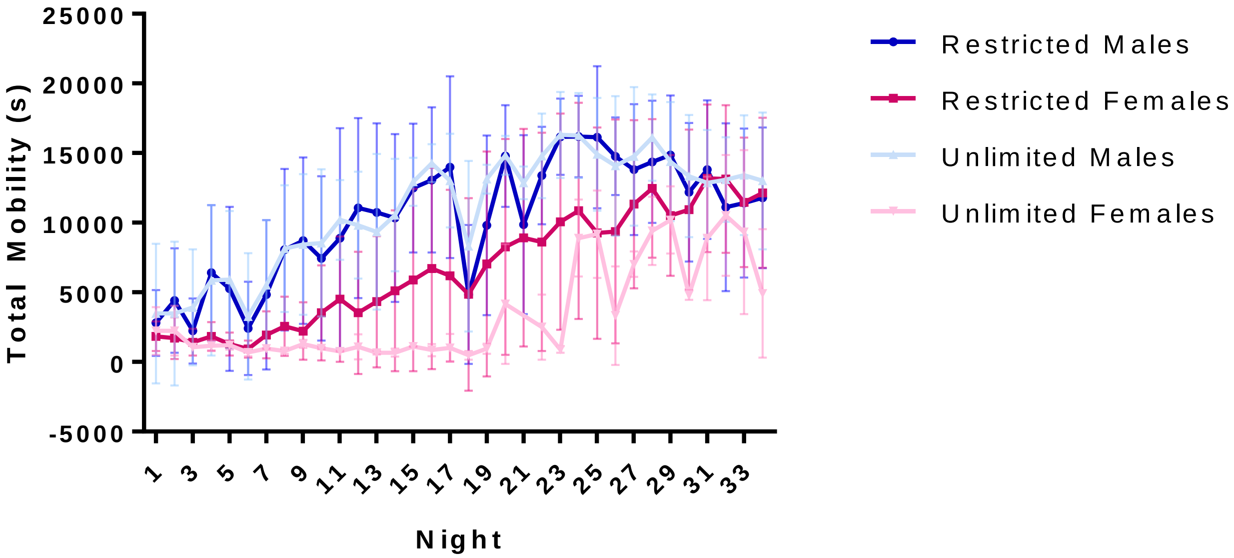

Figure 3.6 Spring nocturnal migratory restlessness behaviour of males and females across food groups. Females receiving unlimited food exhibited less migratory restlessness behaviour than females with limited food access. Mobility is representing restlessness behaviour. Points represent mean values and errors bars represent SEM.

Overall, temperature treatment had stronger effects in spring compared to winter (Figure 3.7).

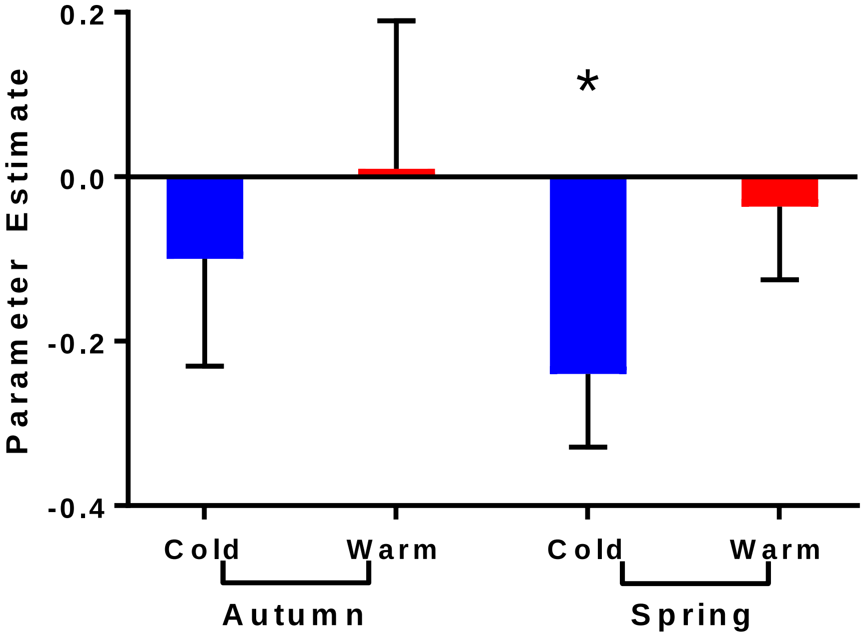

Figure 3.7 Parameter estimates of temperature treatment in autumn and spring. Temperature treatment had stronger effects in spring. Blue bars represent cold treatments (4 °C) and red bars represent warm treatments (24 °C). Error bars represent SEM.

3.3.2.2 Body composition

Fat and lean mass content both increased across time ($F_{2,34}$=6.541, p=0.004; $F_{2,34}$=4.158, p=0.024), but did not differ between food groups ($F_{1,17}$=0.235, p=0.634).

3.4 Discussion

Temperature had different effects on nocturnal migratory restlessness in white-throated sparrows across autumn and spring seasons. During the autumn migratory season, all six top models for migratory restlessness included temperature treatment, but parameter estimates did not significantly differ from zero. This suggests that temperature had an influence on migratory restlessness, but that the effect size was small relative to within-treatment variation between temperature treatments. The small parameter estimates between temperature treatments in autumn may have resulted from birds needing more time to adjust to captivity. It can take several days for birds to adjust to being in captivity, thus this may have obscured potential temperature effects. If anything, cold treatments appeared to decrease restlessness behaviour rather than increase these behaviours, which was opposite to predictions. However, this trend was not significant. Additionally, since birds were caught from the wild and manipulations began 24 h later, food availability may not have had an effect. Close proximity to capture date can also explain why there were no differences in fat mass content between food groups. White-throated sparrows deposit the majority of their energy stores during pre-migratory hyperphagia (Odum et al. 1961), thus their fat stores were likely already present and may not have been further influenced by captive food availability.

Although temperature treatment had minimal effects on migratory restlessness in autumn, it had stronger effects in spring. The parameter estimate for the cold treatment was significantly different from zero, and both warm and cold treatment significantly interacted with trial night, indicating that the effects of temperature varied over time. In the spring, restlessness behaviour was lower on cold nights. This likely relates to decreased activity in winter conditions, thus birds may be less motivated to leave their wintering grounds where food resources are more abundant if the weather is cold. Additionally, females exhibited less restlessness behaviour in the spring compared to males. This could be explained due to different pressures between sexes to arrive at the breeding grounds. In many species, males arrive on breeding grounds earlier to establish territories before females arrive (Morbey and Ydenberg 2001). A previous study in white-throated sparrows found males arrived to a spring stopover site 11 days earlier than females (Beauchamp 2018). Females may therefore be less motivated to migrate under cold conditions, especially if fewer resources would be available on the breeding grounds. Consistent with this, females with unlimited food availability exhibited less restlessness than food-restricted females (Figure 3.6). Limited resource availability can induce changes in migratory behaviour, including extending migratory stopovers (Gwinner et al. 1990). If females are already less motivated to arrive at their breeding grounds under cold conditions, unlimited resource availability on the wintering grounds may make them even less eager to begin their migration.

Although resource availability influenced the intensity of migratory restlessness, there did not appear to be an interaction between fat reserves and temperature manipulation. This suggests that birds are metabolizing and storing fat differently depending on food availability. Increases in feeding rates and decreases in metabolic rates allow migrating birds to deposit high levels of body fat. A previous study found no difference in feeding rates between migratory and non-migratory white-throated sparrows (Stuber and Bartell 2013), thus this further supports birds are likely metabolizing and storing food differently across seasons. It is possible there were no differences of food group in autumn because birds had already put on the majority of their fat resources prior to the beginning of the experiment.

Additionally, morph was an important variable in one of the top spring models, however, parameter estimates were not significantly different than zero. There are few reports of morph differences in migratory restlessness behaviour. In two studies that examined morph differences on migratory restlessness behaviour there was no difference between morphs (Kuenzel and Helms 1974; Kelly 2018), however, tan-striped individuals exhibited higher nocturnal migratory restlessness when infected with malaria compared to infected white-striped birds (Kelly 2018). Thus, further research is necessary to determine what, if any, differences in migratory behaviour exist between white-striped and tan-striped morphs.

Few studies have now examined the effects of temperature on nocturnal migratory restlessness behaviour in white-throated sparrows, with differing results. A previous study of autumn nocturnal migratory restlessness behaviour found that birds showed no restlessness behaviour in warm temperature conditions (24 °C) and increased migratory restlessness at cold temperatures (Berchtold et al. 2017). Although this study had a similar design, there were major differences in methodologies. Berchtold et al. (2017) began assessing restlessness behaviour late in the migration season (21-26 October), used infrared beam breaks to quantify migratory restlessness, and all birds received *ad libitum* food access (Berchtold et al. 2017). Because the Berchtold et al. (2017) study was conducted late in the migration season birds may have responded differently to temperature due to endogenous timing mechanisms. Alternatively there may have been a larger proportion of younger birds in that study. Regardless, further experiments would be required to determine why Berchtold et al. (2017) found strong effects of warm temperatures and I did not. A second previous study analyzed spring nocturnal migratory restlessness in white-throated sparrows. Metcalfe et al. (2013) found that increased barometric pressure and cold temperatures decreased migratory restlessness. However, this study had limitations, including measuring only one hour of restlessness behaviour following lights off, and using IR beam breaks to quantify behaviour (Metcalfe et al. 2013). Although this study did not examine the effect of temperature independent of pressure changes, the observed decrease in migratory behaviour under cold conditions was consistent with my study.

Analyzing restlessness behaviour for the entire duration of the night allows us to confidently infer the behaviour exhibited. Birds may not all choose to depart at consistent times throughout the night, thus analyzing restlessness behaviour across time is beneficial. This study was the first to experimentally manipulate temperature across seasons to assess migratory restlessness behaviour in birds with different resource availabilities. Noldus EthoVision software allows for a higher degree of accuracy when measuring restlessness behaviour, as there is limited room for error or biases and the ability to analyze from dusk to dawn. This technology provides additional insight into captive migratory behaviour for the entire duration of the night with finer details which traditional beam break technology cannot provide. I demonstrated that temperature has differential effects between autumn and spring, with stronger effects in spring. In addition, temperature effects interacted with sex and food availability in spring, but not in autumn. This may be due to different selection pressures acting across each season. Millions of bird mortalities have been documented due to cold conditions (Newton 2007), however, it is difficult to infer that these deaths were a direct result of cold temperatures or a result of changes in atmospheric conditions or resource availability. This study provides further evidence that birds use temperature directly as a cue to influence migratory behaviour, and thus, can have direct influences on survival in migratory species.

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Chapter 4

4 Natural storm exposure and the effects of food availability on physiological responses of songbirds

4.1 Introduction

Extreme weather events can pose severe challenges to a bird's survival and reproductive success. Inclement weather events can have different impacts depending on the life-history stage of the individual, negatively affecting breeding (Krause et al. 2016b, Martin et al. 2017), migration (Newton 2007, Gupta and Das 2016), moult (de Bruijn and Romero 2013), and overall survival. The intensity of the response to such environmental perturbations can differ depending on the availability of resources and past experiences of the individual, and birds must therefore be able to modulate their stress response in many dynamic environmental conditions (Nephew et al. 2003).

What defines an extreme weather event can differ drastically depending on the academic field. For example, climatologists designate an extreme event as drastically changing conditions across a frequency distribution curve, usually within 5% at either end of the distribution (Meehl et al. 2000). Among biologists, a true definition of an extreme weather event does not exist (Wingfield et al. 2017). Defining such events with respect to biological systems can depend on what is experienced as extreme for different individuals, species and ecosystems across spatial and temporal scales. For example, very hot temperatures would not be considered extreme for species residing in desert regions that are physiologically adapted and responsive to such conditions. However, this same event would be considered extreme for species residing in the Arctic. There can also be within-species variation in responses to climatic events, with individual responses varying depending on overall health, sex, life-history stage, social status, energy reserves, or resource access (Wingfield 1985a, Swanson 1990, Dolby 1999). The climatological definition of extreme weather thus does not account for biological variation within the responses of different ecosystems, species, or individuals, and creating a definition or threshold for what is considered extreme within biological systems is impossible.

The allostasis model provides a potential solution to the challenge of individual variation in response to extreme weather, and can provide a framework for determining what is considered ‘extreme’ for an individual in different contexts (McEwen 2013, Wingfield 2013b, Krause et al. 2017). I thus use allostasis as a framework to determine whether birds were experiencing allostatic overload. Glucocorticoid hormones are a significant part of coping mechanisms deployed in response to inclement weather events (Sapolsky et al. 2000, Holberton et al. 2003, Wingfield 2013a). Baseline levels of corticosterone allow an individual to cope with a range of commonly experienced environmental conditions. These levels tend to rise as external conditions deteriorate and allostatic load increases (Wingfield et al. 2017). Allostatic overload may be reached when an extreme event, including an inclement weather event, occurs and the allostatic pathways and mechanisms are no longer able to keep the body in a stable state (McEwen 2002). Allostatic overload can happen particularly often during the winter season with limited food supply (see section 1.4.2). Within the allostasis framework, the perturbation resistance potential (PRP) represents a key concept for an individual to sustain daily functions. The PRP represents the difference between the cumulative resources available and the sum of costs of seasonal existence energy and daily task energy (e.g., foraging, territory maintenance; Wingfield et al. 2017). Thus, keeping a high PRP will be most beneficial to an individual if perturbations within the environment arise. If the PRP reaches critically low levels, an emergency life-history stage is activated to enhance survival, often including temporary disruption of the current life-history stage, such as migration or reproduction (Wingfield et al. 1998).

The specific coping strategies employed during natural storms at different points along the life history stage remains relatively unexplored. The strategy employed likely depends on the current life history stage, and the facultative physiological responses may differ due to current body condition, trade offs of employing a certain strategy, costs and benefits of fleeing, energy expenditure, and available resources (Carey and Dawson 1999, McEwen 2002, Wingfield and Ramenofsky 2011b). The coping mechanisms or responses of birds to inclement weather has only recently been studied in controlled settings (Breuner et al. 2013, Metcalfe et al. 2013, Boyer 2015), however, there have been few experimental studies investigating these effects under natural conditions with experimental control of individuals. We therefore have not yet identified the effects of natural inclement weather on birds and how allostatic load is impacted. Poor weather conditions can have negative effects on birds, but they must somehow cope with such conditions by attempting to maintain a stable physiological state. In this study, I explored the physiological responses of white-throated sparrows (*Zonotrichia albicollis*) to unpredictable natural weather conditions, using birds held in aviaries and fed unlimited or fixed diets. I took blood samples every few days to characterize how corticosterone varies across different outdoor weather conditions. I used different food amounts in each treatment to manipulate energy availability and thus relative allostatic load. I tested the hypothesis that physiological responses induced by natural storm exposure will differ depending on food and energy reserves. Taking into account the perturbation resistance potential, food availability should impact allostatic load. I predicted that food-restricted birds would enter allostatic overload before birds given unlimited food access and exhibit higher levels of corticosterone. I also predicted that food-restricted birds should have higher fat reserves and overall body mass. Finally, I predicted that birds exposed to natural inclement weather receiving unlimited food should experience lower allostatic load and thus not alter body composition or corticosterone levels compared to food-restricted birds.

4.2 Methodology

I used white-throated sparrows as my study species because they commonly experience winter storms in their home ranges. Although they are migratory songbirds, white-throated sparrows are exposed to inclement winter weather, including cold temperatures and snow. See section 2.2.1 for additional information.

4.2.1 Capture and housing conditions

Twenty-four white-throated sparrows were caught in mist nets near Long Point, Ontario from 2 October to 3 October 2017 (Environment Canada Scientific Collecting Permit, CA 0244). Birds were transported to the Advanced Facility for Avian Research at the University of Western Ontario in London, Ontario the same day. On arrival, I weighed birds and measured tarsus length. Birds were then housed in individual cages (33 cm x 36 cm x 38 cm) on racks in outdoor aviaries. The aviary roof was covered by transparent panels to provide protection from precipitation, and some wall panels reduced wind within the aviary structures. Birds were otherwise exposed to ambient weather and lighting conditions. Each cage was equipped with a food cup, water bottle, and small shelter. The shelter had two sides (7 cm x 15 cm) and a roof (7 cm x 7 cm). Twelve birds were randomly assigned to each of two adjacent aviaries visually isolate from each other by a white sheet of plastic placed on the walls. The placement of individual cages was identical in each aviary. Consistent with previous studies (Chapters 2, 3, 5), birds were fed either unlimited food amounts or a limited 8 g of food per day which was previously determined to maintain healthy body condition in these species. Birds were fed a 50:50 mix of ground Mazuri Small Bird Maintenance Diet (catalogue number 56A6, Brentwood, MO, USA) and Premium Budgie Seed (Hagen). Diets were randomized within each outdoor aviary. This experiment was approved by the Animal Care Committee of the University of Western Ontario.

4.2.2 Procedure

To test how birds responded to inclement weather, I periodically took physiological samples as birds were exposed to natural changes in weather during late autumn/early winter. I held birds in individual cages in outdoor aviaries from 9 November 2017 through 6 December 2017, after which the daily high temperature started to decrease below 0 °C. The average daily high temperature was 3.9 °C for the duration of the experiment. Throughout the duration of the experiment, I tracked storm systems as they passed through London, ON. Pressure systems were tracked using www.wunderground.com. Weather Underground has a predictive feature that forecasts future changes in temperature, precipitation, and, most importantly, barometric pressure. Most forecasting applications do not include barometric pressure as part of the forecast, but rather just provide a historical log of it. Predictive barometric pressure conditions allowed me to schedule Quantitative Magnetic Resonance scans and blood sampling a few days in advance. I attempted to take measurements as close as possible to both storm events (low barometric pressure, cloud cover) and fair weather events (high barometric pressure, no cloud cover).

4.2.3 Blood sampling and hormone analysis

I took blood samples to obtain baseline corticosterone levels in the morning every 2-3 days. Based on predicted barometric pressure, I tried to ensure an even distribution of blood sampling on high pressure and low pressure days. Only 4-6 birds were bled each day and individual birds had blood sampling repeated no closer than 7 days apart to avoid drawing excess blood from any individual.

Blood was taken from the alar vein in the wing within 3 minutes of entering the aviaries. The vein was punctured using a 26-gauge needle and blood was collected in heparinized microcapillary tubes. To stop bleeding, cotton balls were applied with slight pressure to the vein. Blood was immediately placed on ice and spun down within 30 minutes of collection. Plasma was separated from red blood cells by being spun down in an IEC Micro-MB centrifuge for 11 minutes. Plasma was extracted and stored in a -30 °C freezer until hormone assays could be completed. Corticosterone levels were later analyzed using an enzymeimmunoassay kit validated for use in sparrows (Wada et al. 2007). See section 2.2.5 for additional information on EIAs.

4.2.4 Body composition

I ran Quantitative Magnetic Resonance (QMR) scans in the afternoon every 2-3 days on birds that did not undergo a blood sample that day. QMR scans were conducted on both high and low pressure days, consistent with the blood sampling schedule. On a day that birds in one aviary had blood taken, birds in the other aviary would be scanned in the QMR instrument to avoid significant disturbance. The next weather event day, the measures would be switched.

4.2.5 DNA extraction, genetic sexing and genetic morphing

Once the experiment was completed, I obtained a blood sample from each bird from the alar vein to genetically determine sex and morph. See section 3.2.4 for additional information on sexing and morphing procedures.

4.2.6 Weather variables

I collected weather data from Environment Canada Historical Weather Archives (http://climate.weather.gc.ca/historical_data/search_historic_data_e.html). I collected weather archives between 9 November 2017 through 6 December 2017, including data for temperature (°C), dew point temperature (°C), relative humidity (%), and barometric pressure (kPa) from the London, ON airport weather station. I obtained solar radiation (W/m^2) readings from historical weather archives from the Department of Geography at the University of Western Ontario. I pooled all weather data for 6 h prior and 12 h prior to the beginning of a physiological measure. For example, if a blood sample was obtained at 10:00am on 9 November 2017, I collected weather data from 4:00am to 10:00am (6 h grouping) and 10:00pm on 8 November 2017 to

10am (12 h grouping) that day. For each time frame, I calculated the mean and relative change of each weather variable.

4.2.7 Statistical analysis

Since it is difficult to place an arbitrary definition of what an extreme weather event for specific species (Wingfield et al. 2017), I did not designate outdoor conditions as either ‘inclement’ or ‘fair’. To explore which, if any, of the weather variables were related to my measures, I conducted an exploratory analysis using individual regressions for each variable. High collinearity amongst the weather variables precluded using linear mixed model or multiple regression approaches. For each physiological measure (corticosterone, fat mass, lean mass), I ran linear regression models in GraphPad Prism (Version 7.04) for each weather variable (temperature, dew point temperature, relative humidity, barometric pressure, solar radiation), including the 6 h and 12 h means and relative changes. Within each model, I separated birds receiving limited food availability and unlimited food availability. I also included sex within each model, but excluded sex from final statistical models since I did not detect any sex differences.

4.3 Results

4.3.1 Corticosterone

There were no detectable effects of the 6 h and 12 h mean or change in temperature (Figure 4.1), dew point temperature, relative humidity, barometric pressure (Figure 4.2) or solar radiation on corticosterone. There were also no effects of food availability on corticosterone levels. I present the linear regression tabular results of temperature (Table 4.1) and barometric pressure (Table 4.2) on corticosterone only, as these weather variables were of most relevant interest.

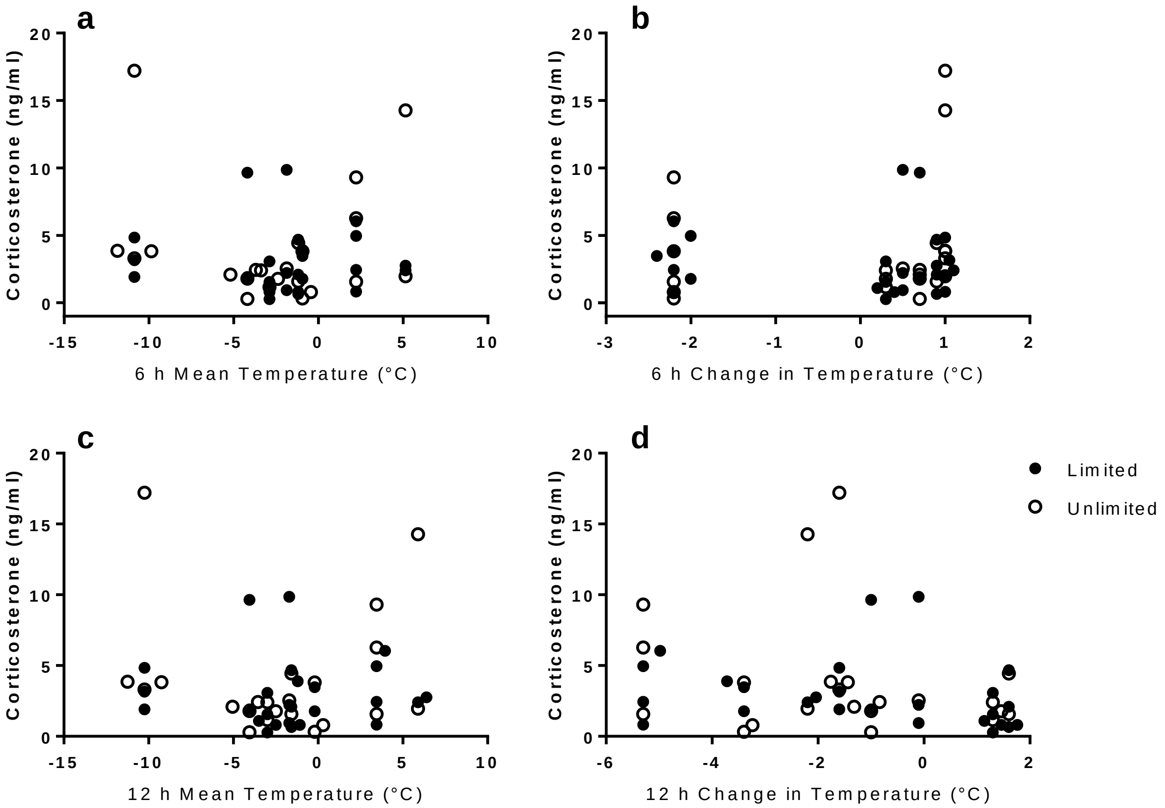

Figure 4.1 The relationship of temperature and corticosterone of white-throated sparrows exposed to natural weather conditions in outdoor aviaries. a) mean temperature (°C) 6 h before measure, b) change in temperature (°C) 6 h before measure, c) mean temperature (°C) 12 h before measure, and d) change in temperature (°C) 12 h before measure. Filled circles indicate birds receiving limited food and open circles represent birds receiving unlimited food access.

Table 4.1 Results of linear regression models testing the effects of temperature (T) on corticosterone. Results include 6 h mean temperature, 6 h change in temperature, 12 h mean temperature, and 12 h change in temperature in birds receiving limited or unlimited food amounts.

Source	r^2	Numerator df	Denominator df	F	Sig.
6 h mean T: Limited Food	0.002	1	24	0.005	0.824
6 h mean T: Unlimited Food	<0.0001	1	20	0.912	0.912
6 h change in T: Limited Food	0.003	1	24	0.009	0.761
6 h change in T: Unlimited Food	0.011	1	20	0.238	0.630
12 h mean T: Limited Food	<0.0001	1	24	0.008	0.926
12 h mean T: Unlimited Food	<0.0001	1	20	0.001	0.966
12 h change in T: Limited Food	0.051	1	24	1.306	0.2645
12 h change in T: Unlimited Food	0.049	1	20	1.051	0.317

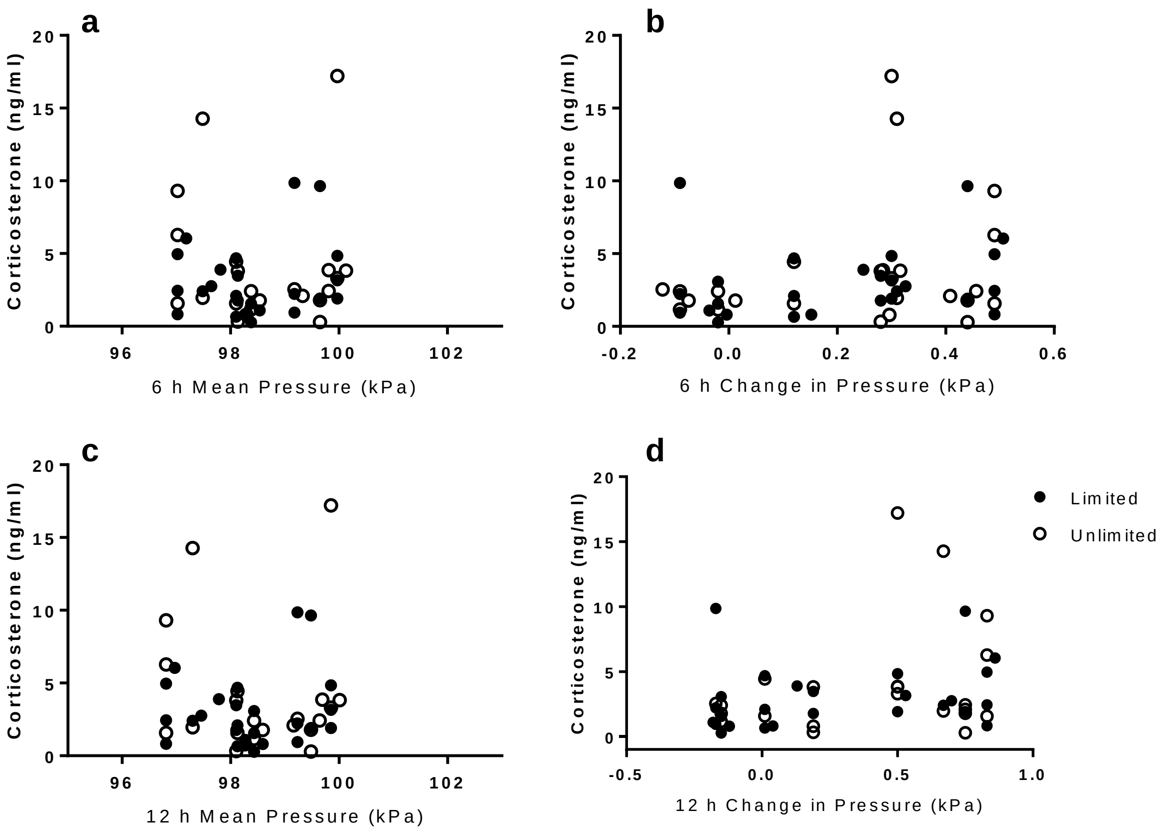

Figure 4.2 The relationship between barometric pressure and corticosterone of white-throated sparrows exposed to natural weather conditions in outdoor aviaries. a) mean pressure (kPa) 6 h before measure, b) change in pressure (kPa) 6 h before measure, c) mean pressure (kPa) 12 h before measure, and d) change in pressure (kPa) 12 h before measure. Filled circles indicate birds receiving limited food and open circles represent birds receiving unlimited food access.

Table 4.2 Results of linear regression models testing the effects of barometric pressure (P) on corticosterone. Results include 6 h mean pressure, 6 h change in pressure, 12 h mean pressure, and 12 h change in pressure in birds receiving limited or unlimited food amounts.

Source	**r^2**	**Numerator df**	**Denominator df**	**F**	**Sig.**
6 h mean P: Limited Food	0.032	1	22	0.400	0.736
6 h mean P: Unlimited Food	0.003	1	20	0.066	0.799
6 h change in P: Limited Food	0.053	1	24	1.355	0.255
6 h change in P: Unlimited Food	0.058	1	23	1.426	0.244
12 h mean P: Limited Food	0.020	1	24	0.507	0.482
12 h mean P: Unlimited Food	0.007	1	20	0.150	0.701
12 h change in P: Limited Food	0.068	1	24	1.755	0.197
12 h change in P: Unlimited Food	0.072	1	20	1.557	0.226

4.3.2 Fat mass

There were no detectable effects of the 6 h and 12 h mean or change in temperature (Figure 4.3), dew point temperature, relative humidity, barometric pressure (Figure 4.4) or solar radiation on fat mass. There were also no effects of food availability on fat mass. Here I also present the linear regression tabular results of temperature (Table 4.3) and barometric pressure (Table 4.4) on fat mass only.

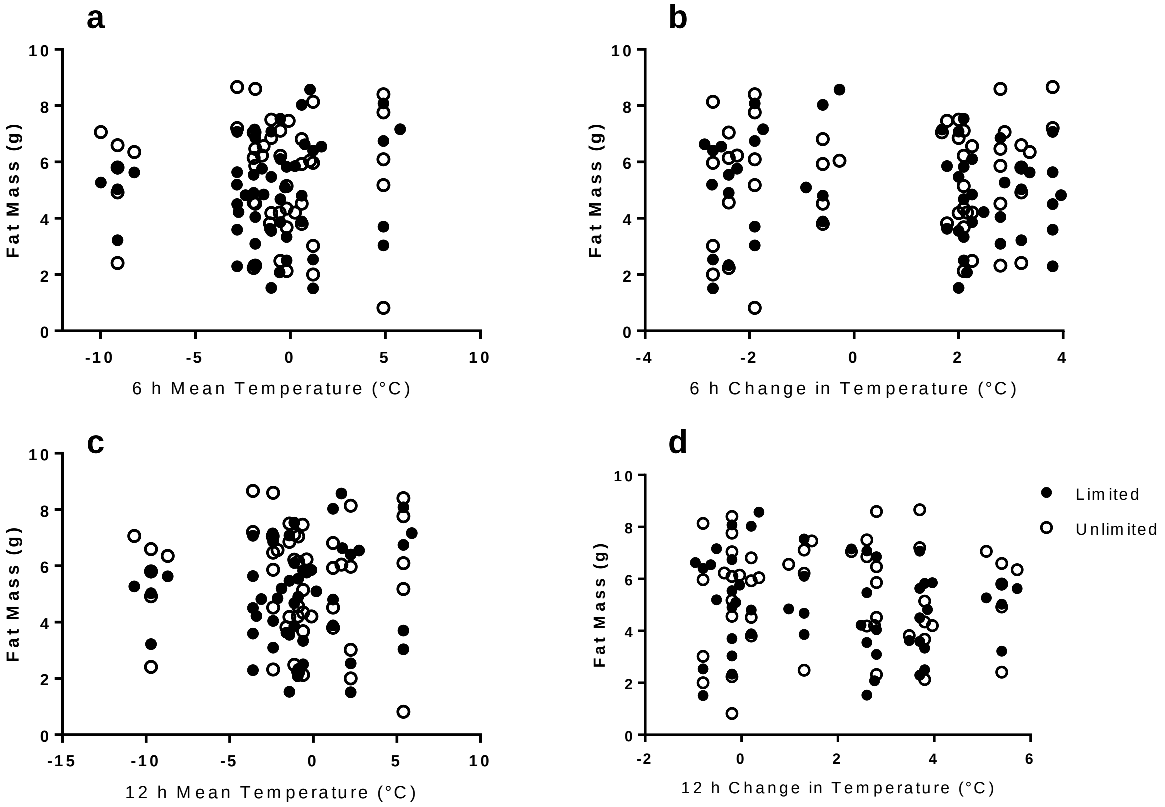

Figure 4.3 The relationship of temperature and fat mass of white-throated sparrows exposed to natural weather conditions in outdoor aviaries. a) mean temperature (°C) 6 h before measure, b) change in temperature (°C) 6 h before measure, c) mean temperature (°C) 12 h before measure, and d) change in temperature (°C) 12 h before measure. Filled circles indicate birds receiving limited food and open circles represent birds receiving unlimited food access.

Table 4.3 Results of linear regression models testing the effects of temperature (T) on fat mass. Results include 6 h mean temperature, 6 h change in temperature, 12 h mean temperature, and 12 h change in temperature in birds receiving limited or unlimited food amounts.

Source	**r^2**	**Numerator df**	**Denominator df**	**F**	**Sig.**
6 h mean T: Limited Food	0.011	1	49	0.575	0.451
6 h mean T: Unlimited Food	0.003	1	46	0.144	0.705
6 h change in T: Limited Food	0.022	1	49	1.14	0.290
6 h change in T: Unlimited Food	<0.0001	1	46	0.001	0.974
12 h mean T: Limited Food	0.013	1	49	0.417	0.668
12 h mean T: Unlimited Food	0.004	1	46	0.222	0.639
12 h change in T: Limited Food	0.013	1	49	0.675	0.415
12 h change in T: Unlimited Food	0.010	1	46	0.480	0.491

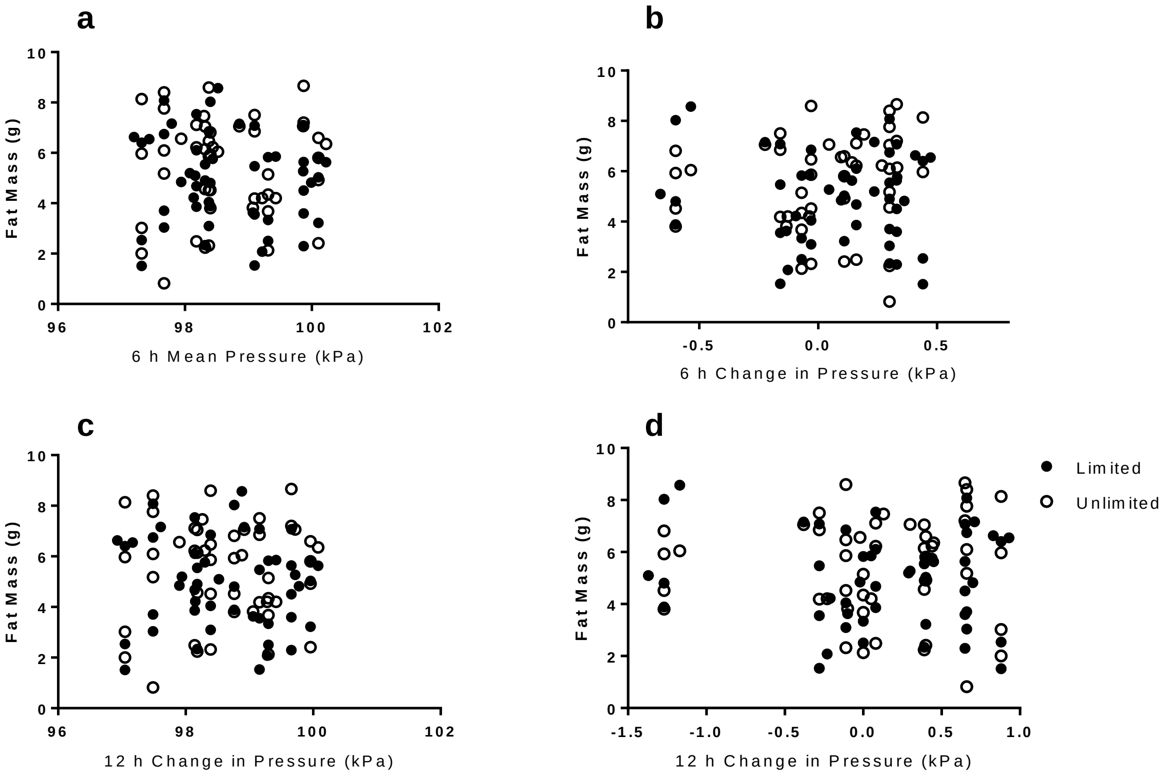

Figure 4.4 The relationship of barometric pressure and fat mass of white-throated sparrows exposed to natural weather conditions in outdoor aviaries. a) mean pressure (kPa) 6 h before measure, b) change in pressure (kPa) 6 h before measure, c) mean pressure (kPa) 12 h before measure, and d) change in pressure (kPa) 12 h before measure. Filled circles indicate birds receiving limited food and open circles represent birds receiving unlimited food access.

Table 4.4 Results of linear regression models testing the effects of barometric pressure (P) on fat mass. Results include 6 h mean pressure, 6 h change in pressure, 12 h mean pressure, and 12 h change in pressure in birds receiving limited or unlimited food amounts.

Source	**r^2**	**Numerator df**	**Denominator df**	**F**	**Sig.**
6 h mean P: Limited Food	0.015	1	49	0.761	0.387
6 h mean P: Unlimited Food	0.001	1	46	0.081	0.777
6 h change in P: Limited Food	0.008	1	49	0.424	0.517
6 h change in P: Unlimited Food	0.022	1	44	1.025	0.316
12 h mean P: Limited Food	0.009	1	49	0.469	0.496
12 h mean P: Unlimited Food	0.001	1	46	0.059	0.808
12 h change in P: Limited Food	0.012	1	49	0.606	0.440
12 h change in P: Unlimited Food	<0.0001	1	46	0.017	0.896

4.3.3 Lean mass

There were no detectable effects of the 6 h and 12 h mean or change in temperature (Figure 4.5), dew point temperature, relative humidity, barometric pressure (Figure 4.6) or solar radiation on lean mass. There were also no effects of food availability. I present the linear regression tabular results of temperature (Table 4.5) and barometric pressure (Table 4.6).

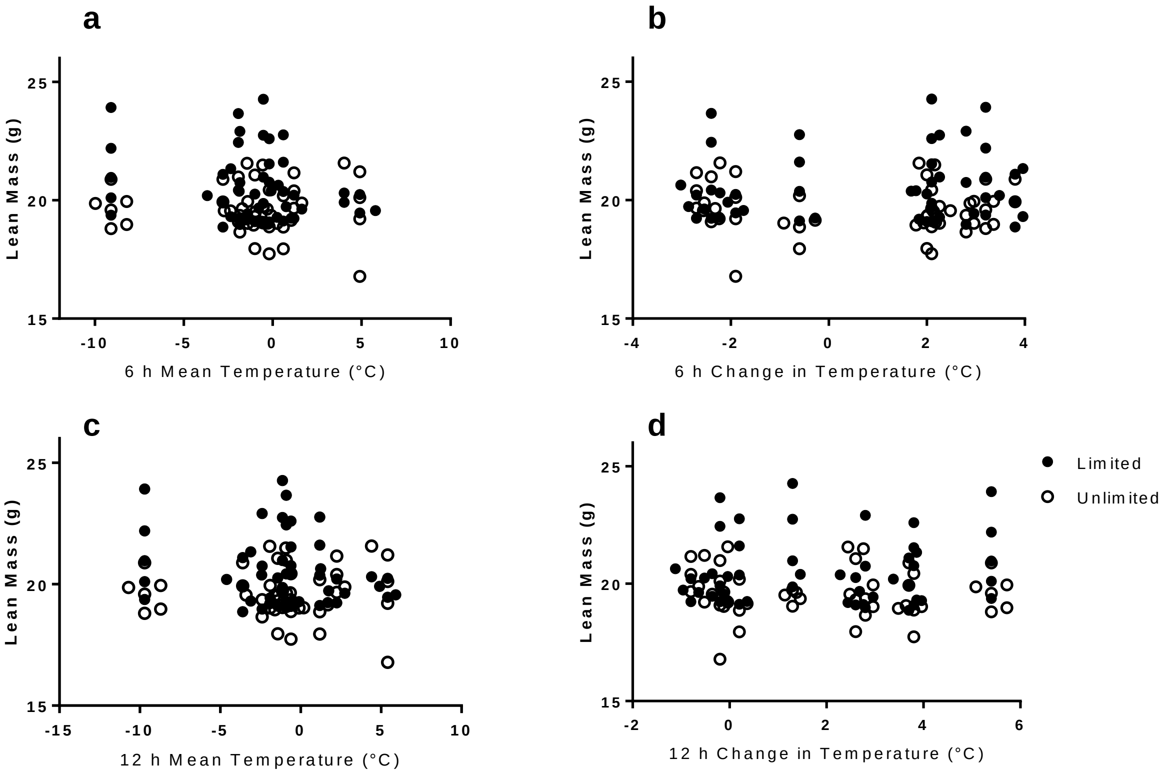

Figure 4.5 The relationship of temperature and lean mass of white-throated sparrows exposed to natural weather conditions in outdoor aviaries. a) mean temperature (°C) 6 h before measure, b) change in temperature (°C) 6 h before measure, c) mean temperature (°C) 12 h before measure, and d) change in temperature (°C) 12 h before measure. Filled circles indicate birds receiving limited food and open circles represent birds receiving unlimited food access.

Table 4.5 Results of linear regression models testing the effects of temperature (T) on lean mass. Results include 6 h mean temperature, 6 h change in temperature, 12 h mean temperature, and 12 h change in temperature in birds receiving limited or unlimited food amounts.

Source	**r^2**	**Numerator df**	**Denominator df**	**F**	**Sig.**
6 h mean T: Limited Food	0.047	1	49	2.419	0.126
6 h mean T: Unlimited Food	<0.0001	1	46	0.007	0.931
6 h change in T: Limited Food	0.008	1	49	0.400	0.529
6 h change in T: Unlimited Food	0.003	1	46	0.172	0.680
12 h mean T: Limited Food	0.043	1	49	2.242	0.140
12 h mean T: Unlimited Food	<0.0001	1	46	0.0002	0.986
12 h change in T: Limited Food	0.008	1	7	0.299	0.601
12 h change in T: Unlimited Food	0.005	1	7	0.0009	0.975

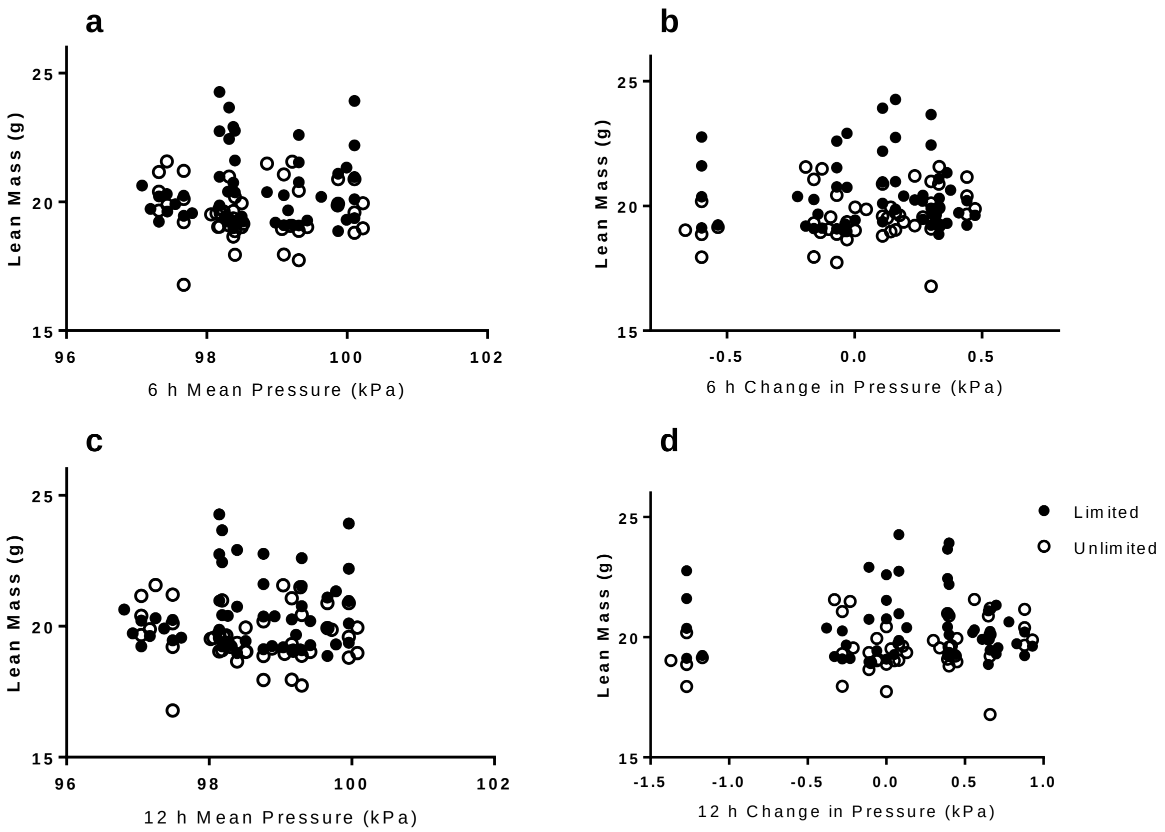

Figure 4.6 The relationship of barometric pressure and lean mass of white-throated sparrows exposed to natural weather conditions in outdoor aviaries. a) mean pressure (kPa) 6 h before measure, b) change in pressure (kPa) 6 h before measure, c) mean pressure (kPa) 12 h before measure, and d) change in pressure (kPa) 12 h before measure. Filled circles indicate birds receiving limited food and open circles represent birds receiving unlimited food access.

Table 4.6 Results of linear regression models testing the effects of barometric pressure (P) on lean mass. Results include 6 h mean pressure, 6 h change in pressure, 12 h mean pressure, and 12 h change in pressure in birds receiving limited or unlimited food amounts.

Source	r^2	Numerator df	Denominator df	F	Sig.
6 h mean P: Limited Food	0.005	1	49	0.267	0.607
6 h mean P: Unlimited Food	<0.0001	1	45	0.039	0.843
6 h change in P: Limited Food	<0.0001	1	49	0.024	0.876
6 h change in P: Unlimited Food	0.061	1	46	3.029	0.088
12 h mean P: Limited Food	0.006	1	49	0.324	0.571
12 h mean P: Unlimited Food	0.006	1	46	0.305	0.583
12 h change in P: Limited Food	0.003	1	49	0.165	0.686
12 h change in P: Unlimited Food	0.062	1	46	3.082	0.085

4.4 Discussion

I was unable to detect any changes in corticosterone, fat mass or lean mass in birds exposed to natural storms in outdoor aviaries. There were no detectable changes in corticosterone, fat mass or lean mass related to the 6 h or 12 h mean temperature, dew point temperature, relative humidity, barometric pressure, or solar radiation. There were also no detectable changes in these physiological measures related to the overall 6 h or 12 h change in the aforementioned weather factors. There were no detectable differences of food availability on corticosterone, fat mass or lean mass.

During the winter, birds are well prepared to deal with predictable seasonal weather (Carey and Dawson 1999). It appears that the birds in my study were able to completely buffer themselves against weather conditions in ways I could not detect. For example, even though birds didn't raise corticosterone levels, birds could be modifying metabolic rate or heart rate, or liberating energy stores independent of corticosterone (Nephew et al. 2003, Breuner et al. 2013). It is also possible that the limited food availability presented to some birds was still a reliable source of food, thus leading to a lack of physiological responses. Sparse food availability can induce a stress response in birds (Breuner and Hahn 2003), but given that even body composition was unaffected by winter weather, the food availability given to even limited treatment birds was not a true food restriction or limitation. Despite the feeding regime, birds had relatively high fat loads (see Figure 4.4). This limited food amount was likely still a more reliable source and a greater amount of food than birds are accustomed to in the wild when challenged with inclement weather.

Previous research in the field has found physiological effects of extreme weather on songbirds, but they often are season and sex specific (e.g., Wingfield 1985a, b; Romero et al. 2000, Ouyang et al. 2015). I also looked for sex differences within the physiological measures but did not detect any obvious sex differences. Thus, weather conditions were not more challenging for males or females.

One explanation for my null results is that there may have simply not been enough inclement weather naturally occurring during the period of my study. There were no extreme weather events within the time frame of this study. In the 12 h prior to body composition measurements, the maximum change in temperature was 5.4 °C, with the average change of just 1.9 °C. A recent example in London, ON of an extreme shift in weather took place in January 2019, where daily high temperatures drastically rose from -26 ℃ to 7 ℃ within just hours (EC 2019). During these conditions, it is likely that the physiological responses of birds in outdoor aviaries would be much more extreme. There were also very subtle changes in barometric pressure during my study. Within climatology, a 'weather bomb' is a term that describes a severe weather event with a change in 2.4 kPa within 24 hours (Sanders and Gyakum 1980). Although relatively rare, Ontario has previously experienced weather bombs in winter (Environment Canada 2016). The largest 12 h change in pressure was only 0.88 kPa in the present study. Given that the conditions throughout the time period wherein measurements took place were relatively mild, it is perhaps not surprising that effects were not detected.

To explore all possible relationships, I ran alternative statistical models to investigate findings. I ran linear mixed models but the approach was limited given the collinearity of the weather variables. I also investigated running a principal components analysis to combine weather variables which may have accounted for the collinearity of the weather variables, but this statistical approach veered away from determining which weather factor influences physiological responses, which was the main focus of this research project. Thus, I reported regression coefficients to avoid potential error due to highly correlated weather variables. After extensive exploratory analyses, I was unable to find any reliable associations between my physiological measures and weather data.

In summary, I was unable to detect any physiological changes in the 6 h and 12 h mean and change of weather factors did not influence birds in outdoor aviaries. It is likely predictable food availability played a role in this, in addition to birds being able to appropriately respond to winter storms. The food availability, even in limited treatments, was still a reliable source of food, likely still higher than food amounts in the wild. This, in combination with a relatively mild season, did not cause a stress response detectable in corticosterone or body composition in birds exposed to these conditions.

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Chapter 5

5 Physiological responses to acute exposures of differential inclement weather cues across seasons

5.1 Introduction

Broad-scale seasonal changes in weather are predictable to many animals, including birds. Abrupt, short-term changes in weather are less predictable as animals may have less time to prepare for a rapid change in environmental conditions. These short-term changes, including inclement weather and storms, can have many negative impacts, including reducing resource availability, decreasing habitat quality, forcing abandoning of territories and/or life-history stages, and reducing immune function and overall health (Wingfield et al., 2017). Although birds time their life-history stages to optimize reproductive success and overall survival, unpredictable, short-term environmental changes can alter physiological and behavioural responses which increase energy demands, leading to an acute stress response.

One negative effect of inclement weather on birds is reduced energy stores, or body condition. Severe weather can reduce foraging success due to high winds or precipitation (Carey and Dawson 1999), and thus indirectly reduce body condition. In birds with minimal energy reserves, severe weather can lead to shifts in corticosterone levels and associated behavioural responses (Breuner and Hahn 2003), collectively leading to an acute stress response. Repeated exposure to acute stressors can lead to chronic activation of the stress-response system (Gross 2014). Chronic stress can cause dramatic changes in physiological and behavioural responses, including corticosterone levels, body composition, and overall movement (Romero 2012). After time, chronic stress can activate an emergency life-history stage and an individual will enter allostatic overload (see section 1.4.2 for more detail on allostasis).

Part of the vertebrate stress response includes glucose mobilization, which is energetically costly (Wingfield et al. 1998). In birds, the hyperglycemic response due to acute stress can vary depending on factors including species, time of day, food availability, and the intensity of the stressor (Malisch et al. 2018), similar to changes in corticosterone levels. When exposed to acute stressors, the sympathetic nervous system and HPA axis are activated (see section 1.4.1 for more detail), quickly leading to elevated levels of epinephrine, norepinephrine and glucocorticoids, and thus collectively promoting glucose mobilization (Sapolsky et al. 2000, Wingfield and Sapolsky 2003, Malisch et al. 2018), also referred to as stress hyperglycemia. Catecholamine release through the HPA axis mediates the breakdown of glycogen to glucose, which increases the availability of glucose to target tissues (Malisch et al. 2018). Glucocorticoids increase glucose concentrations by converting lipids to glycogen. When lipid and energy reserves are minimal, muscle and other tissues can be catabolized for gluconeogenesis. Thus, glucose availability is an important mediator in the acute stress response system, that could potentially respond to stressors such as inclement weather.

The intensity of the physiological response to an environmental perturbation can vary depending on the intensity of the stressor and the overall health of the individual at the time of the stressor (Malisch et al. 2018). The behaviour of the individual may also vary depending on this intensity, and additionally depending on past experiences and the social status of the individual (Sapolsky et al. 2000). Additionally, the novelty of an acute stressor can also influence the magnitude and duration of the stress response (Nephew et al. 2003). For example, European starlings (*Sturnus vulgaris*) had an increased heart rate when exposed to novel anthropogenic stressors compared to stressors they had encountered previously (Nephew et al. 2003). However, these same stressors all elicited an increase in corticosterone, indicating that different responses to stressors can be modulated differently and independently of each other. Thus, a complete understanding of how animals respond to stressors requires assessing multiple response variables.

How birds respond to stressors, including inclement weather, is often flexible and context dependent. During a storm, white-crowned sparrows (*Zonotrichia leucophrys)* with corticosterone implants took longer to return to their breeding site after temporary abandonment than birds with lower corticosterone levels. During fair weather, sparrows with corticosterone implants did not leave their breeding site, but did increase their overall movement (Breuner and Hahn 2003), suggesting that corticosterone levels can differently influence behaviour under different weather conditions. However, repeated exposure to acute changes in temperature and artificial rain in European starlings did not cause a change in corticosterone levels or heart rate (de Bruijn et al. 2017), suggesting that these acute changes in weather cues did not elicit a chronic stress response. In addition, responses to stressors vary seasonally, as the costs and benefits of a glucocorticoid response to a stressor may vary between different life history stages (Remage-Healey and Romero 2000, Romero 2002, Krause et al. 2016a). Thus, there are flexible responses to acute stress. Similarly to an endocrine profile not existing among wild birds (Dickens and Romero 2013), it appears a physiological/behavioural profile also does not exist.

In this experiment I sought to understand how birds respond to an acute stressor; abrupt changes in weather cues. I measured multiple physiological and behavioural responses to acute exposures to inclement weather cues during different seasons and in birds with differing food availability. This study tested the hypothesis that acute exposures to inclement weather cues will elicit an increased stress response in a context dependent way, such that the response would vary depending on season and food availability. I predicted that birds' corticosterone levels, glucose levels and overall activity should increase when exposed to acute inclement weather cues, especially when food was limited. I also predicted there should be a greater response in the breeding season compared to the winter due to increased energetic demands associated with reproduction. To test these predictions, I exposed birds fed either unlimited or restricted food access to acute inclement weather cues, including abrupt changes in temperature and barometric pressure, during winter and spring.

5.2 Methodology

5.2.1 Study species and housing

I brought 24 white-throated sparrows into captivity between 2 October 2017 and 3 October 2017 (Environment Canada Scientific Collecting Permit 0244). Birds were immediately housed in outdoor aviaries and used in another project until 5 December 2017 (see Chapter 4). For more information on capture and housing of these individuals, see section 4.2.1. I brought birds inside from the outdoor aviaries on 6 December 2017 and housed them in a free-flight aviary for four weeks and manually changed photoperiod once per week to reflect outdoor conditions. I then moved birds back into individual cages in one of two environmental chambers kept at 14 °C. I kept all birds on their randomly assigned diet (unlimited or limited food) from when they initially entered the facility. Twelve birds received an unlimited amount of a 50:50 mix of ground Mazuri Small Bird Maintenance Diet (catalogue number 56A6, Brentwood, MO, USA) and Premium Budgie Seed (Hagen), and the remaining 12 birds were assigned a predetermined limited about of 8 g of 50:50 mix of ground Mazuri Small Bird Maintenance Diet (catalogue number 56A6, Brentwood, MO, USA) and premium budgie seed. I manually adjusted photoperiod once per week in the environmental chambers to match the natural outdoor sunrise/sunset schedule (~10L:14D). All birds were held in environmental chambers under these conditions until 22 January 2018 when experimental manipulations began. This experiment was approved by the Animal Care Committee of the University of Western Ontario.

5.2.2 Procedure

I exposed birds to acute weather cue manipulations each day over a two-week timeframe in both the winter and spring season. For each manipulation, I moved a group of 4 birds in individual cages into the hypobaric climatic wind tunnel plenum for approximately 24 h. The birds remained in the plenum from approximately 12:00pm to 11:00am the next day. Birds were housed in identical cages in the environmental chambers and the wind tunnel plenum. In the plenum, I exposed birds to two acute environmental manipulations: one in the afternoon from approximately 14:30pm to 15:30pm and one the next morning from approximately 9:30am to 10:30am (Figure 5.1). Each manipulation took place over a 1-hour period. When I moved birds into the tunnel, the temperature was held at 14 ℃ to be consistent with the home chamber conditions. Of the 24 birds total, each individual bird entered the tunnel twice over a 2-week period. Environmental manipulations consisted of either a decrease in temperature alone, a decrease in barometric pressure alone, or a decrease in both temperature and barometric pressure (Table 5.1). The schedule for manipulations was randomized. I decreased temperature from 14 ℃ to 4 ℃ and decreased barometric pressure from ambient to 96 kPa. Immediately following the manipulation, I returned the birds to ambient pressure and 14 ℃. Following the morning acute exposure, I moved the group of 4 birds to their home environmental chambers and I would immediately move the next group of 4 into the wind tunnel for the upcoming afternoon acute manipulation. These acute weather variable manipulations were 1-hour exposures to drastic decreases in barometric pressure alone, temperature alone, or barometric pressure and temperature combined. Between winter and spring experiments, photoperiod was adjusted to reflect outdoor conditions once per week and all birds received identical diets.

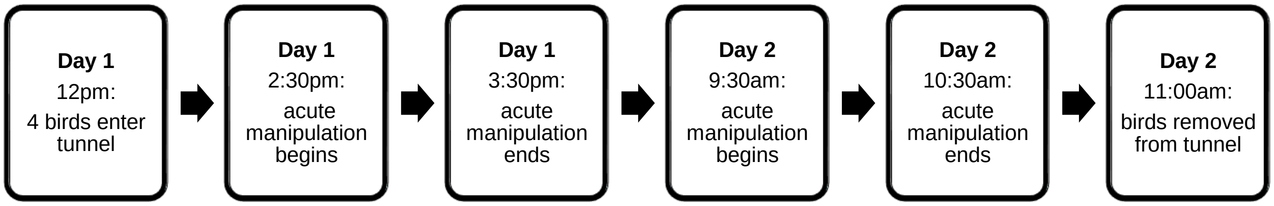

Figure 5.1 A timeline showing each acute environmental manipulation lasting 24 h.

Table 5.1 Acute weather manipulations used for treatment groups in white-throated sparrows during winter and spring.

Acute 1 h Treatment	Temperature (°C)	Pressure (kPa)
Temperature alone	14 → 4	None
Pressure alone	None	Ambient → 96.0
Both	14 → 4	Ambient → 96.0

5.2.3 Blood collection for glucose and corticosterone

Immediately following each 1-hour morning manipulation, I took blood samples from each bird to obtain corticosterone levels and blood glucose levels. I did not take blood samples after the afternoon acute exposures to avoid withdrawing too much blood from each bird and repetitive wounding. I took blood from the alar vein in the wing with a 26-gauge needle and collected it in heparinized microcapillary tubes. All samples were collected within 3 minutes of researchers entering the wind tunnel. Before centrifugation, a pinhead amount of blood was placed on a FreeStyle Lite human glucose monitoring strip, which was validated as a superior alternative to colorimetric kits in white-throated sparrows (Malisch et al. 2018). The glucose levels were immediately recorded for each bird in mmol/L. I then placed the remaining blood sample on ice and then centrifuged them to separate plasma from red blood cells. Plasma was then stored in a -30 ℃ freezer until blood collection was complete. Corticosterone levels were measured in plasma using an enzymeimmunoassay (EIA) kit (see section 2.2.5 for more detail on EIAs).

5.2.4 Behavioural analysis

Two video cameras (Supercircuits, model PC182XS) were set up in the wind tunnel plenum to quantify overall movement [total distance moved (cm) and total time moving (s)] and feeding behaviour [feeding duration (s) and latency to feed (s)]. The Noldus EthoVision XT software used centre-point detection settings to track each individual with static subtraction. See section 2.2.6 for additional details on static subtraction and Noldus analyses.

5.2.5 Statistical analysis

All data for glucose, corticosterone and behavioural responses were analyzed in SPSS (IBM, Version 25.0) with linear mixed models. Bird ID was entered as a random effect for all models.

For glucose and corticosterone linear mixed models, sex, morph, food group, acute treatment (temperature alone, barometric pressure alone, or both), day and their interactions were entered as fixed effects for both winter and spring experiments. If factor interactions were not significant, they were removed from the model. I ran a second model for both glucose and corticosterone to compare winter and spring levels with sex, morph, food group, acute treatment, and season as fixed effects.

For behavioural measures, I ran four separate models for each behavioural response [total distance moved (cm) and total time moving (s)] and feeding behaviour [feeding duration (s) and latency to feed (s)] in winter and spring. For each of these models, I entered sex, morph, food group, acute treatment, day, and their interactions as fixed effects. If factor interactions were not significant, they were removed from the model. For each behavioural response, I also ran a second linear mixed model to compare winter and spring and added season as a fixed effect.

5.3 Results

A summary of results from all measures (glucose, corticosterone, feeding duration, latency to feed, movement duration and total distance moved) can be found in Table 5.20.

5.3.1 Glucose

There were no significant main effects on glucose in the winter (Table 5.2). In spring, there was no effect of acute treatment, but there was a significant main effect of sex (Table 5.3). Males had higher glucose levels than females. There were no overall differences in glucose levels between seasons or food group (Table 5.4).

Table 5.2 Fixed effects of manipulations on glucose in birds exposed to acute weather manipulations in winter. There were no significant effects.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Sex	1	17.264	0.939	0.346
Morph	1	19.033	0.214	0.649
Food Group	1	15.909	0.727	0.407
Acute Treatment	2	21.681	1.711	0.204

Table 5.3 Fixed effects of manipulations on glucose in birds exposed to acute weather manipulations in spring. Significant effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Sex	*1*	*12.911*	*5.759*	*0.032*
Morph	1	9.934	3.934	0.076
Food Group	1	8.876	1.592	0.239
Acute Treatment	2	21.964	0.340	0.715

Table 5.4 Fixed effects of manipulations on glucose in birds exposed to acute weather manipulations across seasons. There were no significant effects.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Season	1	45.901	1.146	0.290

5.3.2 Corticosterone

In winter, sex and acute treatment had significant main effects on corticosterone (Table 5.5). Females had higher corticosterone levels than males (Figure 5.2). Birds exposed to acute changes in both temperature and pressure had higher corticosterone levels than birds exposed to temperature alone, but not pressure alone (Figure 5.3; Table 5.6). There were no significant main effects or interactions in spring (Table 5.7). There were no differences in corticosterone levels between seasons ($F_{1,76.66}$=0.60, p=0.411).

Table 5.5 Fixed effects of manipulations on corticosterone of birds receiving acute weather manipulations of temperature alone, barometric pressure alone, or temperature and barometric pressure combined in winter. Significant interactions are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Sex	*1*	*18.822*	*6.842*	*0.017*
Morph	1	19.977	1.400	0.251
Food Group	1	18.195	0.001	0.978
Acute Treatment	*2*	*20.387*	*4.485*	*0.024*

Table 5.6 Pairwise comparisons of manipulations on corticosterone between acute treatments: 1 (temperature alone, T), 2 (pressure alone, P), and 3 (both temperature and pressure, T & P). Significant effects are italicized.

(I) Treatment	(J) Treatment	Mean Difference (I-J)	Std. Error	df	Sig.
1 (T)	2	-0.0892	0.721	19.949	0.230
	3	*-2.210*	*0.711*	*20.887*	*0.007*
2 (P)	1	0.892	0.721	19.949	0.230
	3	-1.228	0.716	20.342	0.101
3 (T & P)	*1*	*2.120*	*0.711*	*20.887*	*0.007*
	2	1.228	0.716	20.342	0.101

Table 5.7 Spring fixed effects of manipulations on corticosterone of birds receiving acute weather manipulations of temperature alone, barometric pressure alone, or temperature and barometric pressure combined. There were no significant effects.

Source	Numerator df	Denominator df	F	Sig.
Sex	1	34	0.034	0.854
Morph	1	34	1.917	0.175
Food Group	1	34	0.339	0.564
Acute Treatment	2	34	1.064	0.356

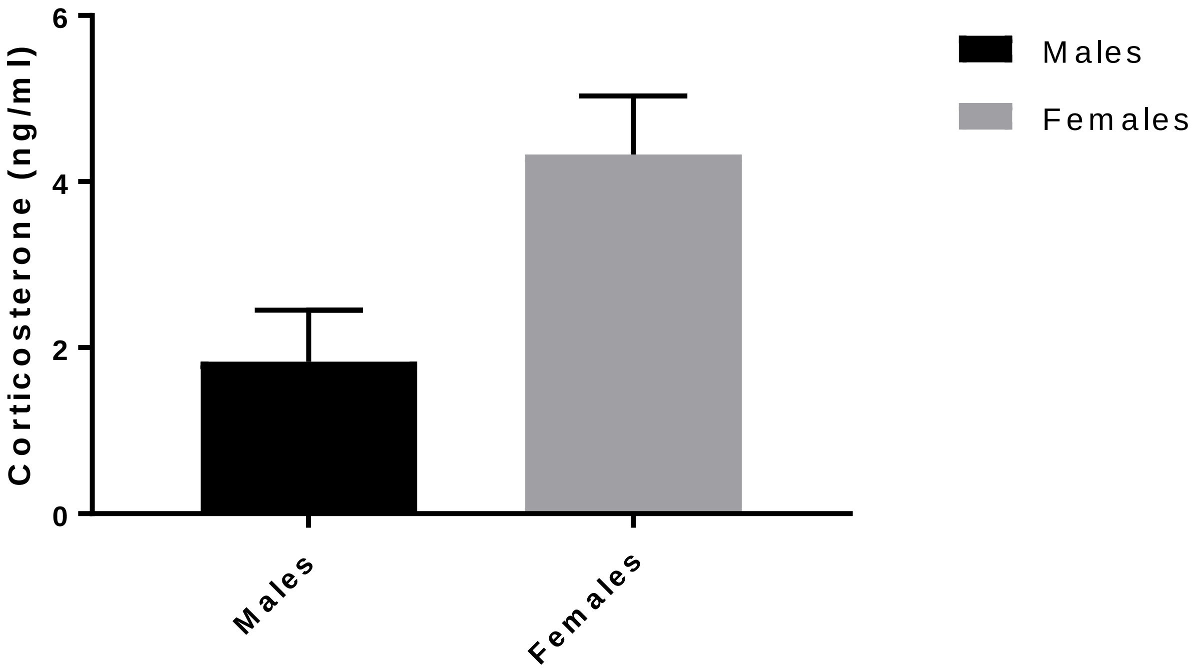

Figure 5.2 Winter corticosterone levels are lower in males compared to females in white-throated sparrows exposed to acute weather manipulations. Error bars represent SEM.

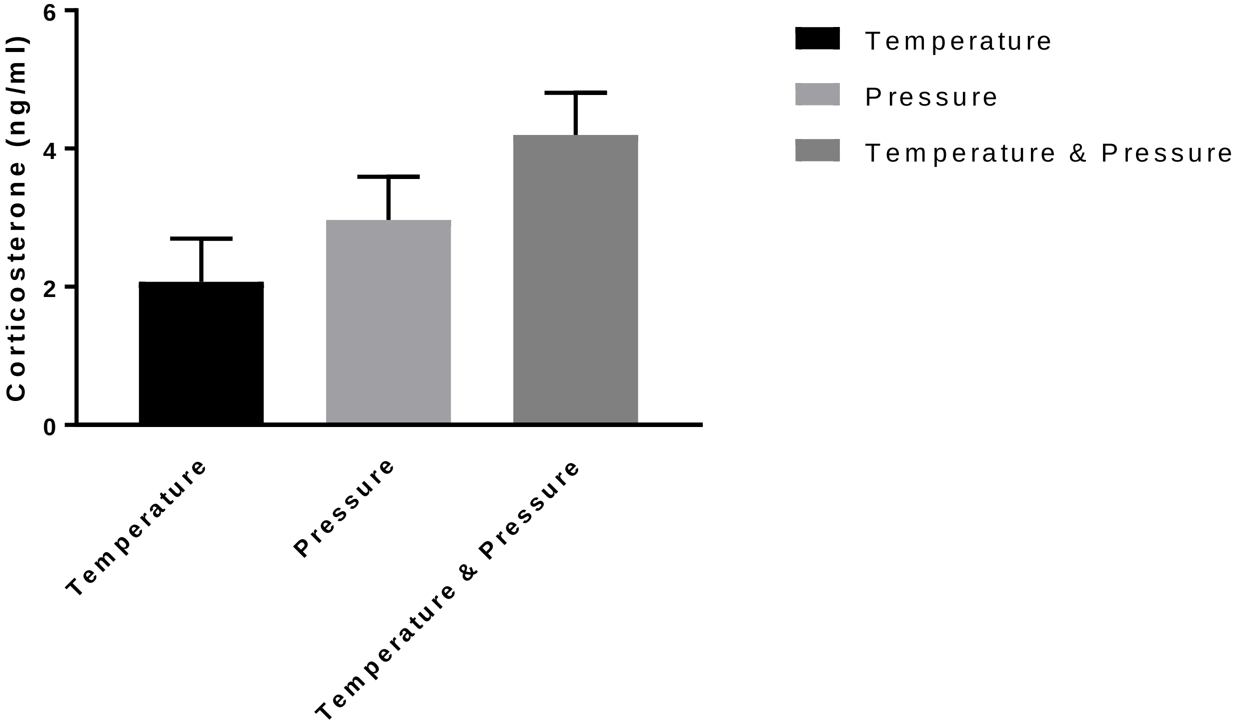

Figure 5.3 In the winter, white-throated sparrows exposed to acute changes in temperature and pressure combined had higher corticosterone levels than sparrows exposed to temperature alone, but not pressure alone. Error bars represent SEM.

5.3.3 Behavioural responses

5.3.3.1 Distance moved

In winter, there were significant main effects of acute treatment and food group (Table 5.8). Birds exposed to changes in both temperature and pressure moved a greater distance than birds exposed to temperature alone, but not pressure alone (Figure 5.4). Additionally, birds exposed to changes in pressure alone moved more than birds exposed to changes in temperature alone. Birds receiving limited food moved a greater distance than birds receiving unlimited food access (Figure 5.5). There were no significant main effects in spring, however, acute treatment was approaching significance (Table 5.9). Additionally, birds moved more in the winter than spring (Figure 5.6; Table 5.10).

Table 5.8 A summary of fixed effects of total distance moved in response to acute weather manipulations in winter. Significant effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Sex	1	14.854	0.797	0.386
Morph	1	15.521	1.276	0.276
Food Group	*1*	*13.144*	*4.880*	*0.046*
Acute Treatment	*2*	*19.148*	*3.773*	*0.042*

Table 5.9 The fixed effects of distance moved in birds exposed to acute weather cue manipulations in spring. There were no significant effects.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Sex	1	21.013	0.035	0.852
Morph	1	20.664	0.56	0.815
Food Group	1	19.742	0.949	0.342
Acute Treatment	2	19.719	3.357	0.056

Table 5.10 Fixed effects of distance moved in birds exposed to 3 acute manipulations between winter and spring. Significant effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Season	*1*	*62.570*	*18.933*	*<0.0001*

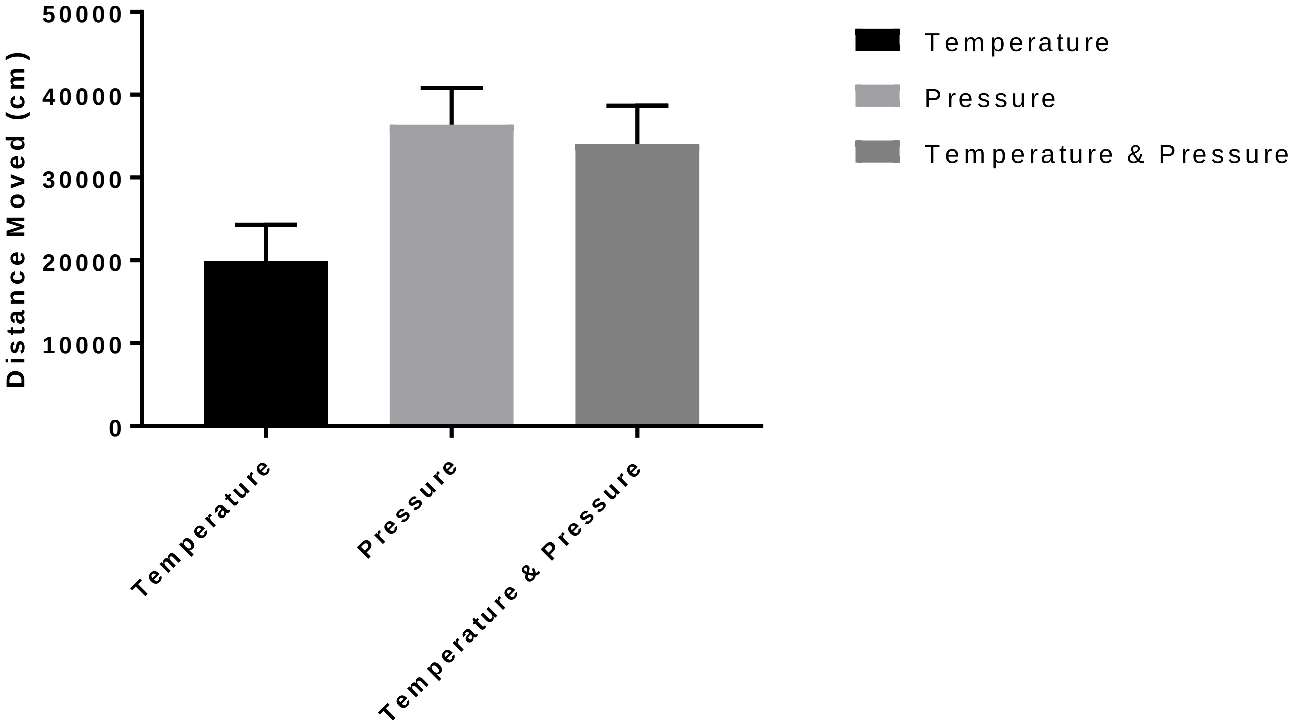

Figure 5.4 In winter, white-throated sparrows exposed to acute changes in both temperature and pressure moved a greater distance than birds exposed to temperature alone, but not pressure alone. Error bars represent SEM.

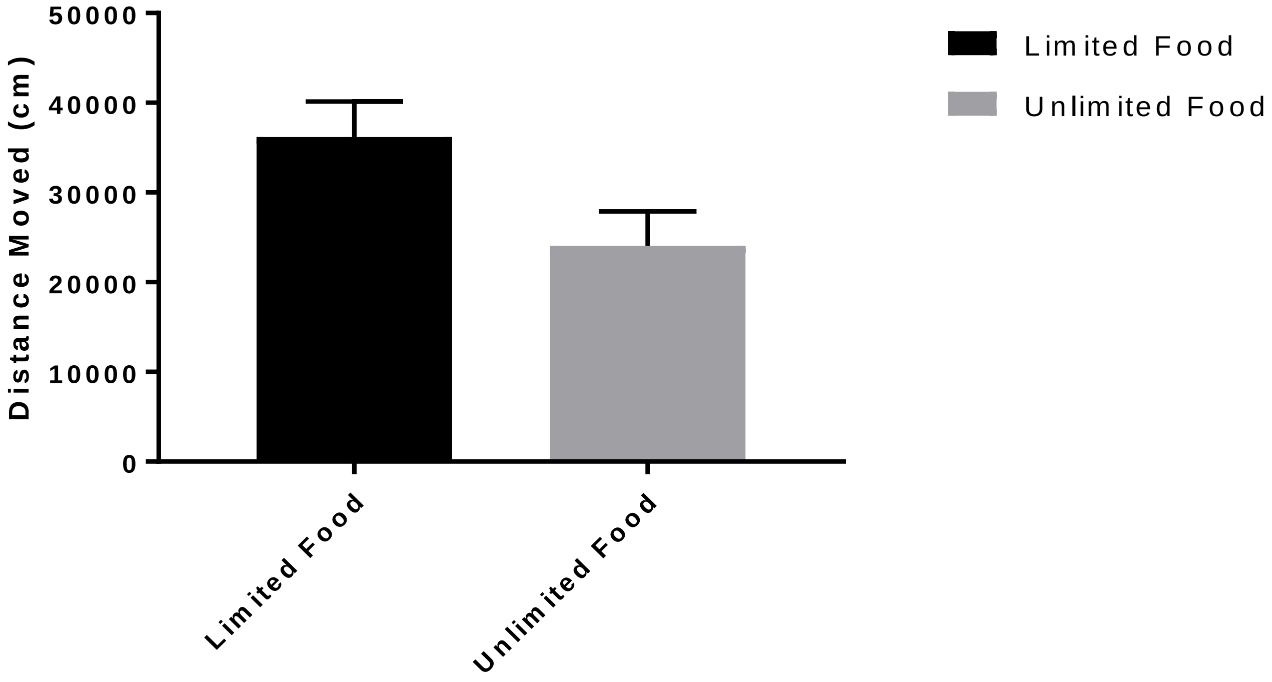

Figure 5.5 In winter, white-throated sparrows receiving limited food access moved more distance than sparrows receiving unlimited food access when exposed to 1 h acute weather manipulations. Error bars represent SEM.

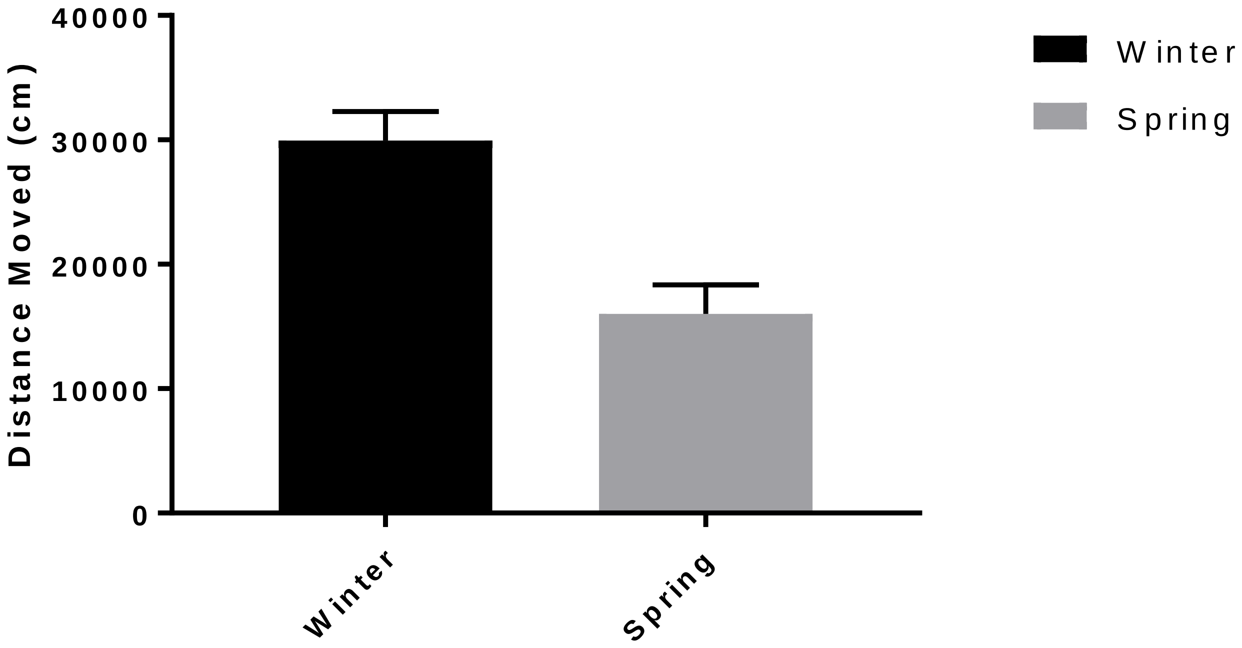

Figure 5.6 White-throated sparrows moved more distance in winter compared to spring when receiving acute weather cue manipulations over a 1 h period. Error bars represent SEM.

5.3.3.2 Feeding duration

In winter, there were significant main effects of food group (Table 5.11). Birds given limited food spent more time feeding than birds given unlimited food access (Figure 5.7). In spring, tan-striped individuals spent much more time feeding than white-striped (Figure 5.8; Table 5.12). Overall, birds spent more time feeding in winter than spring (Figure 5.9; Table 5.13).

Table 5.11 Fixed effects of feeding duration of birds exposed to 3 different acute weather manipulations and different food availabilities in winter. Significant effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Sex	1	36	1.214	0.278
Morph	*1*	*36*	*3.285*	*0.078*
Food Group	*1*	*36*	*18.496*	*<0.0001*
Acute Treatment	2	36	0.751	0.479

Table 5.12 A summary of fixed effects of feeding duration in birds exposed to 1 h acute weather manipulations in spring. Significant effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Sex	1	20.126	1.003	0.328
Morph	*1*	*20.314*	*5.214*	*0.033*
Food Group	1	18.956	0.452	0.509
Acute Treatment	2	25.533	1.874	0.174

Table 5.13 Fixed effects of feeding duration between winter and spring of birds exposed to identical acute weather manipulations. Significant effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Season	*1*	*78*	*34.417*	*<0.0001*

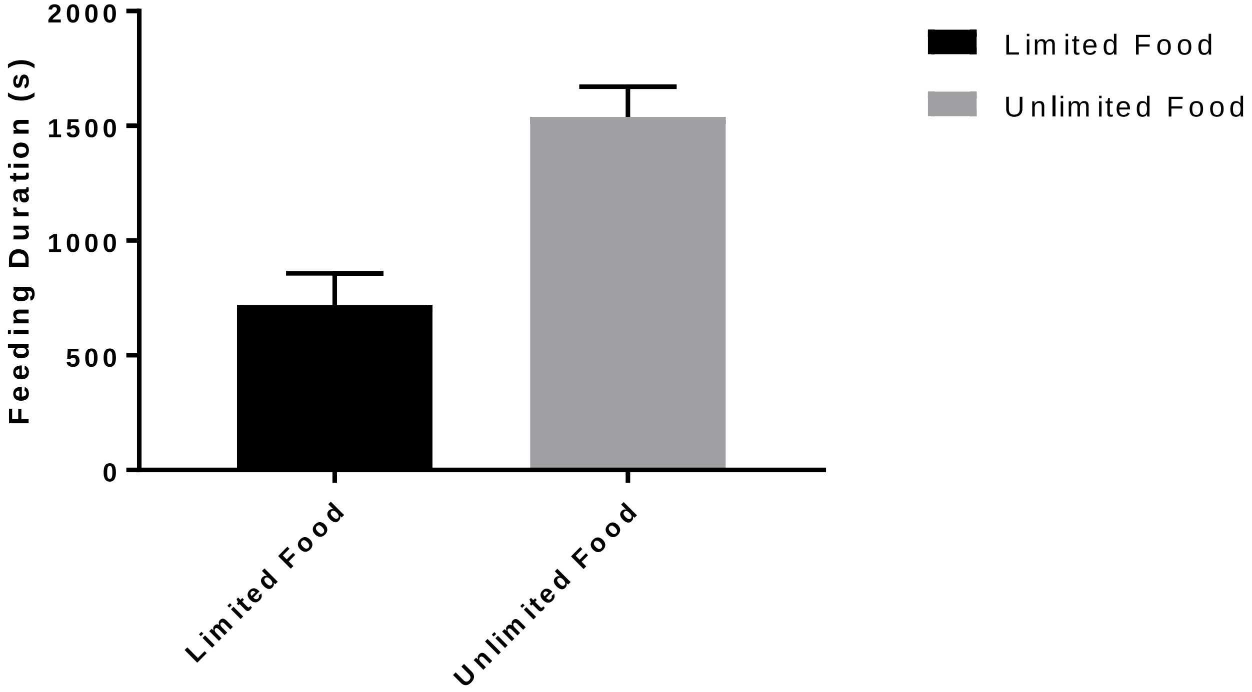

Figure 5.7 In winter, white-throated sparrows receiving unlimited food access spent more time feeding during acute weather manipulations than sparrows receiving limited food access. Error bars represent SEM.

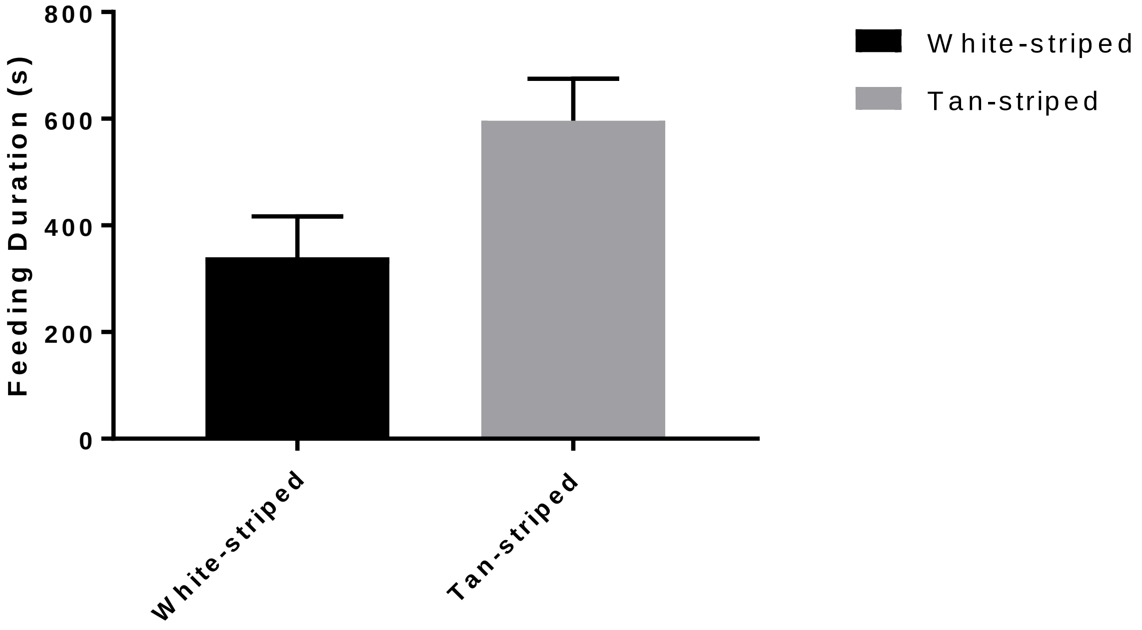

Figure 5.8 In spring, tan-striped white-throated sparrows spent more time feeding during 1 h acute manipulations than white-striped individuals. Error bars represent SEM.

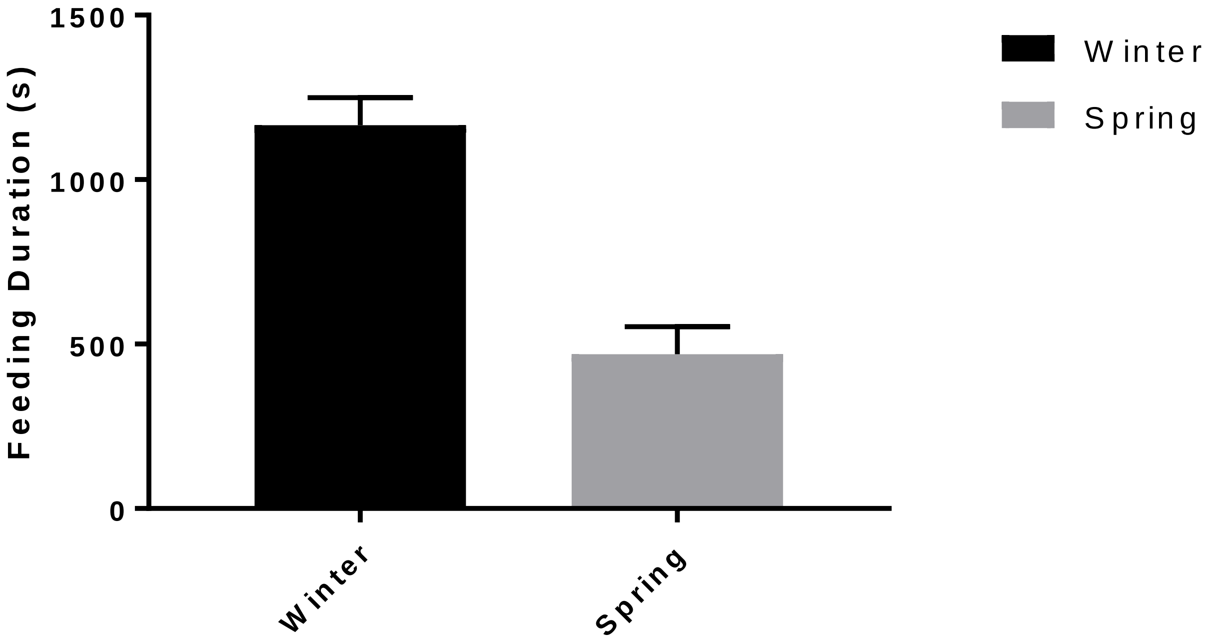

Figure 5.9 White-throated sparrows spent more time feeding in the winter than the spring when exposed to acute changes in weather cues. Error bars represent SEM.

5.3.3.3 Latency to feed

There were no significant effects in the latency to feed in winter (Table 5.14). In spring, birds receiving acute changes in temperature alone approached food cups faster than birds receiving changes in pressure alone and birds receiving changes in both variables (Figure 5.10; Table 5.15). Birds took longer to approach food cups in spring than winter (Figure 5.11; Table 5.16).

Table 5.14 A summary table of the fixed effects in the latency to feed of birds exposed to acute weather manipulations in winter. Significant effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Sex	1	21.126	0.202	0.658
Morph	1	21.394	0.012	0.913
Food Group	1	19.648	2.399	0.137
Acute Treatment	2	22.643	0.685	0.514

Table 5.15 A table highlighting the fixed effects in the latency to feed in the spring of birds exposed to 3 acute weather manipulation treatments. Significant effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Sex	1	19.312	1.858	0.189
Morph	1	18.972	2.131	0.161
Food Group	1	18.438	0.225	0.641
Acute Treatment	*2*	*15.677*	*6.756*	*0.008*

Table 5.16 The fixed effects of latency to feed across winter and spring. Significant effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Season	*1*	*62.811*	*32.159*	*<0.0001*

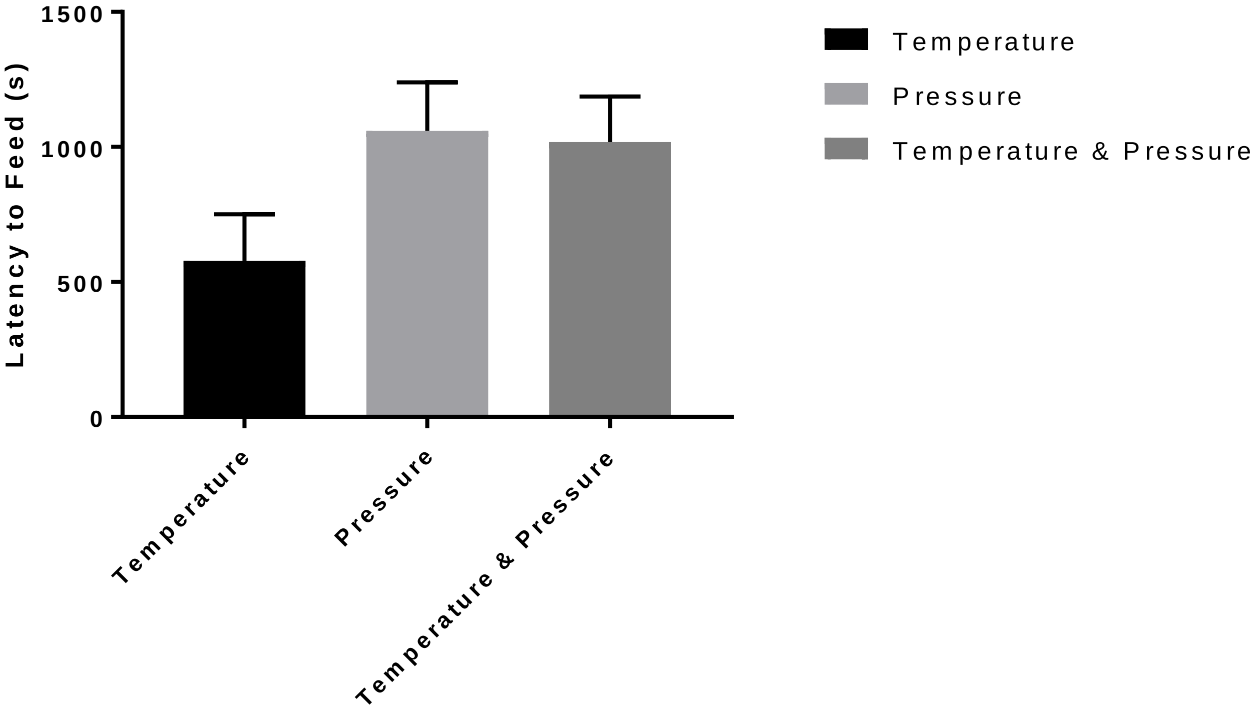

Figure 5.10 In spring, white-throated sparrows receiving acute manipulations of temperature alone approached food cups more quickly than sparrows receiving changes in pressure alone and birds receiving changes in both variables. Error bars represent SEM.

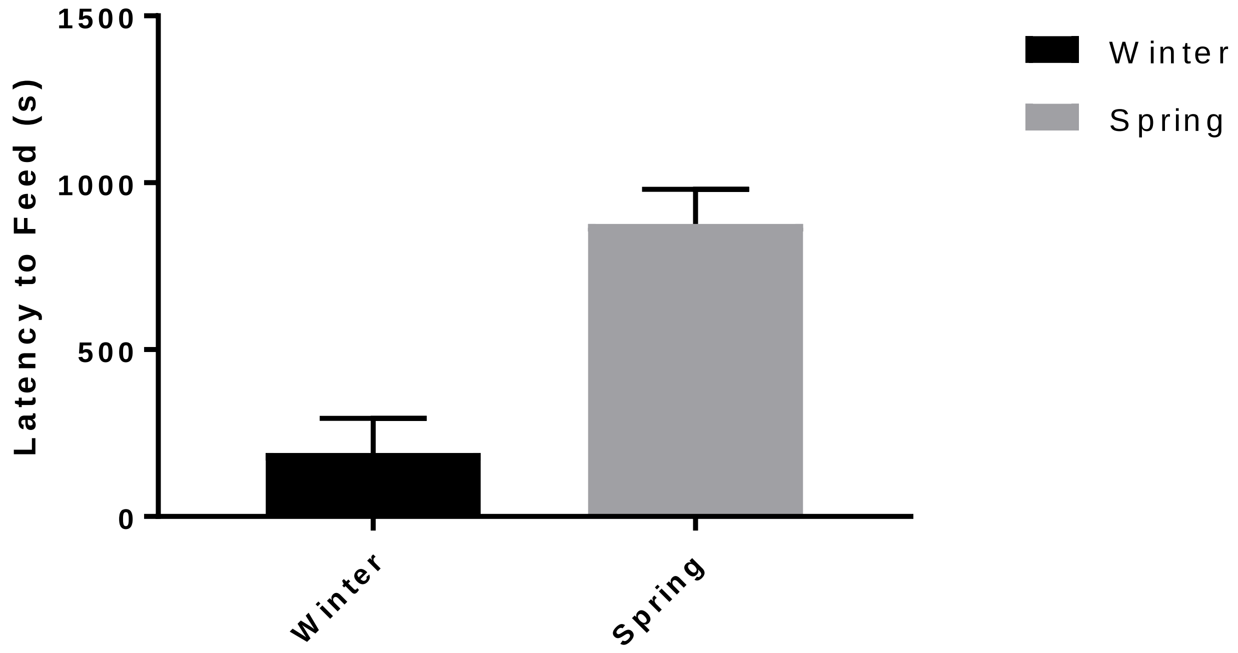

Figure 5.11 Birds exposed to acute weather manipulations approached their food cups more quickly in winter than spring. Error bars represent SEM.

5.3.3.4 Movement duration

In winter, birds receiving limited food access moved more throughout the 1 h acute manipulation than birds receiving unlimited food access (Figure 5.12; Table 5.17). In spring, acute treatment had significant main effects (Table 5.18). Birds exposed to temperature alone moved more than birds exposed to both temperature and pressure changes combined (Figure 5.13). Birds moved for a longer duration in winter than spring (Figure 5.14; Table 5.19).

Table 5.17 A summary table of the fixed effects of movement duration in birds exposed to 1 h acute changes in temperature alone, pressure alone, and temperature and weather combined in winter. Significant effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Sex	1	16.027	0.971	0.339
Morph	1	17.143	3.510	0.078
Food Group	*1*	*14.171*	*11.651*	*0.004*
Acute Treatment	2	22.876	2.705	0.088

Table 5.18 Fixed effects of movement duration birds exposed to acute weather manipulations in spring. Significant effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Sex	1	20.114	0.001	0.975
Morph	1	19.747	0.074	0.788
Food Group	1	19.112	0.073	0.789
Acute Treatment	*2*	*16.933*	*8.018*	*0.004*

Table 5.19 Fixed effects of movement duration in birds exposed to identical acute weather manipulations between winter and spring. Significant effects are italicized.

Source	**Numerator df**	**Denominator df**	**F**	**Sig.**
Season	*1*	*63.564*	*28.140*	*<0.0001*

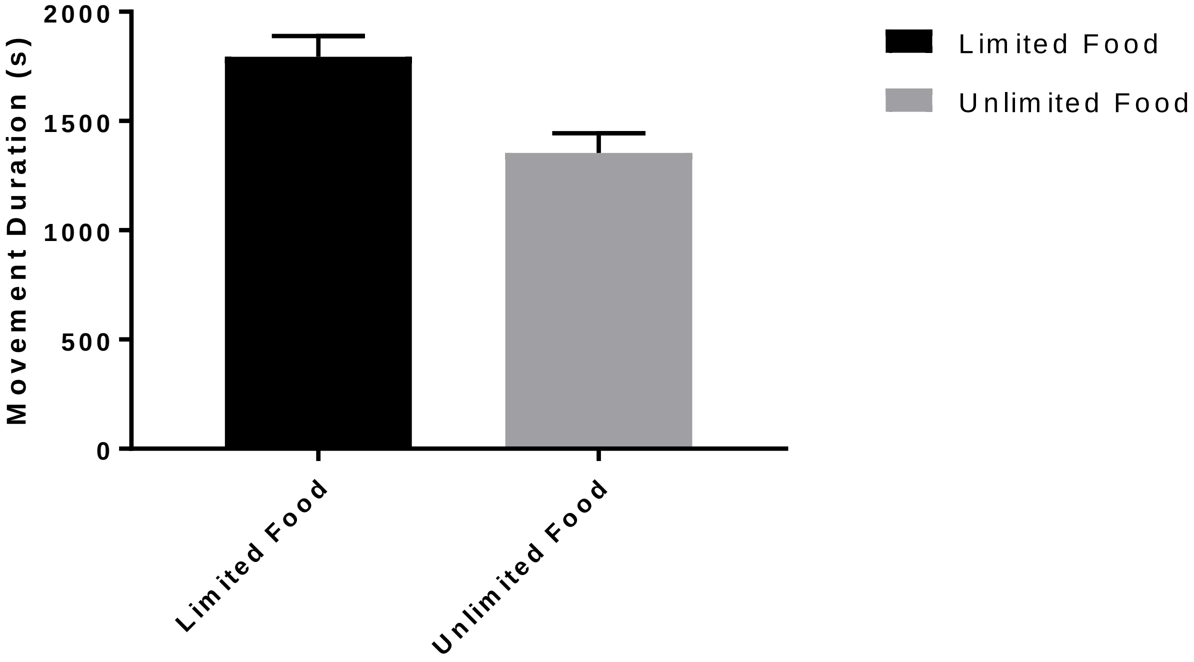

Figure 5.12 In winter, white-throated sparrows receiving limited food access moved more throughout the 1 h acute manipulation than birds receiving unlimited food access. Error bars represent SEM.

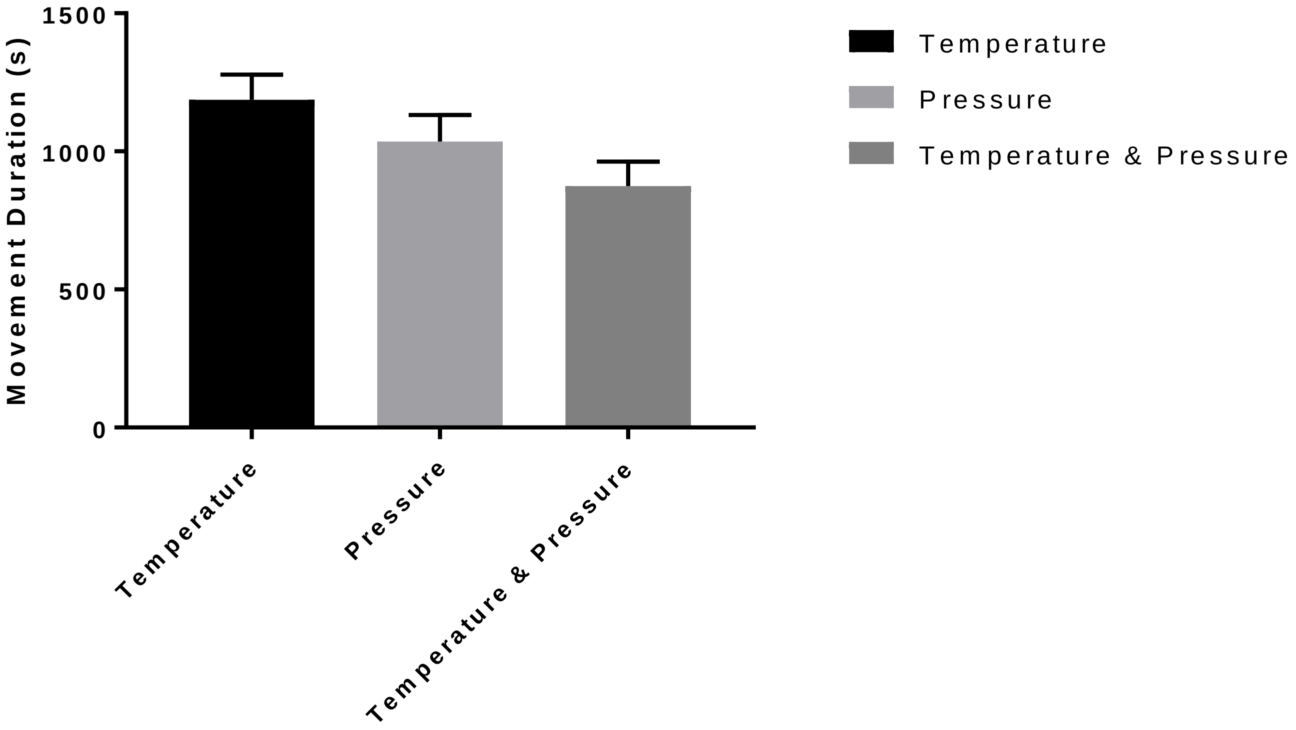

Figure 5.13 In spring, white-throated sparrows exposed to temperature alone moved more than birds exposed to both temperature and pressure changes combined. Error bars represent SEM.

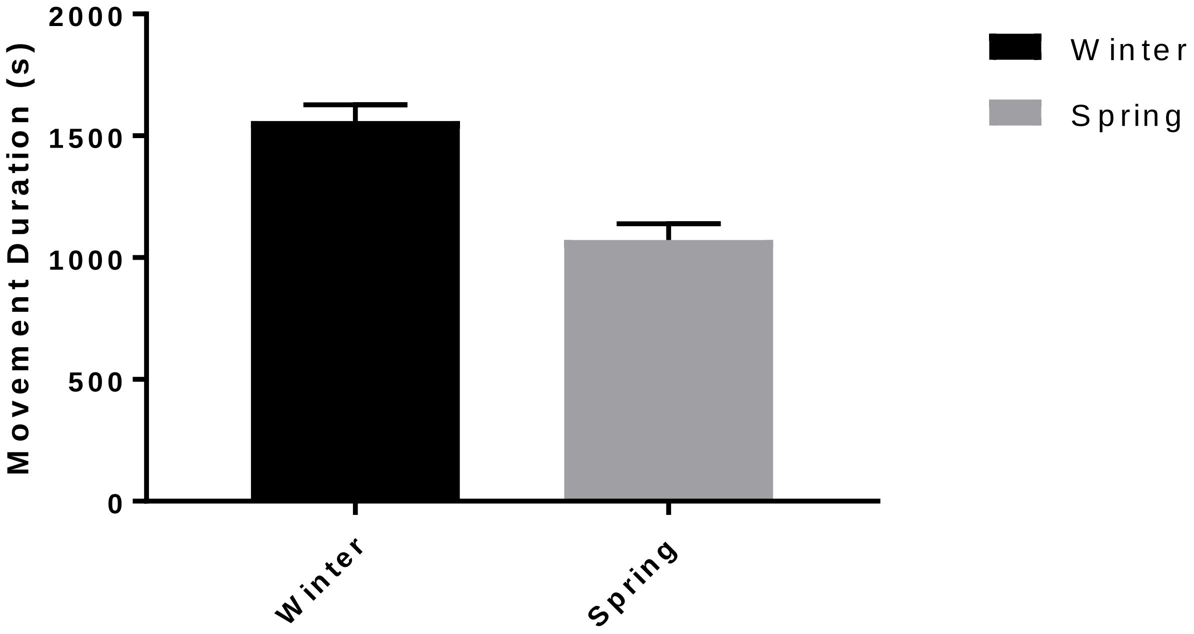

Figure 5.14 White-throated sparrows moved for longer durations in winter when exposed to 1 h acute weather cue manipulations than birds exposed to 1 h acute weather cue manipulations in spring. Error bars represent SEM.

Table 5.20 A table summarizing the different physiological (glucose, corticosterone) and behavioural (feeding duration, latency to feed, distance moved, movement duration) responses to acute weather manipulations of temperature alone (T), pressure alone (P), and temperature and barometric pressure combined (T & P) in winter, spring, and across seasons.

Measure	**Winter**	**Spring**	**Across Seasons**
Glucose	No differences.	Males had higher glucose levels than females.	No differences.
Corticosterone	Females had higher corticosterone levels than males. Higher corticosterone in birds exposed to both T & P than birds exposed to T (not P).	No differences.	No differences.
Feeding Duration	Limited food birds increased feeding duration compared to unlimited food birds.	Tan-striped birds increased feeding duration compared to white-striped birds.	Birds increased feeding duration in winter compared to spring.
Latency to Feed	No differences.	Birds exposed to T alone decreased latency to feed than birds exposed to P alone and T & P.	Birds decreased latency to feed in the winter.
Distance Moved	Birds exposed to both T & P moved more than birds exposed to T (not P). Birds exposed to P alone moved more than birds exposed to T. Limited food birds increased distance moved.	No differences.	Birds moved more in the winter.
Movement Duration	Limited food birds increased time moving.	Birds exposed to T alone increased time moving compared to birds exposed to T & P.	Birds moved for longer in the winter.

5.4 Discussion

The goal of this study was to understand how birds respond to 1 h acute changes in temperature alone, barometric pressure alone, and temperature and barometric pressure combined. I predicted that corticosterone levels, glucose levels and overall activity should increase when exposed to acute inclement weather cues, especially if birds were given limited food access. I also predicted a seasonal difference in these responses, as energetic demands differ throughout winter and spring. I found there were differential physiological and behavioural responses to acute weather manipulations within and across seasons. Overall, there were more responses to acute weather manipulations in winter than spring, but there were specific differences of measures observed between winter and spring.

5.4.1 Winter

Corticosterone levels were higher in birds exposed to acute manipulations of both temperature and pressure compared to birds that were exposed to acute decreases in temperature alone. Changes in temperature alone was not a strong enough cue to elicit a response through the HPA axis, but a combination of weather cues (temperature and pressure) did elicit a response via the secretion of glucocorticoids. A combination of changes in acute weather variables (temperature and pressure) also influenced the overall distance moved, as birds in this combination treatment moved more compared to temperature alone. A previous study found white-crowned sparrows exposed to a 1 h acute stressor of depleted food access also exhibited an increase in baseline corticosterone levels (Krause et al. 2017), suggesting that reduced food availability even over a short time frame can influence a rapid elevation in baseline corticosterone. However, food availability did not have an influence on corticosterone levels in this study, perhaps because the limited amount of food given to birds was still a reliable enough source to birds such that it was not perceived as a source of stress. When birds have access to food resources, and thus adequate fat and energy reserves, bunkering down in microclimates such as shrubs or among dense foliage is a common response during inclement weather (Carey & Dawson 1999). An increase in locomotor activity in birds exposed to acute changes in temperature and pressure may be attributed to attempting a facultative movement or migration to escape the impending storm or an escape strategy to take cover during the impending storm. Birds exposed to acute changes in pressure alone also moved more than birds exposed to temperature only, further supporting that barometric pressure, either alone or combined, may be more influential than temperature alone in the winter. Interestingly, corticosterone levels and distance moved were not detectably different in pressure alone, suggesting that a combination of cues is most influential in eliciting a response in the HPA axis. In a study by Metcalfe et al. (2013), white-throated sparrows similarly exposed to decreases in pressure alone moved more often than birds exposed to other treatments, however, these alternative treatments differed from the present study, including increases in pressure and decreases in temperature combined, and decreases in pressure and increases in temperature combined (Metcalfe et al. 2013). Barometric pressure may not be the most influential cue that a winter storm is approaching as previously suggested (Breuner and Hahn 2003, Metcalfe et al. 2013), but changes in multiple weather cues may be more reliable when detecting an approaching winter storm. However, there were differential responses of physiological and behavioural measures between acute treatments, suggesting that specific responses may be mediated by different cues.

Food amounts also influenced the behavioural responses to acute weather manipulations in winter. Birds given limited food amounts during 1 h acute manipulation increased their feeding duration, total distance moved, and overall movement duration compared to birds receiving unlimited diets, suggesting that regardless of acute treatment, birds with limited food resources were preparing for the approaching simulated storm. This suggests that each acute treatment was enough of a stressor to elicit behavioural responses, even if physiological responses were not detected.

5.4.2 Spring

Acute weather cue treatments (temperature alone, pressure alone, and temperature and pressure combined) had different effects on birds in the spring than the winter. In spring, birds exposed to decreases in temperature alone decreased their latency to approach food cups compared to acute treatments of pressure alone and temperature and pressure combined. Additionally, birds exposed to temperature alone increased time spent moving compared to birds undergoing acute treatments of both temperature and pressure. Increased movement has been previously documented as a food seeking behaviour in birds (Astheimer et al. 1992, Lynn et al. 2003, Fokidis et al. 2011), thus it makes sense that an increase in locomotor activity and faster approaches to food cups are both observed. In winter, the acute treatment of temperature and pressure combined elicited more responses, but it appears that temperature alone elicits stronger responses in the spring. These findings suggest that there may be differences in the perceived cues depending on the season. For example, decreases in temperature and pressure in winter may elicit a stronger response because both of these cues combined can be associated with inclement weather that can cover food resources for ground-feeding birds with snow. In the spring, decreases in barometric pressure and associated precipitation may not be perceived as stressful, as precipitation associated with these changes will not temporarily limit food resources. Thus, drastic changes in temperature alone may be enough to elicit behavioural changes in the spring.

Corticosterone levels were not influenced by experimental manipulations in the spring. These findings are consistent with a previous study of acute decreases of barometric pressure, wherein these changes did not influence corticosterone levels in sparrows (Breuner et al. 2013). Acute decreases in temperature and exposure to artificial rain in European starlings did not elicit a change in corticosterone levels (de Bruijn et al. 2017), however, a similarly designed study found increased levels of corticosterone in starlings exposed to the same acute temperature change (de Bruijn and Romero 2013). The former study suggests no detectable change in corticosterone reflect a downregulation in the stress response system (de Bruijn et al. 2017), however, body condition may also be a factor. The magnitude of the stress response, and thus, corticosterone secretion to a stressor is related to the body condition of the animal (Breuner and Hahn 2003). If birds' body condition was not negatively influenced by limited food availability, then activation of the HPA axis is therefore not likely. Thus, overall body condition may not have deteriorated between food groups in spring which did not cause secretion of glucocorticoids.

Glucose was not influenced by acute weather manipulations in winter or spring. It does not appear to be fueling increases in mobility as there were no detectable changes within or across seasons. Dependence on glycogen or glucose energy in cold stress in minimal compared to the reliance on fat in birds (Carey and Dawson 1999). In spring, males had higher glucose levels than females, but there were no other detectable sex differences in any measure. Further research is necessary to understand why this sex difference appeared in spring only, however I found no evidence of hyperglycemia in response to inclement weather cues.

5.4.3 Seasonal differences

There were no detectable physiological responses that differed across seasons. There were, however, differences in several behavioural responses between winter and spring. Birds moved a greater distance, spent more time in motion, increased their feeding duration, and approached food cups more quickly in the winter compared to spring. These findings suggest there may be increased demands in winter to cope with inclement conditions. As noted above, inclement weather in winter likely has a greater effect on food availability. Birds may be prepared to increase foraging in response to winter storms than spring storms, when there is a greater risk to foraging at the same time as higher energy demands for thermoregulation.

There were more physiological and behavioural responses to acute weather manipulations in winter than spring. Although birds were singing when the spring experiment began, I did not check whether birds were exhibiting migratory restlessness or had fully entered breeding condition. It is therefore not clear if the energetic costs of entering spring migratory condition and/or reproductive preparations were a factor. Birds in breeding condition may be more sensitive to storm exposure as resources and energy normally designated for reproduction would have to be reallocated to storm survival. Alternatively, since the perturbation resistance potential is smaller in the winter (i.e., there is less energy available to an individual; Wingfield et al. 2017), birds are likely preparing for the storm through preventative behavioural measures. Increased foraging is a classic behavioural response to approaching storms (Carey and Dawson 1999, Breuner and Hahn 2003) that I observed in the winter treatments only.

In summary, responses of white-throated sparrows to inclement weather cues varied between winter and spring, and differed between the cues presented (Table 5.20). In general, sparrows had a greater response to storm cues in winter than spring, in contrast to the null results observed in Chapter 4. In the outdoor aviary study (Chapter 4), birds would have been exposed to more gradual changes in, and a greater number of, inclement weather cues. Birds appeared able to cope with these changes with no observable hormonal or behavioural responses. In this experimental study effects were observed likely due to the more rapid changes in cues and reduced predictability of them. Thus, acute responses to inclement weather clearly depend on the season, and a variety of external and endogenous factors.

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Chapter 6

6 General Discussion

The last five years have been the warmest on record and had some of the most severe weather events ever recorded (NOAA 2018). This drastic rise in severe weather globally is alarming, and this predicted increase in severity and frequency of inclement weather conditions through global change draws concern for the adaptability and ultimate survival of many species. Despite the concern for many taxa, the focus within this thesis remains on birds. It is clear that birds are able to cope with and respond to inclement weather in many circumstances (Carey and Dawson 1999, Wingfield et al. 2017), but as environmental conditions become more severe, the adaptive coping responses of many species may be pushed to their limit. The degree of variation in adaptive traits within a population may influence whether some species are able to deal with weather extremes and others may exceed an abiotic tolerance threshold. More frequent extreme weather conditions will likely shift behavioral and physiological mechanisms to the limits of current phenotypic plasticity in birds. Widespread mortalities of landbirds in Australia have been documented by the thousands in recent years attributed solely to extreme heat waves (McKechnie et al. 2016), further highlighting the vulnerability of birds to extreme weather events.

Birds respond to a variety of weather cues, including temperature, barometric pressure, precipitation, wind, and cloud cover (Carey and Dawson 1999, Newton 2007), however, these highly correlated cues observed in field studies do not allow insight to what specific cue is driving the response. The focus of the study of responses of birds to inclement weather has been in observational field studies. Such observational studies are unable to draw conclusions about which specific weather variables, or the changes in such variables, are mainly responsible for physiological and behavioural responses. Within this thesis, I therefore examined the effects of recurrent inclement weather cues (Chapter 2), and also acute exposure to inclement weather cues (Chapter 5) in a controlled setting to investigate the responses of birds to individual weather cues. I also investigated how temperature alone can influence migratory behaviour (Chapter 3). To complement these experimental studies, I also examined the effects that natural storm systems had on birds in a controlled setting (Chapter 4). Using such experimental studies, my doctoral research investigated a general question: how do white-throated sparrows respond to repeated exposure of inclement weather cues? This thesis additionally investigated how the annual life-cycle and availability of food influences physiological and behavioural responses to inclement weather cues.

6.1 Exposure to simulated inclement weather cues

Chapter 2 was a follow-up study to a previously conducted experiment in which I increased the frequency of simulated winter storm exposure from the original study. The responses to more frequent simulated storm cues were quite different: birds exposed to inclement weather cues once per week increased their fat and lean mass. In contrast, birds exposed to inclement weather cues twice per week had lower corticosterone levels and fat mass, even though they spent more time feeding. Thus, increasing the frequency of storm exposure from once per week to twice per week may therefore exceed a physiological threshold for tolerance among white-throated sparrows, and physiological and behavioural responses can differ based on the frequency of exposure to inclement weather conditions.

Considering that birds modify responses when exposed to recurrent, long-term environmental perturbations, I also wanted to characterize the responses to inclement weather cues presented in acute settings (Chapter 5). This project also allowed insight to whether certain cues alone or combined cause different responses. I found that acute exposure to decreases in temperature alone, barometric pressure alone, and both temperature and barometric pressure combined elicited different responses, all of which were season specific. In the winter, acute exposure to decreases in temperature and pressure elicited higher corticosterone levels and a greater distance moved than if birds were exposed to decreases in just temperature. In the spring, birds exposed to decreases in temperature alone elicited greater behavioural responses than birds exposed to decreases in both temperature and pressure. These results suggest that birds may have a stronger response to certain weather cues depending on the season. Thus, acute responses to inclement weather appear to depend on the season, and a variety of external and endogenous factors.

6.1.1 Seasonal effects

Within this thesis, responses of white-throated sparrows to acute inclement weather cues varied between winter and spring, as noted above. In general, birds elicited more responses to storm cues in winter than spring. Flexible responses of the stress response requires an individual to modulate their resistance of acute stress, shift their actual response to stress for more flexibility, and quickly respond and recover from the environmental perturbation once it has passed (Wingfield 2013b). At certain times of the year when energetic demands may be less (i.e., summer months), the acute stress response may differ compared to times of the year when energetic demands are greater (i.e., winter months), as individuals become more resistant (Wingfield 2013b). Modulation of the response to acute stress can include processes whereby individuals become more resistant to labile perturbation factors at certain times of the year when the adaptive value of the emergency life-history stage may be less. That was likely exhibited in Chapter 5, as I observed these strong seasonal effects. Based on this, if Chapter 2 was repeated during the spring, I predict that there would be less intense effects in the spring than observed in the winter.

In contrast, for migratory restlessness there were stronger responses to temperature treatments in the spring than the autumn (Chapter 3), however, this may have been a result of the timing of birds entering captivity masking effects normally observed in autumn. Interestingly, however, manipulating acute exposure to temperature alone in spring (Chapter 5) influenced the latency to feed and movement duration of birds. There may be a relationship of changing temperature variables in spring that influence the behaviour of white-throated sparrows, since Chapter 3 also observed detectable differences based on changes in temperature alone, whereas decreases in both temperature and pressure in the winter may indicate more severe conditions may occur, in the form of snow covering food resources.

Previous findings suggest that a change in barometric pressure is the most influential and reliable cue that indicates the presence of a storm (Ahrens 2012; Metcalfe et al. 2013), allowing the changes observed in a laboratory to accurately represent responses that would also occur in the wild. Chapters 2 and 5 further confirm that birds can use changes in temperature and barometric pressure as reliable cues that inclement weather is approaching, but the specific weather cue causing these responses may be season- and sex-specific, and additionally differ depending on food availability.

6.1.2 Food availability effects

Birds are well adjusted to respond to and cope with inclement weather when resources are available and when they are not in energetically costly periods, such as moult (Romero et al. 2000). Additionally, the response of birds to inclement weather fluctuates depending on an individual's allostatic load (Wingfield 2013b). Birds within my thesis studies likely did not enter allostatic overload, as the amount of resources available to them never caused a negative energy balance (Wingfield et al. 2011). There were minor detectable differences in physiological or behavioural measures between food groups throughout the entire thesis. Food availability only influenced behavioural responses of birds experiencing acute weather cue exposure in the winter, but not the spring (Chapter 5). However, food treatment did not influence behavioural or physiological measures in birds chronically exposed to inclement weather cues (Chapter 2), birds exposed to natural outdoor conditions (Chapter 4), or birds exposed to different temperature treatments in autumn migratory condition (Chapter 3). Within Chapter 3, food treatment did have a sex effect, wherein females receiving unlimited food availability exhibited less migratory restlessness behaviour than females receiving limited food in the spring, but no overall main effects.

A limited food amount of 8 g per day likely did not induce nutritional or energetic deficiencies in birds in any of these projects, suggesting that this limited amount was not restricted enough to negatively influence body condition or energy reserves in individuals. Exposure to inclement weather cues had a stronger effect than food group throughout Chapters 2-5. Food availability was still a reliable source of food for birds, which may have contributed to limited detectable responses based on limited resource availability. Future projects identifying differences in responses should choose more drastic limited amounts, or food-restricting birds altogether.

6.2 Exposure to naturally occurring weather systems

Although there was a stronger response of acute exposure in the winter, this was not observed with birds in outdoor aviaries exposed to natural outdoor settings. In Chapter 4, birds were exposed to more gradual changes in inclement weather cues compared to any other study. Birds were also exposed to more changes in weather conditions, especially considering natural diurnal temperature variation. However, birds appeared able to cope with these changes with no observable hormonal or behavioural responses.

Persistently poor weather conditions are likely required to initiate a stress response (Romero et al. 2000). During this experimental time frame, there were no extreme weather events that would have challenged the response of these songbirds. The inclement conditions that were experienced were well within the ability of birds to cope physiologically. Thus, not detecting any physiological responses highlights the ability of birds to appropriately cope and limit immediate physiological responses when environmental conditions remain predictable.

6.3 Future directions

Although weather within a region may present itself as extreme to humans, birds residing within these regions are often highly adapted to live in such environments. However, these adaptive responses can be pushed beyond their limits when persistent unpredictable environmental perturbations tax an individual. A higher allostatic load and the potential to enter allostatic overload remains a concern as extreme weather continues to persist (Wingfield and Ramenofsky 2011a). Changing weather patterns as a result of global climate change can vastly impact birds through both direct and indirect pathways (Romero et al. 2000, Walther et al. 2002, Parmesan 2006). Shifting climate norms are affecting physiological and behavioral mechanisms that birds use to cope with environmental perturbations, but the acute experimental conditions presented within this thesis were not extreme enough to induce such a state. I did, however, document a potential physiological threshold by increasing inclement weather exposure to twice per week, indicating that the increased frequency of predicted extreme weather events will negatively influence responses of birds. Depending on the current life history stage, sex, body condition, and/or available resources, the level of influence on these responses can differ.

Integrating controlled laboratory studies with natural observational studies will aid in further investigation into the responses of birds to inclement weather at different stages of the annual life cycle. For example, telemetry and the use of radio-tags or other tracking devices is an advancing technology that can aid this understanding. Telemetry towers, such as Motus Wildlife Tracking System (see Müller et al. 2016) can provide information on animal movement and link this data to intrinsic and extrinsic conditions, including the presence of unfavourable weather conditions. Following the precise movement of individuals and using local weather data specific to the animal's location will help provide insight into how birds respond to different weather conditions. For example, a low pressure system without precipitation may cause an animal to reside within sheltered microclimates, but a low pressure system accompanied with significant precipitation may induce facultative movement or migration until the inclement conditions have passed.

6.4 Concluding remarks

While observational studies are important to document broad-scale responses of wildlife to shifting weather patterns, experimental studies that can simulate severe future weather conditions are now becoming more important. Future work must continue to investigate the effects of global change on different species, across different life-cycles, and under different habitat qualities. Although these relationships may seem dire, presenting these findings may facilitate implementing conservation strategies under drastic climate change with unknown future political climates.

Many gaps still currently exist in the literature demonstrating direct links between biological responses and climatological variables due to the complexity of conducting field studies on this topic. My doctoral research fills gaps in the current literature assessing the responses of birds to inclement weather in a controlled setting, but yet additionally provides more evidence that the responses of birds depends on a number of factors. Controlling weather cues allows us to determine which specific cues are eliciting a response. Observational and laboratory studies will be key to bridge the gap of uncertainties in the predicted climate scenario. Although direct links concluding the relationship between climate shifts and biological responses may not be published in the literature, many studies still support and provide evidence that birds are responding to changes in weather patterns (Breuner and Hahn 2003, Breuner et al. 2013, Metcalfe et al. 2013). Understanding these links and interactions will be critical for species survival and conservation in the future of global change, which is what this thesis also aims to participate in.

Combined, these projects provide further evidence in the complexity of responses of birds to inclement weather. These responses are dependent upon a variety of factors, including food availability, duration of exposure, season and, in some cases, sex. Thus, it is difficult to draw a linear conclusion from these studies. This thesis reflects other multi-directional findings within the published literature. For example, corticosterone has been documented to increase, decrease, or not change in response to inclement weather cues (Dickens and Romero 2013), highlighting that birds must use a variety of cues to respond to inclement weather, and that multiple other factors including season, sex and food availability can influence this response. Thus, further research is needed to understand how external and endogenous factors interact to modify birds' responses to inclement weather.

6.5 References

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Curriculum Vitae

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Education:

2015 – 2019	Doctor of Philosophy, Biology: Ecology and Evolution with Specialization in Environment and Sustainability University of Western Ontario, London, ON
2013 – 2015	Master of Science, Biology: Ecology and Evolution University of Western Ontario, London, ON
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Course Instructor Teaching Appointments:

Winter 2019	Sessional Co-Instructor: Psychology 3226B – Hormones and Behaviour
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Conference Presentations:

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June 2017	**Boyer, A.** & MacDougall-Shackleton, S.A. "Comparing effects of recurrent inclement winter weather cues on white-throated sparrows". Oral Presentation. Animal Behavior Society Conference, Toronto, ON
May 2016	**Boyer, A.** & MacDougall-Shackleton, S.A. "Effects of recurrent inclement winter weather cues on white-throated sparrows". Oral Presentation. Canadian Society of Zoologists Conference, London, ON

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May 2015	**Boyer, A.** & MacDougall-Shackleton, S.A. “Effects of recurrent inclement weather cues of white-throated sparrows (*Zonotrichia albicollis*)”. Oral Presentation. Ontario Ecology, Ethology, and Evolution Colloquium, York University, Toronto, ON
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Oct 2014	**Boyer, A.** & MacDougall-Shackleton, S.A. “How is climate change impacting avian species?”. Oral Presentation. Rotman Institute of Philosophy Annual Conference on Climate Change: Knowledge and Models in Climate Science, University of Western Ontario, London, ON
Oct 2014	**Boyer, A.** & MacDougall-Shackleton, S.A. “Effects of recurrent inclement weather on a songbird species”. Poster Presentation. Latornell Conservation Symposium, Alliston, ON
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Peer-Reviewed Publications:

May 2019	Hernandez, A., Babcock, S., **Boyer, A.** (2019) “She’s too young to be here”: Perceptions of a young female university professor. Case Study. Teaching Innovation Projects Journal. [submitted, in review]
Apr 2017	Moser-Purdy, C., MacDougall-Shackleton, S.A., Bonier, F., Graham, B., **Boyer, A.,** Mennill, D.J. (2017) Male song sparrows have elevated testosterone in response to neighbors versus strangers. Hormones and Behavior. 93: 47-52

General Publications:

Nov 2018	Is Your Cat Safe Outdoors? Cat and Bird Interaction Brochure (2018) City of London, Environmental and Ecological Planning Advisory Committee
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Academic Awards & Scholarships:

Apr 2019	AER Graduate Student Scholarship in Environment & Sustainability, Private Donor through University of Western Ontario
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Leadership and Outreach:

Mar 2019	BirdSafe for UWO Booth Attendant, EnviroCon Sustainability Fair, London, ON
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2016 – 2019	Great Canadian Shoreline Cleanup Team, London, ON
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Organizing Committees:

2015 – 2019	EnviroCon – Centre for Environment & Sustainability Student Organizer University of Western Ontario
2017 – 2018	Ontario Ecology, Ethology and Evolution Colloquium (OE3C) Co-Chair 2018
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Associations & Affiliations:

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Internship Programs:

2010 – 2012	WDIV Detroit – Meteorology Department: Student Intern NBC News Corporation, Detroit, MI
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