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Effects of Recurrent Inclement Winter Weather Cues on White-Throated Sparrows (Zonotrichia albicollis)

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Graduate Program in Biology
A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science

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(Thesis format: Monograph)

by

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Abstract

Climate change has been linked to an increasing frequency of inclement weather and winter storms. As such, it is important to understand the effects changing weather patterns have on avian species. I investigated the effects of recurrent inclement winter weather cues on glucocorticoid hormones and behaviour of a native Canadian songbird, white-throated sparrows (*Zonotrichia albicollis*). I used a hypobaric climatic wind tunnel to simulate storms by altering barometric pressure and temperature accordingly, and measured behavioural responses, body composition, and baseline corticosterone levels in birds exposed, or not exposed, to weekly simulated storms. After environmental manipulations, experimental birds had significantly higher fat and lean masses. Baseline corticosterone levels decreased over time in both groups, and time spent at food cups increased over time in both groups as well. Thus, although manipulations did not have a detectable effect on baseline corticosterone, it did affect body composition. This research provides novel experimental evidence that birds detect changing weather patterns and respond appropriately, and indicates that repeated exposure to inclement weather cues directly affects birds' energy reserves.

Keywords

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

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1 Literature Review and Introduction

All plants and animals are subject to seasonal and short-term variations in abiotic conditions. Abiotic factors are the non-living components that impact ecosystems, such as temperature, precipitation, light and nutrient availability. All species have a specific tolerance range and limit to abiotic factors that dictates dispersal and colonization, geographic distribution, reproductive success, population dynamics, and overall survival (Pidwirny 2006). Species thrive in specific geographic locations due to the surrounding abiotic factors, however, species' abilities to tolerate such factors are now being compromised as a result of global change. While species have evolved adaptations to cope with inclement conditions, climate change may be pushing some species to their tolerance limit with respect to climatic abiotic factors, especially depending on the degree of variability of different adaptive traits that currently exist in the population. As climate change advances, abiotic factors such as temperature, precipitation, wind and storms are being impacted and increasing in severity and frequency (NOAA: NCDC 2015). Species must now adapt their tolerance limits in order to thrive in their current geographical ranges.

Changing weather patterns can affect most animals, making it an increasingly important topic to study with the onset of climate change altering many abiotic factors. The following literature review will revolve around avian species and their responses to inclement weather and changing weather patterns. I will discuss the environmental factors that change during inclement weather and seasonal shifts, the effects that inclement weather has on the physiology, morphology and behaviour of birds, and the

mechanisms that drive such changes. I will also discuss the cues used to detect oncoming inclement weather in birds.

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). During winter, 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, polar air mass, creating extremely cold temperatures. These systems cause changes in the air's moisture content (relative humidity, dew point), shifts in wind speed and direction, decreasing barometric pressure, and significant snowfall and resultant ice cover (Ahrens 2012).

Studies of the effects of inclement weather on wild animals are becoming more widespread as climate change occurs and inclement weather becomes more common. Weather and climate differ in respect to the time period of reference. Weather refers to the current outdoor conditions on a daily scale, and climate refers to the atmospheric conditions across a long period of time, usually 30 years. Climate change is typically characterized by fluctuating air and ocean temperatures, shifts in average precipitation totals and patterns, and more severe weather over an extended period of time (Environment Canada 2014). In Canada, increased air temperatures and shifts in precipitation patterns have already led to a higher frequency of extreme weather events than seen in previous years, including heat waves, heavy precipitation and flooding, a

sharp increase in thunderstorms and unstable air, and diminishing ice cover (EC 2014). Globally, climate change is affecting natural systems and animal populations through changes in global temperatures and annual precipitation levels (Easterling *et al.* 2000; Parmesan & Yohe 2003). Forty-one percent of 1598 species of plants and animals sampled have already been affected by an increase in average global temperature by just 0.6 °C (Parmesan & Yohe 2003). This number of affected species has increased since 2002, as a further increase of global temperatures rose to 0.99 °C above average in 2013 (NOAA: NCDC 2015). Since records began in 1880, 2014 was the warmest year ever recorded (NOAA: NCDC 2015), even though the central and eastern United States and Canada experienced record-breaking low temperatures throughout the past few winter seasons. Average global temperatures are expected to increase further in coming decades (IPCC 2014), 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 (Beniston & Stephenson 2004; Easterling *et al*. 2014; IPCC 2014), which may be a result of an impacted jet stream (Francis & Vavrus 2015). 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 supply us with accurate meteorological forecasts depending on their location (Saucier 2003). Jet stream patterns are now weakening due to a greater proportion of warming temperatures at lower 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 & Vavrus 2015).

Changes in global climate patterns, including increasing temperature, precipitation, and frequency of extreme weather events are having profound effects across several 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 high mortality incidences among species (Newton 2007), however, even if inclement weather does not directly cause mortality, it can act indirectly by negatively affecting the reproductive success of an entire population (Wingfield 1985a), food availability (Boyle, Norris & Guglielmo 2010), and/or suitability of habitats, leading to further population declines. The following section describes further the effects that climate change and inclement weather have on species, and focuses particularly on an unanswered fundamental question in ecology (Sutherland *et al.* 2013): in the face of rapid environmental change, what determines whether species adapt, shift their ranges, or go extinct? Although there is a plethora of data showing adaptations (Nussey *et al.* 2005; Bradshaw & Holzapfel 2006; Parmesan 2006), range shifts (Thomas & Lennon 1999; Zuckerberg *et al.* 2011; James & Abbott 2014), and extinctions (Easterling *et al.* 2000; Parmesan 2006; Freeman & Class Freeman 2014), there is limited research looking at the mechanisms underlying why or how an adaptation, shift, or extinction is occurring. There is an overwhelming number of interactions occurring at several levels of an ecosystem which lessen the ability to make accurate, scientific predictions.

The occurrence of inclement weather is natural and 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 & Abbott 2014), territorial defense (Carey & Dawson 1999), mate acquisition (Wingfield 1985a; b; Vitousek & Romero 2013), and survival (Romero, Reed & Wingfield 2000; Takagi 2001; Walther *et al.* 2002; Parmesan 2006). Thus, detecting and responding appropriately to inclement weather is important to overall fitness and survival for most animals. There are a plethora of cues that many animals can use to detect an impending storm, including cloud cover, barometric pressure, temperature, wind, infrasound, and precipitation (Carey & 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 winter storm, there is also 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. The most reliable cue used by vertebrates to detect an incoming storm is barometric pressure (Breuner *et al.* 2013; Metcalfe *et al.* 2013). Prior to an incoming storm, barometric pressure can decrease anywhere between 2-12 kPa over just 24 h (Ahrens 2012).

1.2 Impacts of inclement weather on birds

Poor weather conditions can have adverse effects on individual species and also 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 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 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 & Dawson 1999; Parmesan & Yohe 2003). These conditions can create life threatening conditions, and may continue to cause lasting problems that persist after the storm.

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. There are two main classifications of bird migratory strategy: 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). Obligate migration is innate and occurs each calendar year in the spring and winter (Newton 2012). Severe weather along obligate migratory paths can create obstacles for birds, especially those travelling over water with nowhere to stop and take shelter. 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). Billions of avian fatalities can be accounted for by

inclement weather along the migratory path (Newton 2007). 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. 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). Additionally, significant population 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 their fall migrations (Butler 2000), further supporting the idea that successful migrations are being negatively impacted by the increase in frequency and severity of storms. Although there is strong evidence supporting this, radar records of migrating birds shows a 50% decrease in the number of birds migrating even on clear days (Gill 2007). This decline of migrating species, even on clear days, is still likely due to an increase of inclement weather prior to the beginning of migration that is impacting the ability of birds to successfully migrate. Although severe weather conditions can negatively impact populations, certain weather conditions may actually create ideal conditions for some migrants. Strong winds, if travelling in the correct direction, may aid migrants by allowing them to travel further with less energy use. Soaring or flying along such favourable tail winds can increase the travelling speed and also reduce energy expenditure (Shamoun-Baranes & van Gasteren 2011), however, if winds become too

strong and tempestuous conditions persist, fatal accidents may occur. Storms are becoming more frequent and severe, lessening the likelihood of favourable conditions aiding migrants along their path.

1.2.2 Impacts on reproduction

Reproduction can be delayed or eliminated as a result of inclement weather prior to and/or during the breeding season. Reproductive hormone concentrations can be decreased or delayed, or total abandonment of the breeding territory may occur as a result of poor weather conditions. For example, male song sparrows (*Melospiza melodia*) in New York were found to experience a delay in testicular development and decreased levels of circulating testosterone after a particularly harsh winter season and severe early-spring storms, but no impact on corticosterone levels (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 "normal" weather conditions. Such changes did not impact corticosterone levels, indicating that although changes occurred, it was not necessarily considered "stressful" to male song sparrows (Wingfield 1985a). The same severe winter also impacted female song sparrows, however, the effects differed. Females also 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 only stressful to females. This indicates that depending on the sex, reproduction may be influenced differently as a result of inclement weather. 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 in addition to a delay of

increased circulating reproductive hormones (luteinizing hormone and testosterone; Wingfield, Moore, & Farner, 1983), further supporting that inclement weather can interrupt the reproductive cycle.

1.2.3 Impacts on rearing young

Inclement weather can pose several challenges when birds are trying to successfully raise nestlings. Nestling survival increases overall fitness and reproductive success of a breeding pair, thus inclement weather can directly reduce fitness. Snow cover can create obstacles for successfully 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 & Dawson, 1999). In the same study described above (section 1.2.2), song sparrows were additionally impacted after an early-summer storm by negatively impacting their ability to successfully feed young. A severe storm that depleted their resources was accompanied by a significant decline in body composition and an increase in corticosterone levels in males (Wingfield 1985a), which was the opposite of the effects observed after the severe winter storm. The same storm affected females differently, indicating that life cycles can be impacted differently between sexes due to inclement weather. In females, corticosterone levels were not impacted from the early-summer storm – the opposite effect of males (Wingfield 1985b). This difference was likely observed because males were the main provider of food at the time of the early-summer storm, as at this stage females feed themselves but not young. In addition to impacting sexes differently during the rearing stage, inclement weather can impact individuals differently depending on the time of year and reproductive state (Wingfield *et al.* 1983;

Romero *et al.* 2000; Romero 2002). In the pre-breeding season, inclement weather had no effect on glucocorticoid hormone (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). Bull-headed shrikes (*Lanius bucephalus*) showed a positive correlation between nestling deaths and total severe precipitation per day (Takagi 2001), indicating further that rearing young becomes more difficult under inclement conditions. Thus, once young are in the nest, inclement weather appears to induce a stress response and impair reproduction in many songbird species.

1.2.4 Impacts on extinctions

Species may become extinct if the rate of climate change is greater than that of adaptations occurring to cope with changing abiotic conditions. Extinctions are also occurring where there is an inability to respond to increasing temperatures via poleward or altitudinal range expansions, whether because of physical geographic barriers, insufficient habitat, or a lack of mobility among species (Parmesan 2006).The number of extinctions stemming from climate change has been increasing at an alarming rate over the past 100 years (Easterling *et al.* 2000). Polar and mountaintop species are being affected the most, as species have gone extinct due to shrinking ranges from climate change (Parmesan 2006). Species that are more resilient, or more able to successfully respond physiologically, behaviourally, or morphologically, to environmental perturbations are less likely to be affected by extirpation or extinction (Wingfield 2013). However, in some cases extinction may be unavoidable whether a species is resilient or not. For example, species that reside on mountaintops will only be able to undergo

altitudinal shifts to a certain extent before they reach the summit of the mountaintop and have nowhere else to go. The white-winged robin (*Penoethello sigillatus*), mountain gerygone (*Gerygone cinerea*), crested satinbird (*Cnemophilus macgregorii*), and crested berrypecker (*Paramythia montium*) have all shifted their mountaintop ranges to the highest altitudinal location possible in their home of New Guinea (Freeman & Class Freeman 2014). A further rise in average temperature of 1 °C will lead to the extinction of all four species, which is predicted to occur within the next 50 years (Taylor *et al.* 2014). By 2100, the extinction of these four tropical birds of New Guinea will be inevitable, in addition to another 10-15 bird species pushed to extinction atop the same New Guinea mountaintops as a direct result of climate change (Taylor *et al.* 2014). Extirpations are now occurring as a result of the El Niño Southern Oscillation (ENSO), which are expected to occur more often and with more severe effects in the years to come (NOAA: NCDC 2015). El Niño years give rise to changes in the Pacific Ocean temperatures, precipitation patterns, and ocean currents. In addition, ENSO also affects weather conditions globally at a smaller scale. Warmer waters from the western Pacific flow eastward toward Ecuador and Peru during ENSO years, displacing colder waters with much warmer water temperatures (Ahrens 2012). These conditions are creating cascading effects across the continent that affect several species. Warm waters off the coast of Ecuador and Peru create unsuitable conditions for anchovies – the primary food source of local seabirds. A decline in seabirds' primary food source is leading to decreased populations, and in some places, local seabird extinctions. Changes in water temperature and precipitation patterns in a particularly bad ENSO year resulted in the total extinction of all seabirds on Christmas Island in the Pacific (Gill 2007). It is

inevitable that inclement weather will occur, whether climate change is advancing or not, and will likely cause harm to many species. It is important to note, however, that extirpations and extinctions are occurring at a more rapid rate than any other time in recent history, and these numbers have been linked to the rise in global temperatures and extreme weather patterns (Parmesan & Yohe 2003).

1.2.5 Impacts on wildlife in general

In addition to having an impact on avian species, 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, Codella & Cowell 1987; Heupel, Simpfendorfer & Hueter 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 climactic conditions, i.e., decreasing barometric pressure, low temperature, and low relative humidity than compared to short-breeding species (Oseen & Wassersug 2002).

In addition to having an impact on terrestrial animals, inclement weather can also affect many marine animals, particularly those residing in shallow waters (Heupel *et al.* 2003; Crinall & 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 & 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.

1.3 Responses of birds to inclement weather

With global change contributing to higher frequencies of storms and inclement weather, avian species must cope with short-term changes, adapt to such changing environmental conditions in both the short- and long-term, or go extinct (Beniston & Stephenson, 2004; Newman *et al*., 2011). 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 among individual species 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 variability 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.

Surviving winter months for temperate bird species can become a challenge if temperatures drop too low or there is a severe shortage of food. It becomes critical for birds to make behavioural, physiological, and morphological adjustments when they experience severe winter weather, otherwise they may die. There are two main mechanisms by which species can respond to climate change or changing weather patterns: adaptive evolution and/or phenotypic plasticity. Adaptive evolution involves genetic changes that increase reproductive success and survival in a population and are passed onto future generations. Evolutionary adaptations are primarily occurring on the interior of species ranges to match those on the exterior or most northern limits (Parmesan 2006). Phenotypic plasticity involves the ability of a species to change their behaviour, morphology, and/or physiology in response to changing environmental conditions (Bradshaw & Holzapfel 2006). Determining whether changes in range and/or phenology are attributed to adaptive changes in genetic composition or to phenotypic plasticity can be difficult as complete genetic analyses are required for each study. This section will look at both mechanisms; however, as phenotypic plasticity is more commonly observed, it will receive more focus.

1.3.1 Genetic adaptations

Adaptive evolution as a direct result of climate change involves genetic changes via natural selection. When rapid changes in climate occurs, populations can experience

different selection pressures than previously. If the selection pressure is outside the norm of a species, species can persist via evolutionary adaptation, which requires genetic variation. Variation can already exist in the population, arrive from another population, or arise via mutation. Genetic adaptation may not always be possible if the environment has progressed negatively during a short period of time and the rate of evolution may not occur fast enough for a population to persist.

Adaptive evolution has been observed across many bird populations (Bradshaw & Holzapfel 2006) including great tits (*Parus major*). Due to warming temperatures, great tits' main food supply (caterpillars) were emerging earlier in the season than normal, resulting in a lack of food once nestlings hatched, and ultimately, contributing to the inability of adults to feed their young. As a result of differential lifetime reproductive success and variation among alleles, there has been a change in great tits' egg-laying date to a more foraging-rich time, at least in some populations (Nussey *et al.* 2005). A change in the frequencies of laying dates, which are assumed to be under genetic control, occurred as a result of differential reproductive success of birds with different laying dates. Also due to changing climactic conditions, resource use is rapidly evolving at expanding range margins (Parmesan 2006). Also as a result of differential lifetime reproductive success, blackcaps (*Sylvia atricapilla)* have shifted their range to warmer territories where breeding and nesting activities are greater. Blackcaps residing in cooler regions have evolved genetic differences compared to those birds who are living in warmer climate, including earlier gonadal development, earlier arrival to breeding grounds, and larger clutches that maximized their fitness (Bearhop *et al.* 2005).

1.3.2 Phenotypic plasticity

Phenotypic plasticity involves the alteration of behaviour, morphology, and/or physiology within an individual's lifetime to adjust to recent environmental changes. In the presence of more severe winter weather, birds must be able to appropriately respond to keep warm and dry for survival. Preparing for the cold winter season involves multiple complex processes in birds. There are several avian winter strategies for regulating thermogenesis to maintain good overall body condition and regulate internal temperatures. During winter, birds are able to increase their external cold resistance through acclimatizing (Carey & Dawson 1999). Acclimatized birds are able to maintain a stable internal temperature in cold conditions approximately 6-7 hours longer than compared to summer months (Carey *et al*. 1989). This means that wintering birds can withstand polar temperatures without needing to expend extra energy for thermoregulation. During this time, birds also increase their fat stores and lower their metabolic rates (Carey & Dawson 1999). Birds are also plastic in the sense that their endocrine systems are impacted differently depending on the time of year, availability of food, sex, and reproductive state (Wingfield 1985a; b).

1.3.2.1 Morphological adjustments

Morphological adaptations are an important type of phenotypic responses also used to regulate body temperature. The most important physical attribute for insulation are a full coat of down feathers. Down feathers, which are closest to the skin, are the main insulating feathers, however, exterior contour feathers do provide a level of insulation to birds as well (Gill 2007). Birds produce an oil from the preen gland which, when applied to their feathers via the beak, creates a waterproof coating that is resistant to precipitation.

By keeping the skin dry, birds are able to conserve additional energy from having to further regulate thermogenesis. Prior to each winter season, birds living in temperate/arctic climates enter a molting phase to grow a new batch of feathers to enhance performance and thermogenic capacity (Gill 2007). Molting is a period of time where birds replace older, tattered feathers with fresh, new feathers. This process takes place following breeding and again prior to migration. New feathers are advantageous for water repellency, thermoregulation, flight efficiency, and mate acquisition/preference. Molting is energetically taxing on birds, as they are shedding all their feathers and using most of their available protein and energy to regenerate a complete new set (Gill 2007). Mid-molt, when feathers have been shed but not yet regrown, insulation can become an issue if temperatures drop to abnormal levels or if species live in Arctic regions. Energy must be rerouted to heat production rather than feather regeneration, so molt must be timed accordingly (Romero *et al.* 2000). If this is not an option, molting may have to occur in stages, which takes a longer period of time and a higher expenditure of energy. The large amount of energy expenditure responsible for molting makes avoiding stressors throughout this process, when possible, exceedingly important (de Bruijn & Romero 2013). A study found that corticosterone, the primary glucocorticoid found in birds, increased during molt under cold conditions in three sampled Arctic bird species; Lapland longspurs (*Calcarius lapponicus*), snow buntings (*Plectrophenax nivalis*), and redpolls (*Carduelis flammea*). All three species had increased levels of corticosterone during molt due to frigid temperatures and the high amount of expended energy (Romero *et al.* 2000). Although the timing of molting in temperate birds is now shifting as winter

and spring seasons are shifting in time, it is still critical for birds to be able to undergo morphological adjustments at any time needed.

1.3.2.2 Physiological adjustments

Throughout both diurnal and seasonal cycles, birds can fluctuate their body mass depending on ambient conditions. Throughout the year, variation of weight occurs diurnally in birds. In fall and winter, acquired fat reserves diminish earlier and more quickly in the evening than compared to in the spring. This corresponds to photoperiod and temperature; as it gets darker and colder earlier, the need for energy increases (Lehikoinen 1987). Reserves and energy will continue to deplete until morning when foraging and activities can resume.

Birds residing in cold geographic regions during the winter are fatter than they are during summer or autumn. This seasonal variation of weight is referred to as ‘adaptive winter fattening’ (King 1972). The need for energy is highest during short-wintering days due to temperature and snowfall (Lehikoinen 1987). In most small winter passerines, the fat reserves created are only large enough to sustain them for up to two days of no food (Carey & Dawson 1999) which is why they are sometimes referred to as emergency fat reserves. Creating limited reserves only used in emergencies is likely a result of energy conservation. Minimum daily fat reserves are maintained throughout the entire winter season and subside slowly as spring and summer approach. An increased rate of foraging, and therefore additional fat and energy reserves, has several accompanying potential costs, including increased expenditure of energy to forage and search for food, increased risk of predation by increased exposure, and more difficulty with flight due to heavier masses (Carey & Dawson 1999). Another means of staying warm comes via shivering,

which is the primary strategy for regulating temperature in most birds (Marsh & Dawson 1989). When birds get cold, they tense their muscles and begin to shiver, just as mammals do. In birds, shivering occurs through the use of the flight muscles: pectoralis and supracoracoideus (Marsh & Dawson 1989). These muscles move back and forth and create frictional heat and increase oxygen consumption (Gill 2007). Other strategies birds employ to keep warm include huddling together, residing in microclimates that may include hiding under dense foliage or in cavities, increasing exposure to incoming solar radiation, or, in migrating birds, fleeing the area when possible (Carey & 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 be shifting their physiological adjustments to compensate for the severe winter weather seasons now occurring. Physiological 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 (Gill 2007). The accumulation of fat reserves, which are stored in adipose tissue, muscles, and the body cavity, are used throughout the migratory route so birds can continue flying without needing to stop and waste additional energy searching for food. Creating fat reserves for migratory paths can also become important if inclement weather is experienced along the route and birds are forced to undergo facultative migrations along obligate migratory paths.

1.3.2.3 Range shifts

Phenotypic plasticity is exhibited in the ability of some avian species to shift both in space (e.g., range) and in time (e.g., earlier migration). Such shifts are made in response to fluctuating environmental conditions and survival. Most migrating avian species that have been studied to date show advances in their breeding and migration patterns as a result of changing environmental conditions (Charmantier & Gienapp 2014). There is strong evidence showing northward range shifts of temperate species being directly related to rising temperatures (Thomas & Lennon 1999; Walther *et al.* 2002; Parmesan 2006; Smith *et al.* 2012; Taylor *et al.* 2014). Northward range shifts have been observed among several taxa including butterflies, mammals, amphibians, birds, and plants (Parmesan 2006). More than half of 1598 total species sampled in one study showed northward or altitudinal shifts in their range in the past 30 years (Parmesan & Yohe 2003). In Britain, the northward range of breeding bird species shifted an average 18.9 km over a 20 year period (Thomas & Lennon 1999), corresponding directly to the rate of increasing temperatures occurring in that region. Taylor *et al*. (2014) found shifts in the hybrid zone between black-capped chickadees (*Poecile atricapillus*) and Carolina chickadees (*Poecile carolinensis*). Between 2002-2012, this hybrid zone shifted north at a rate of 0.97 km/year, which directly corresponds to an increase in winter temperatures in the original hybrid zone. While several temperate-zone species are able to expand their range and shift northward, some tropical mountainous species are forced to shift their ranges to higher elevations. In New Guinea, the annual mean temperature has raised 1 °C over the last 50 years. During this time period, 87 bird species shifted their altitudinal ranges by an average of 113 m (Freeman & Class Freeman 2014). To a certain extent, temperate species are able to shift their ranges northward more easily than mountainous

tropical species, assuming these species are not already residing at the poles and appropriate habitat is available. As tropical species shift up mountains, there is less available habitat, and eventually the summit of the mountain is reached. When compared to temperate species, the response of tropical species to increased temperatures are stronger and more significant, indicating tropical species may be more profoundly affected by climate change (Freeman & Class Freeman 2014). This, however, does not reduce the importance of the shifts currently being observed in temperate species.

1.3.2.4 Phenology shifts

The timing of seasonal life history events, or phenology, is also shifting among species across a global scale (Parmesan & Yohe 2003). Changing environmental cues, such as temperature, precipitation and photoperiod are responsible for shifts in phenology. Spring warming is now occurring earlier and fall cooling is occurring later (Parmesan 2006). An earlier arrival of spring means birds arrive at their breeding grounds sooner than normal, singing begins earlier in the season, as well as egg-laying, nesting periods, and fledging (Walther *et al.* 2002). As of 2006, over 800 species had already advanced spring life history events, and/or shifted their range (Parmesan 2006), and this number has continued to rise within the last decade. The magnitude to which species are affected by earlier-occurring seasons correlates to the ability of the individual to adapt appropriately to changes in life history events (Parmesan 2006). Mexican jays (*Aphelocoma wollweberi*) are laying eggs 10 days earlier across a time span of 26 years. These data correspond again with increases in average temperatures in the egg-laying range (Brown, Li & Bhagabati 1999). Earlier seasons are also causing some species to advance the onset of migration and breeding by an average of 2.3 days per decade (Parmesan & Yohe 2003).

Crick *et al.* (1997) found mean egg-laying dates of 20 temperate bird species advanced by an average 8.8 days over 24 years. Thus, changes in weather as a result of global change have already caused several shifts in phenology to occur across many avian species.

1.3.2.5 Maladaptive responses

Species may also respond maladaptively to climate change. This means phenotypic plasticity can occur in response to one changing variable, for example declining temperature. Such an adaptation, however, could result in a negative outcome with respect to another variable, for example successful migration. In blackcaps, responses to earlier hatching dates are maladaptive under global warming conditions, as an earlier hatching date significantly prolonged the duration of molt and advanced autumn migration (Coppack *et al.* 2001). Earlier autumn migration in this species is leading to premature deaths, and the extended molting process is exhausting energy and nutritious reserves. Maladaptive adaptations support the idea that even though populations are present, there are indicators that such populations are stressed and may not persist indefinitely.

1.4 Inclement weather and stress

Drastic changes in environmental surroundings can be a source of stress to birds. Although definitions of stressors 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 & Ramenofsky 1997). However, extreme conditions may not necessarily act as stressors if they are predictable. Many species are able to prepare for extreme

conditions if there are cues that reliably predict such conditions. A single storm may act as an acute stressor to birds, however, 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.

Stressors typically involve conditions that are unpredictable in time and/or space (Wingfield & Ramenofsky 1997). For example, birds may prepare for extreme 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. Even a short-term change in air temperature of just 3 °C in European starlings (*Sturnus vulgaris*) was a significant enough change to act as a stressor and cause an increase in heart rate, corticosterone levels, and perch hopping behaviour (de Bruijn & Romero 2011).

1.4.1 HPA Axis

With seasonal changes and fluctuations in weather conditions, birds are often exposed to different stressors. When birds encounter a stressor, such as abnormal fluctuations in temperature or precipitation, or an increased abundance or severity of inclement weather conditions, both physiological and behavioural responses are activated. Varying hormone levels play a large role in the ability of species to modify behaviour and physiology in response to changes in climate, or environmental conditions. Hormones also play a large role in seasonal changes in birds, including molting, migration and breeding (Wingfield, O'Reilly & Astheimer 1995). Glucocorticoids are mainly responsible for the overall

condition or health of individuals. The primary glucocorticoid found in birds is corticosterone (Holmes & Phillips, 1976). Typically, glucocorticoid levels represent a scale or index of stress, in addition to a reliable measure of overall health as a result of changing environmental conditions. Exposure to stressors activate the avian stress response; a cascade of responses via the hypothalamic-pituitary-adrenal (HPA) axis (Rivier & Vale 1983). First, the stressor must be perceived and processed by the hippocampus, amygdala, and the hypothalamus. This recognition stimulates the paraventricular nucleus (PVN) of the hypothalamus to secrete corticotropin releasing hormone (CRH). CRH is detected by the anterior pituitary, and stimulates release of adrenocorticotropin releasing hormone (ACTH) which in turn stimulates the adrenal cortex to release corticosterone (Holmes & Phillips, 1976). The secretion of corticosterone stimulates two negative feedback loops to the anterior pituitary and the hypothalamus. The HPA axis can take just minutes to activate (Rivier & Vale 1983), depending on the severity of the stressor, and will retreat when the stressor is no longer present.

Elevated corticosterone has a variety of physiological and behavioural effects that allow the organism to cope with a stressor; generally resources are diverted from growth and maintenance to facilitate short-term survival. Corticosterone levels can rise within minutes of exposure to a stressor, such as unsuccessful foraging, defending a territory, the presence of intruders, fleeing from a predator, or inclement weather conditions (Rivier & Vale 1983; Romero *et al.* 2000). Corticosterone levels can fluctuate depending on the age and sex of the species, the severity of the stressor, and the time of year (Wingfield *et al.* 1983; Wingfield 1985a; b; Romero *et al.* 2000). 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). As noted above (section 1.4), even a short-term change of 3 °C activated the HPA axis in European starlings (*Sturnus vulgaris*). This slight change in temperature caused an increase in heart rate, corticosterone levels, and perch hopping behaviour (de Bruijn & Romero 2011). As higher frequencies of storms are causing increased baseline corticosterone levels, further studies must be conducted to determine whether higher baseline stress levels will also weaken immunity, cause organ failure, or lead to premature death, in addition to documenting changes in glucocorticoids over time.

1.5 Predicting inclement weather and the cues used

As extreme weather can pose several challenges to birds, it is important that birds are able to detect the onset of storms in order to properly prepare themselves. Birds can visually detect cloud cover and precipitation (Carey & Dawson 1999), however, once these cues are detected, the storm is likely already present in the area, allowing limited time, if any, to prepare. As discussed previously, a reliable cue that a winter storm is approaching is a steady decline in both temperature and barometric pressure. Birds can predict and respond to oncoming inclement weather by detecting changes in barometric pressure and temperature (Breuner *et al.* 2013; Metcalfe *et al.* 2013) and respond accordingly. The mechanism surrounding how birds can detect oncoming storms through declines in barometric pressure, however, still remains unknown. It is suggested that the paratympanic organ (PTO), a sensory organ in the middle ear, likely plays a role (Breuner

et al. 2013; Metcalfe *et al.* 2013). The PTO was discovered over 100 years ago in birds (Vitali 1911), but its function and origin are still largely unknown. 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. It has recently been suggested that birds may also have the ability to detect infrasound from storms (Streby *et al.* 2015), however, there is not strong enough support in the literature to support this.

Among birds, a main driver in responding to decreasing barometric pressure, and thus a storm, is the availability of food for survival (Breuner & Hahn 2003; Boyle *et al.* 2010). A study of white-ruffed manakins (*Corapipo altera*) showed that birds residing in higher elevations were more likely to migrate down the mountain when exposed to declining pressure, as the availability or accessibility of food is greater and more predictable at lower levels. 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). Also as a response to decreasing barometric pressure, captive sparrow species increased their overall feeding and decreased their feeding latency (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. 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.

1.6 New methods for an emerging field

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 species are responding at many different levels. Several studies have looked at the effects that natural storms have on many species (Wingfield 1985a; Romero *et al.* 2000; Heupel *et al.* 2003), however, there have been limited experiments among birds that have directly manipulated barometric pressure and temperature 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 among captive white-crowned sparrows to identify the effects it had on physiology and behaviour over a short-term period. Within these two subsets, they looked specifically at 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 steroid stress 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 (*Zonotrichia albicollis*) had similar findings (Metcalfe

et al. 2013). Experimentally decreasing barometric pressure led to a decrease in feeding latency, however, this experiment was also a short-term manipulation only lasting 2 weeks. Regardless, this study presents further evidence supporting the ability of birds to 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 (Lehikoinen 1987; Carey & Dawson, 1999) 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 previously, none have looked at 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, 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 important as climate change is advancing and the frequency and severity of storms is increasing (IPCC 2014; NOAA: NCDC 2015). Such studies will add to global change datasets and contribute to future conservation and management strategies. In order 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.

1.7 Objective, hypotheses, and predictions

Recent experimental work has shown that birds do respond to changes in barometric pressure, however, these birds have only been tested under one exposure of the condition. Under natural conditions, animals are subjected to repeated exposure of inclement events throughout the season, which is why I chose to subject birds to repeated manipulations to test how they responded to sequential events. The main objective of my thesis was to determine how birds respond to an increased frequency of simulated winter weather cues with respect to physiology and behaviour in a controlled setting. In particular, I looked at changes in body composition (overall mass, fat mass, lean mass) and baseline glucocorticoid (corticosterone) levels, and I measured overall movement and feeding duration during simulated storms compared with those birds that were not undergoing additional simulated storms. By simulating repeated exposure to inclement winter weather cues, it provides insight from a more realistic ecological perspective and is of importance for understanding how increases in inclement weather may affect species.

I hypothesized that an increased frequency of recurrent inclement weather cues should act as a cumulative chronic stressor for birds, resulting in physiological and behavioural stress responses. When birds perceive and process a stressor, the HPA axis is activated, which increases the production of corticosterone. Inclement weather can act as an acute stressor, but I predict that recurrent inclement weather cues over a long-term period would no longer act as just an acute stressor, but act as a chronic stressor on birds. As a

result, I predicted that birds exposed to additional inclement weather cues would exhibit increased levels of baseline corticosterone levels.

I also hypothesized that birds would respond to recurrent inclement weather cues by altering their overall body composition and increase their fat composition and overall body mass. When an impending storm is perceived, birds respond accordingly in an attempt to successfully survive throughout the duration of inclement weather. Inclement weather can create an unpredictable food supply, which emphasizes the importance of foraging prior to the onset of the storm (Carey & Dawson 1999). In winter, birds create additional fat reserves as an emergency response system. Storms can deplete food resources and create unpredictable foraging conditions, so by creating additional fat reserves, birds are able to ensure energy sources over the next few days.

Finally, I predicted that birds would increase their overall feeding duration as they were exposed to additional inclement winter weather cues. This prediction ties in with the previous prediction of creating additional fat stores. As birds sense declining barometric pressure and temperature, they should be spending more time feeding to obtain additional reserves.

2 Materials and Methods

2.1 Study species

White-throated sparrows are an excellent species with which to study responses to inclement weather cues in captivity, as they experience both winter and spring storms in their natural habitats and home ranges. White-throated sparrows spend their summers in the Canadian boreal woodlands, stretching from the west coast to the east coast (Sauer *et al*., 2014). They winter throughout the eastern United States, from southern Ontario to the Gulf of Mexico (Figure 1) (Falls & Kopachena, 2010; Sauer *et al*., 2014). As predicted by the general increased frequency of storms as a result of climate change, the wintering and spring range of this species is also undergoing a change in the weather patterns it experiences. For example, an abnormal winter storm occurred in Atlanta, Georgia during the 2014 winter season, which is an area with a highly concentrated population of white-throated sparrows. Over 2 inches of snow fell in a 24 h period, while the average annual snowfall is only 2.1 inches (NOAA 2015). In addition to commonly experiencing winter storms, white-throated sparrows also adapt particularly well to captive settings and are thus well suited for experimental studies (Falls & Kopachena, 2010).

a) b)

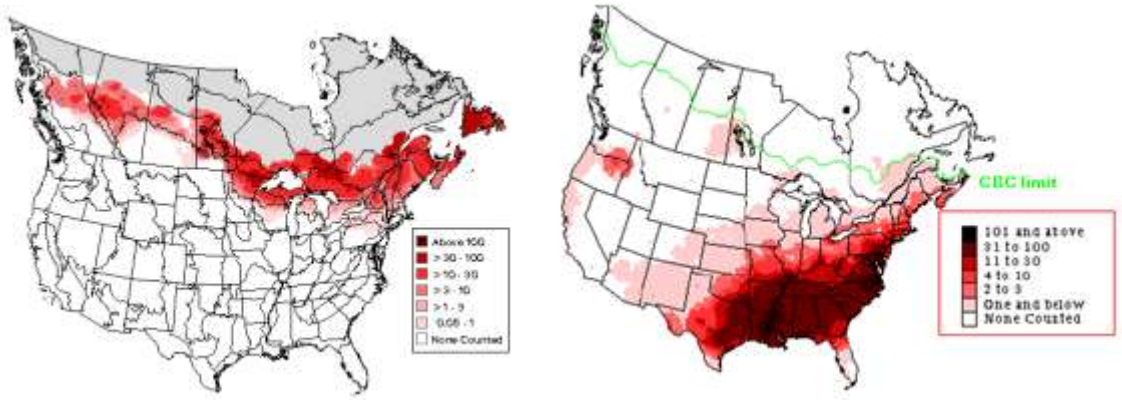

Figure 1: a) The summer breeding grounds of white-throated sparrows in North America from Breeding Bird Survey (BBS) data. b) The wintering grounds of white-throated sparrows in North America from Christmas Bird Count (CBC) data (Sauer *et al*., 2014).

I caught 24 white-throated sparrows during their fall migration using mist nets and seed-baited Potter traps at the experimental field site of Western University in October 2013. Both traps and nets were checked every 30 minutes between 7:30 a.m. and 10:00 a.m., as the highest amount of activity is observed just after dawn.

Birds were brought to the Advanced Facility for Avian Research at the University of Western Ontario and housed in individual cages (13" X 14.5" X 15") at 11 °C and provided an ad libitum source of a 50:50 mixture of ground Mazuri Small Bird Maintenance Diet (catalogue number 56A6, Brentwood, MO, U.S.A.) and premium budgie seed. Upon capture, birds were banded and weighed. Unfortunately, clear identification of morph or age of each bird was not possible as visual identification is difficult when birds are in winter plumage. White-throated sparrows have two different morphs within the same species: white-striped or tan-striped (Lowther, 1961). These morphs exhibit negative assortative mating, with over 90% of the time, white-striped individuals of both sexes mating with tan-striped individuals of both sexes (Falls & Kopachena, 2010). In addition to the median crown being a different colour, differences have also been observed in size and behaviour of each morph. White-striped birds are typically more aggressive than tan-striped birds, in addition to being about 2-3% larger (Falls & Kopachena, 2010). Tan-striped birds also exhibit more parental care compared to white-striped morphs (Tuttle 1990). Unfortunately, clear identification of white-striped and tan-striped morphs is difficult when birds are in basic (winter) plumage, and I could not identify morph with certainty. Similarly, identifying the age of birds as being hatch-year birds (birds born in 2013) or older was not certain based on plumage. Because I could not identify morph and age with certainty, I recorded each bird's mass and wing

length upon capture and assigned birds to treatment groups (see section 2.2 below) pseudorandomly to counterbalance by size and plumage characteristics. Sex was determined genetically using a small blood sample collected from each bird. Further protocol on genetic sexing can be found in section 2.2.5.

The birds' cages were kept on racks within an environmental chamber at 11 °C and under daylight settings matching that of the natural sunrise/sunset schedule outside. The photoperiod was adjusted once per week to reflect outdoor conditions so birds would enter wintering conditions. After being held in captivity for approximately 14 weeks, birds were randomly separated into experimental and control groups of 12 birds each. Each group was housed in a separate environmental chamber, with each bird still held in their own individual cage. Throughout the duration of the time spent in captivity, all birds were held at a constant 11 °C under ambient barometric pressure and kept under a short-winter photoperiod (~10L:14D) reflecting natural outdoor conditions. Across their wintering grounds in the eastern United States, 11 °C is a realistic average temperature during the wintering months for white-throated sparrows (NOAA, 2015), however, this temperature can fluctuate widely depending on storm systems passing through the region.

2.2 Experimental design

All birds were given the same amount of food each day throughout the duration of the experiment. Prior to the beginning of manipulations, the minimum required food for a 24 h period was measured. Birds ingested, on average, 6 g of premium finch seed and Mazuri over 24 hours, so a fixed allotment of 8 g was given to each bird per day. This was done so that birds had sufficient food to not be food restricted, but so that they would not perceive food availability to be unnaturally unlimited.

I assigned birds to two groups (experimental and control) counterbalanced based on wing length and plumage characteristics in an attempt to have age class, morph, and sex evenly distributed between groups.

2.2.1 Experimental Birds

Over a 9-week period beginning in January 2014 at the Advanced Facility for Avian Research, inclement winter weather cues were simulated once per week using a hypobaric climatic wind tunnel. The hypobaric climatic wind tunnel allows for manipulations of temperature, barometric pressure, humidity, and wind. The tunnel can control temperature values between -15 °C and 30 °C and barometric air pressure from ambient (average ~101 kPa) down to ~37 kPa (equivalent to ~7000 m in altitude). By combining specific values of temperature, barometric pressure, humidity, and wind we are able to recreate a typical low pressure system accompanied by a cold front, which usually represents the most severe winter storms (Ahrens, 2012).

Once per week for 9 weeks I subjected experimental birds to a simulated storm (a low pressure system with an associated cold front). All 12 experimental birds were transferred from their home environmental chamber into the wind tunnel plenum in their individual cages for a 24 h period. Prior to bringing birds in, the conditions in the tunnel were replicated to match those of their environmental chamber, i.e. 11 °C, ambient barometric pressure, and ~60 % humidity. Throughout the 24 hour period of being in the tunnel, birds would experience a decrease in temperature from 11 °C to 1 °C and a decrease in barometric pressure from ambient to 96.19 kPa at constant relative humidity. These manipulations were meant to simulate inclement winter weather passing through the region. The environmental changes occurred over a rapid yet realistic time frame that a

severe winter storm would occur on their wintering grounds (NOAA: NCDC 2015). On average, the air temperature declined at a rate of 1.9 °C per hour for approximately 6 hours until values declined from 11 °C to 1 °C. The temperature was held around 1 °C for approximately 14 hours, at which time temperature values increased at approximately 3 °C per hour until the holding temperature of 11 °C was reached. Barometric pressure declined at a continuous rate of approximately 1 kPa per hour, however, the duration of the decline depended on the ambient barometric pressure conditions in London, ON at that time. If London, ON was dominated by a high pressure system on the day of experiments, then barometric pressure would take longer to decline than on days which the study site was dominated already by a low pressure system. The same holds true for the total time it took to return to ambient barometric pressure – the dominating ambient pressure system determined how many hours it took to resume ambient conditions. After the 24 hour experimental period, conditions returned to 11 °C and ambient barometric pressure, birds were transferred back to their home environmental chambers and remained undisturbed for the remainder of the day. Figure 2 shows the environmental manipulations that occurred across the experimental timeframe between January and March 2014.

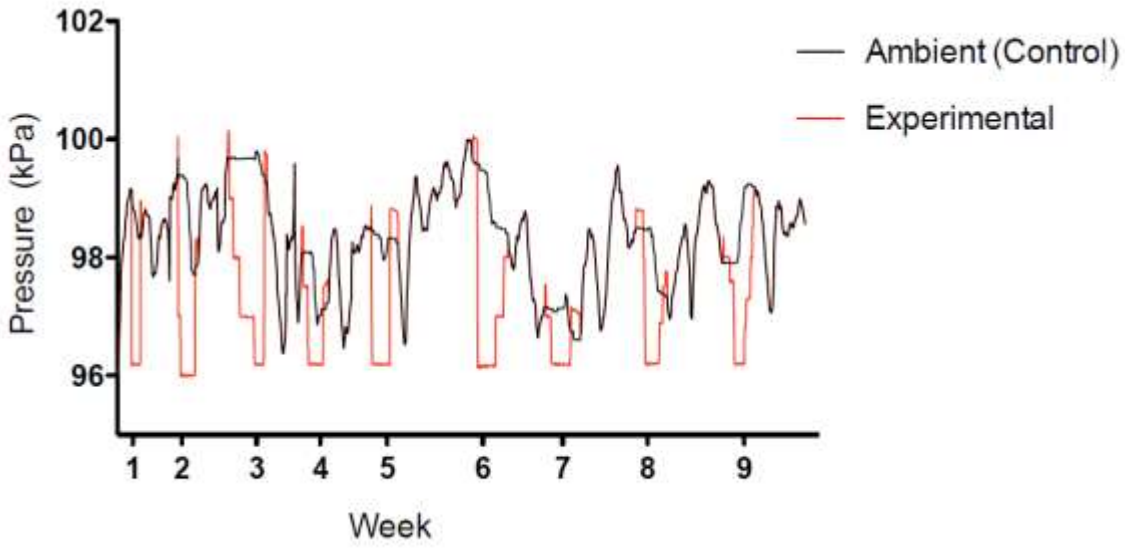

Figure 2: Barometric pressure experienced by experimental white-throated sparrows across 9 weeks. The black line indicates ambient barometric pressure conditions experienced by control birds throughout the experiment and experimental birds when they were not in the wind tunnel. The red line depicts the manipulated barometric pressure values experienced by experimental birds across time.

2.2.2 Control Birds

Control birds were held in identical environmental conditions throughout the duration of the experiment of 11 °C, ambient barometric pressure, ~60% humidity, and on short-wintering days matching natural outdoor photoperiods. To eliminate any differences in stress between the two groups due to changing physical surroundings, control birds were also transferred to the hypobaric climatic wind tunnel once per week for a 24 h period over the 10 week duration. Once in the tunnel, the birds were held at the control temperature of 11 °C and under ambient barometric pressure. After 24 h, birds were brought back to their environmental chambers and left alone for the remainder of the day.

2.2.3 Body Composition

The body composition of each bird was measured using Quantitative Magnetic Resonance (QMR) scans. QMR scans are a painless, noninvasive way to obtain fat mass, lean mass, and total body water in about 3 minutes. Every second week, each bird was weighed and immediately placed in a small plastic tube and inserted into the QMR instrument. The 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 (Mcguire & Guglielmo 2010). Calibration of the instrument occurred each day of scans using 5 and 94 g standards of canola oil to ensure accurate readings to the nearest 0.001 g (Gerson & Guglielmo 2011; Guglielmo *et al.* 2011). After the scan was completed approximately 150 seconds later, the bird would be released back into its individual cage.

2.2.4 Baseline corticosterone

To quantify chronic stress, I measured baseline corticosterone levels in blood samples taken from each bird every other week. Baseline corticosterone levels reflect the relative condition or health of an individual over an extended period of time and increase when vertebrate animals are exposed to cumulative stressors (e.g., recurrent unpredictable environmental perturbations) over a long-term period (Bonier *et al.* 2009). On weeks where blood samples were taken, they were collected 5-6 days (depending on the group) after birds returned to their home chambers to allow birds to recover from the potential acute stress of being transported to and from the wind tunnel. To decrease handling stress, birds that underwent QMR scans one week did not have blood samples taken the same week, and vice versa, as shown in Figure 3. Of the 12 birds in each group, 6 would undergo a QMR scan and the remaining 6 would get a blood sample taken, alternating each week. This ensured that each individual was only subject to one blood sample every other week to reduce the likelihood of baseline levels increasing as a result of continuous handling or numerous blood sample collections. Bi-weekly sampling was chosen to capture variation in corticosterone over the course of the experiment while minimizing handling stress.

Blood samples were obtained within 3 minutes of entering each environmental chamber to ensure that corticosterone was at baseline levels (Romero & Romero 2002). Blood was taken directly from the alar vein found along the wing. Once feathers were removed to reveal the vein, the alar vein was punctured with a 26-gauge needle and approximately 10 µL of blood was collected in heparinized microhematocrit tubes. Bleeding was stopped by applying pressure to the alar vein with a small cotton ball and birds were released back

into their cages once bleeding stopped. Blood samples were immediately put on ice and within 30 minutes of collection were spun down for approximately 10 minutes using an IEC Micro-MB centrifuge to separate red blood cells from plasma. Hematocrit percentage was recorded, and plasma was immediately removed from red blood cells. Plasma samples were put into a -30 °C freezer for storage until all samples were obtained over the 9 week experiment. Upon collection of all blood samples, radioimmunoassays (RIA) were run to obtain baseline corticosterone levels.

Corticosterone was quantified from obtained plasma using a ^{125}I radioimmunoassay that has been previously validated for songbirds (Newman *et al.* 2008) and has been used in white-throated sparrows (Metcalfe, unpublished). Radioimmunoassays measure hormone (antigen) levels in plasma by use of antibodies. Plasma was diluted with steroid diluents at a 1:50 ratio and samples were analyzed by adding 50 µL of diluted plasma to each tube. A known quantity of antigen was made radioactive with ^{125}I. The radioactive antigen was then mixed with a known antibody for that antigen and they bind together. My plasma samples were added and competed to bind with the same antibody. The higher concentration of the sample increases the binding affinity to the antibody and displaces the radioactive antigen. The intra-assay coefficient of variation was 8.6% for a low control and 3.3% for a high control.

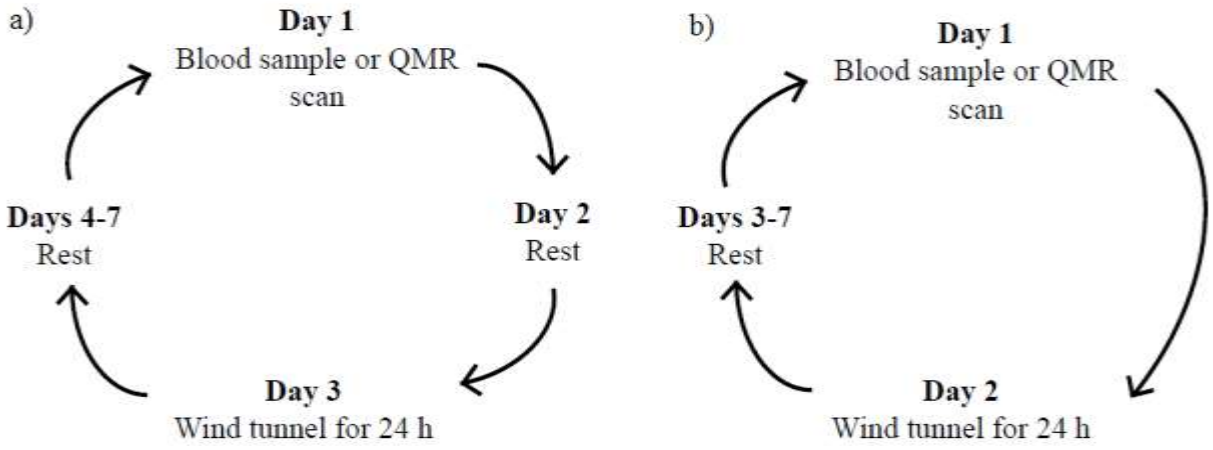

Figure 3: A timeline depicting 1 week of methodology in a) experimental and b) control groups. On day 1, half of each group had a blood sample drawn, while the remaining half underwent a Quantitative Magnetic Resonance (QMR) scan. The following week, the roles were switched so each bird did not undergo a blood sample and QMR in the same week. Each cycle was repeated 9 times for a total of 9 weeks.

2.2.5 DNA extraction and genetic sexing

Each bird was sexed genetically by using a small blood sample obtained at the same time that baseline corticosterone samples were collected from the alar vein. Once collected, a drop of blood was blotted onto a small square of filter paper and left to dry. DNA was extracted using an ammonium-based protocol to salt out proteins, modified from Laitinen *et al*. (1994). The DNA concentration was quantified using a NanoDrop 2000 Spectrophotometer (Thermo Scientific) and diluted with TE to make a stock usable in subsequent polymerase chain reactions (PCR).

The DNA sexing technique targets the chromobox-helicase-DNA-binding gene (CHD-W), the only W chromosome found in birds. The W sex chromosome occurs in females (ZW) but not in males (ZZ), therefore detection of the W chromosome will determine the sex of the individual. I used primers P2 and P8 to amplify portions of the CHD-W gene and CHD-Z gene (Griffiths *et al.* 1998). The gel electrophoresis showed either one band for males or two bands in females.

2.2.6 Behavioural analysis

Behaviour was recorded during the time birds were in the wind tunnel, but not during the other 6 days per week they were in their home environmental chambers. To quantify feeding behaviour, Noldus EthoVision XT cameras and software were installed in the wind tunnel plenum. A total of 4 cameras were set up to record the movement and behaviour of 8 of the 12 total birds per group. Cameras recorded the overall movement and the number of approaches made to the food cup during daylight hours (12PM to 5PM; 7AM to 12PM). Each of the 8 birds being analyzed were identified by the software by using the grey-scale technique. Grey-scaling tracks the darkest image in the frame and

is able to record the overall movement and document the number of approaches to the food cup. The software also records the duration of time that each bird spent in its food cup. I used the software to extract the following variables: distance moved over time and feeding duration. Behavioural analyses did not begin until week 5 of the experiment. Unfortunately, the installation of the Noldus software was untimely for the beginning of my experiment. Due to additional unforeseen technical difficulties in week 6, control birds were placed in the wind tunnel on day 2 and experimental birds entered on day 3 (opposite shifts occurred, see Figure 3). Behavioural analyses were not able to take place on week 6 for control birds but experimental birds were still recorded in week 6. I was still able to collect behavioural data for all experimental birds week 5 to 9, and for control every week omitting week 6. This is still enough data to observe changes in behaviour, although it would have been ideal to observe the entire 10 week duration.

2.2.7 Statistical analysis

Data were analyzed using IBM SPSS Version 22. The effects that recurrent inclement winter weather cues had on baseline corticosterone concentration, body composition, time at the food cup, and overall activity levels were all examined using linear mixed models. Time, group, and their interaction were entered as fixed effects for all models. Individual bird ID was entered as a random effect, although once determined that individual bird ID did not have a significant interaction, random effects were omitted from models. Age and morph were omitted from models as visual observation from feathers were not reliable outside of the breeding season. Sex was omitted as only 2 individuals were female in the entire sample size (n=24).

3 Results

White-throated sparrows were either exposed, or not exposed, to changes in environmental conditions, including temperature and barometric pressure. After environmental manipulations, experimental birds had a significantly higher fat mass, lean mass, and overall mass. Baseline corticosterone levels decreased in time across groups, and feeding duration increased over time among both groups as well.

3.1 Body composition

Over the 10 week experiment, body composition was significantly altered between control and experimental groups. Individuals exposed to repeated storms had a significant increase in overall body mass compared with control (Figure 4; $F_{1,80} = 8.911$, $p = 0.004$). The increase in overall body mass is attributed to an increase in fat mass (Figure 5; $F_{1,80} = 4.597$, $p = 0.035$) compared to control at the end of the treatment, with no main effect of time ($F_{7,80} = 1.231$, $p = 0.296$), and an increase in total lean mass (Figure 6; $F_{1,80} = 5.89$, $p = 0.017$), with no difference across time ($F_{7,80} = 1.164$, $p = 0.333$). Thus, simulating recurrent inclement winter weather cues caused a change in body composition, including increased fat mass, lean mass, and overall mass values.

3.2 Baseline corticosterone

There was a significant decline in baseline corticosterone concentrations across weeks, however, there was no significant difference between groups. Baseline corticosterone significantly declined over time ($F_{1,79.922} = 7.510$, $p = 0.008$), however, no differences in baseline levels were observed between groups (Figure 7; $F_{1,95.671} = 0.848$, $p = 0.360$).

3.3 Behavior

3.3.1 Time spent feeding

The time spent feeding significantly increased over time ($F_{4,63} = 8.455$, $p < 000$), however, was not affected by treatment ($F_{1,63} = 0.007$, $p = 0.934$). Thus, the total feeding duration increased across time (Figure 8).

3.3.2 Distance moved

The overall distance moved was not different between groups or across time (Figure 9). There were no significant effects of total distance moved with respect to time ($F_{4,64} = 1.237$, $p = 0.304$), group ($F_{1,64} = 0.002$, $p = 0.968$), or their interaction ($F_{2,64} = 0.184$, $p = 0.833$). Thus, total distance moved was not affected by changes in barometric pressure or temperature.

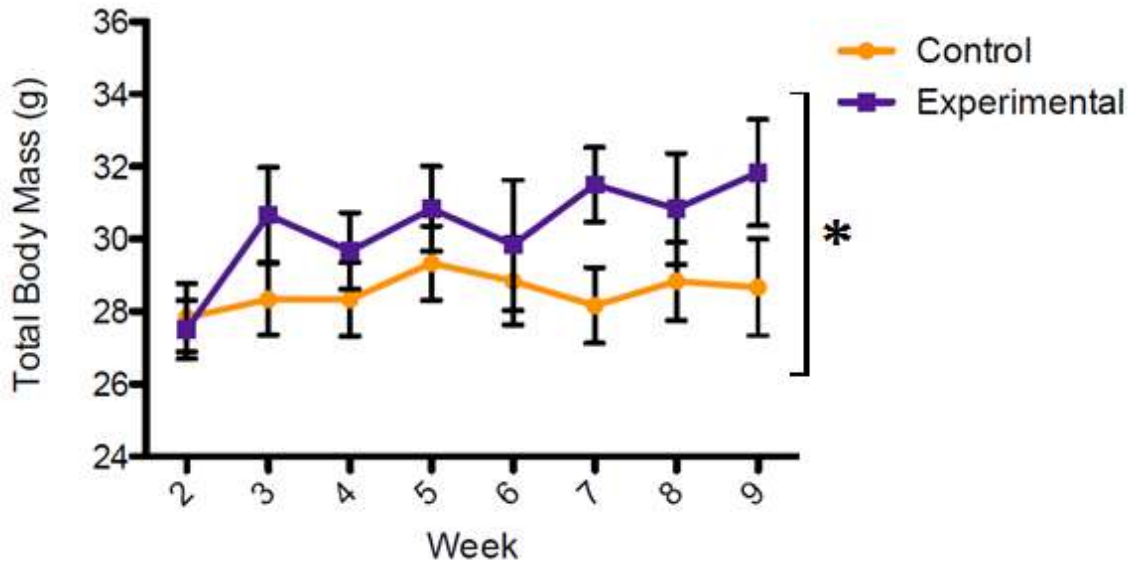

Figure 4: Mean overall body mass of white-throated sparrows exposed, or not exposed, to weekly simulated winter storms. Points indicate weekly means and error bars represent 1 SE of the mean. The asterisk indicates a significant difference between groups (p=0.004).

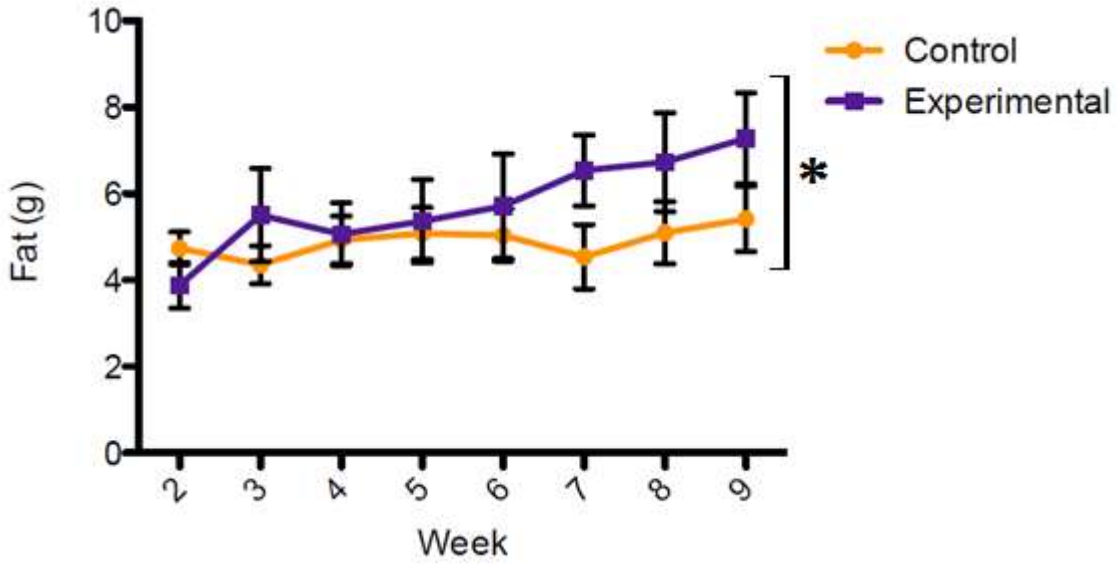

Figure 5: Mean fat mass of white-throated sparrows exposed, or not exposed, to weekly simulated winter storms. Points indicate weekly means and error bars represent 1 SE of the mean. The asterisk indicates a significant difference between groups (p=0.035).

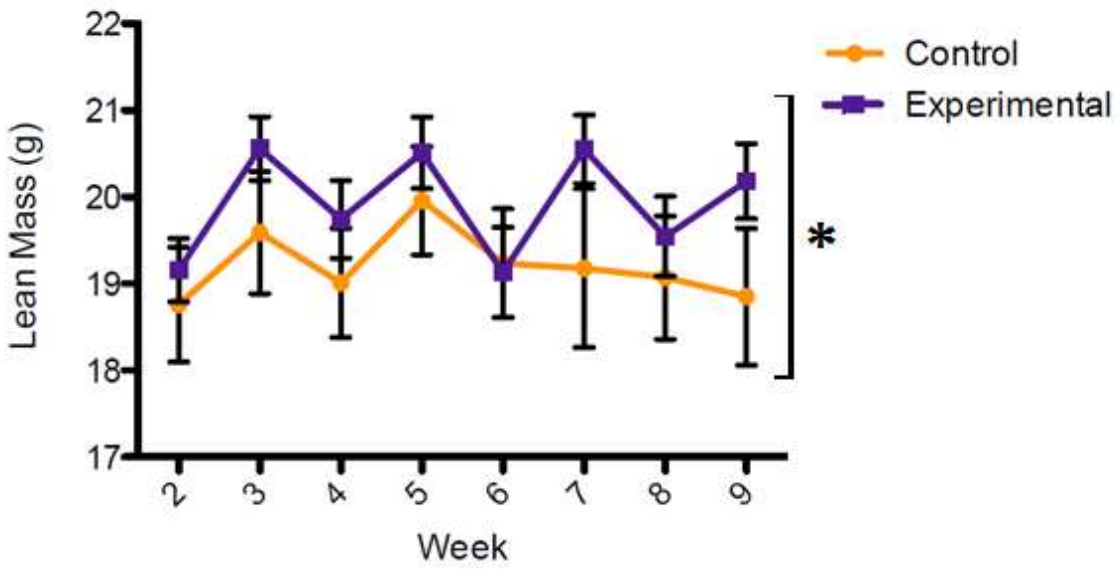

Figure 6: Mean lean mass of white-throated sparrows exposed, or not exposed, to weekly simulated winter storms. Points indicate weekly means and error bars represent 1 SE of the mean. The asterisk indicates a significant difference between groups (p=0.017).

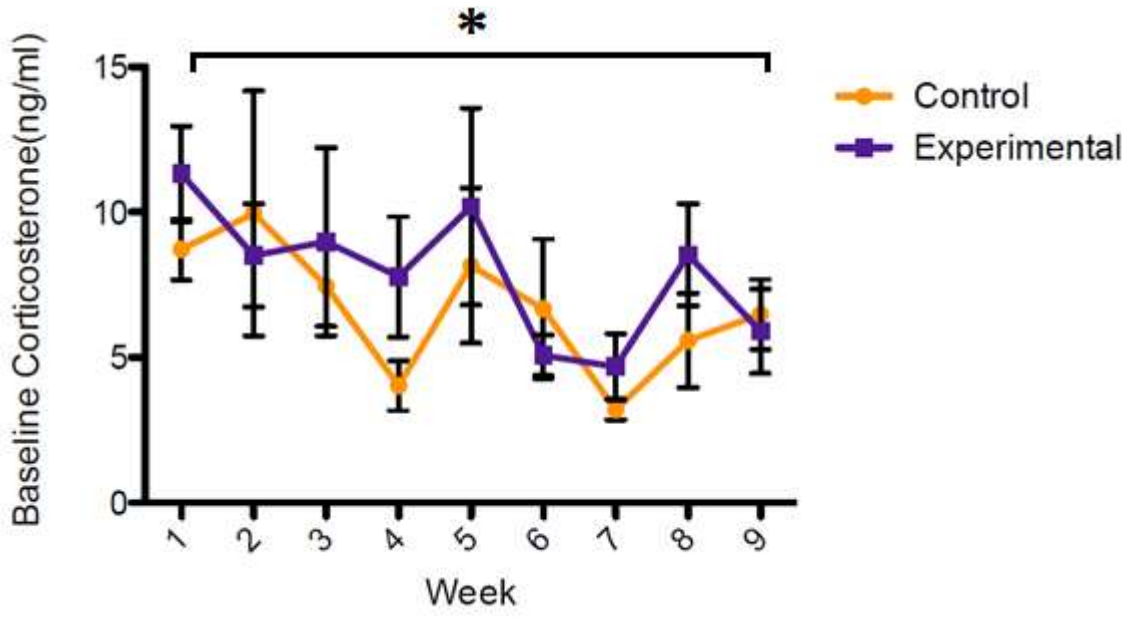

Figure 7: Baseline plasma corticosterone concentration measured in white-throated sparrows exposed, or not exposed, to weekly simulated winter storms. Points indicate weekly means and error bars represent 1 SE of the mean. The asterisk indicates a significant decrease in values across time (p=0.008).

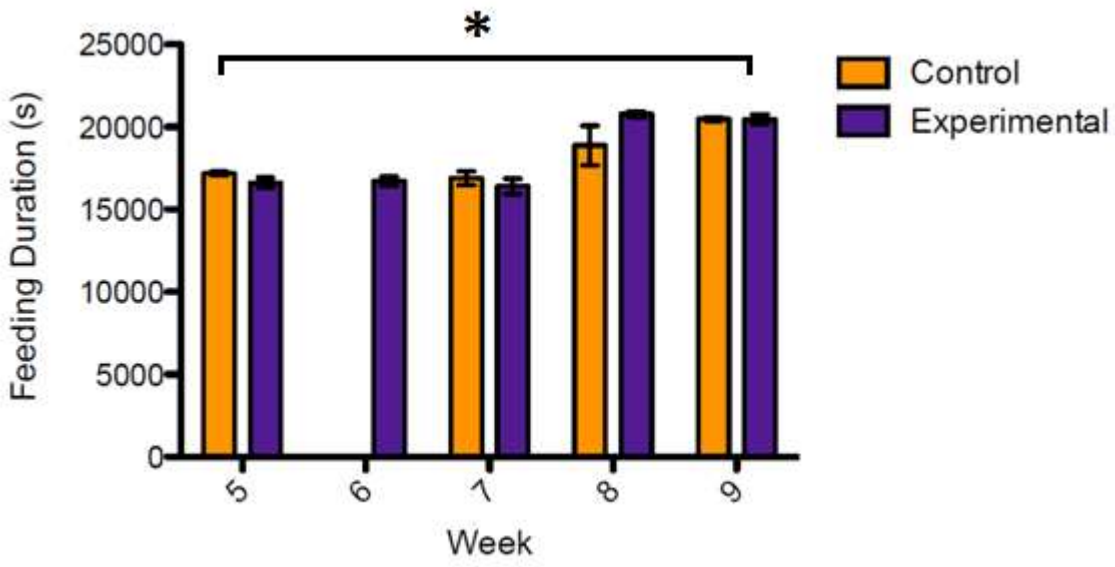

Figure 8: Time spent feeding was measured across time in white-throated sparrows exposed, or not exposed, to weekly simulated storm cues. Feeding time increased across time ($p<0.0001$). Bars indicate mean feeding duration and error bars represent 1 SE of the mean.

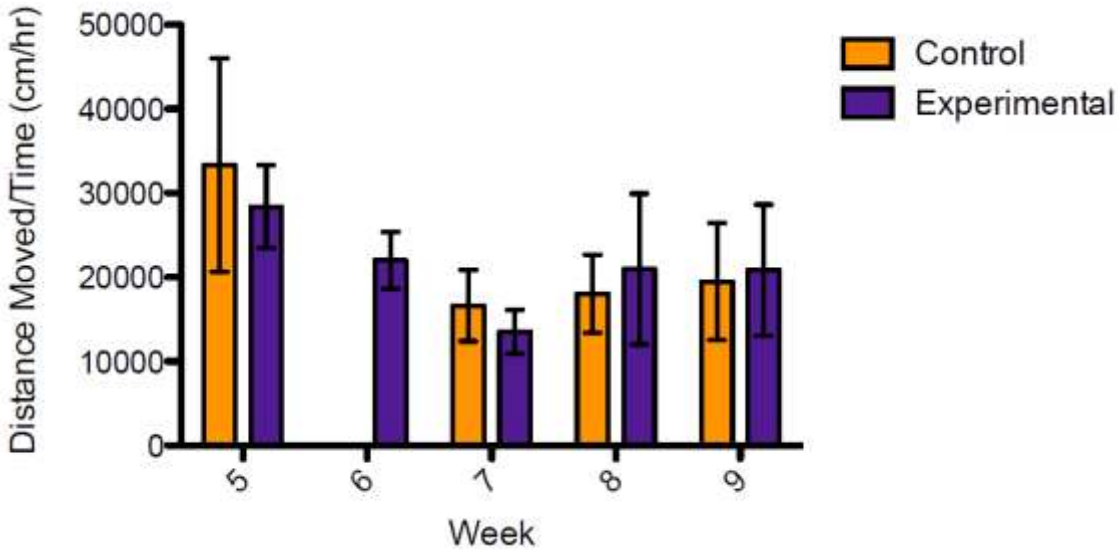

Figure 9: Overall distance moved was measured across time in white-throated sparrows exposed, or not exposed, to weekly simulated storm cues. There were no significant relationships with respect to overall distance moved. Bars indicate mean distance moved and error bars represent 1 SE of the mean.

4 Discussion

Over the 10 week experimental period, baseline corticosterone levels, body composition, and feeding behaviour were all assessed in white-throated sparrows in response to simulated inclement winter weather cues. Birds that were exposed to recurrent simulated winter weather cues did respond, however, not all predictions were met. Recurrent simulated winter weather cues caused an increase in overall mass, lean mass, and fat mass. However, baseline corticosterone levels, the time spent feeding and overall movement while in the wind tunnel were not significantly impacted between groups. The cues associated with one additional storm system per week were enough to elicit a physiological change in body composition, however, these cues did not appear to act cumulatively as a chronic stressor to induce a change in baseline corticosterone levels or behaviour. Thus, this study provides further evidence that birds can sense changes in barometric pressure and temperature as reliable cues of inclement weather and respond accordingly.

One variable that could not be controlled for was ambient weather experienced in London, ON. It would have been ideal for birds not to detect any ambient changes in barometric pressure, however, that could not be achieved. Additionally, changes in ambient conditions could not be controlled for as all individuals were experiencing changes equally, making it impossible to distinguish between changes over time or changes as a result of changing barometric conditions. It was assumed, however, that since birds of both groups were equally experiencing changes in ambient pressure that it should not have had an adverse effect on either group.

4.1 Body composition

Birds that experienced recurrent environmental manipulations had significantly altered body compositions compared to birds that did not undergo environmental changes. Experimental birds had increased fat mass, lean mass, and overall mass. These results provide further evidence that changes in environmental conditions, including barometric pressure and temperature, can impact energy reserves. These changes likely allow birds to respond to new weather conditions. In the winter, a low pressure cold front can bring precipitation in the form of snow through most of white-throated sparrows' wintering range. Since these birds are a 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. Creating fat stores is a common wintertime response to the onset of inclement winter weather to prepare against unpredictable future foraging (Carey & Dawson 1999). My results further validate the hypothesis that inclement winter weather cues will elicit an increase in fat mass, even by just one additional simulated storm per week. Interestingly, lean mass was also higher in experimental birds. The increase in lean mass observed by individuals experiencing winter storm cues could be explained by physiological changes from winter acclimatization. Increased thermogenic capacity can cause variation in the size of whole organ mass, or lean mass (Carey *et al*. 1989). In most birds, shivering is the primary means of regulating thermogenesis (Carey & 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 this function (Swanson 2001) which would result in an increase in lean mass content. Shivering is an energetically costly task, requiring an outlet of additional energy while in

the wind tunnel. The main energy substrate for shivering, and thermogenesis in general, comes from fatty acids (Carey & Dawson 1999), which was likely pulled from the increase in fat mass content also observed. The change in lean mass in my study was likely attributed to the decline in temperature that birds experienced, and not affected by decreases in barometric pressure, however, this remains untested. Overall, changes in body composition indicate that experimental birds sensed the decline in barometric pressure and temperature and underwent physiological changes that could aid in survival.

4.2 Baseline corticosterone

I predicted that an increased frequency of inclement winter weather cues would cumulatively act as a chronic stressor, as each individual simulated storm should have acted as an acute stress event. Since baseline glucocorticoid levels were not significantly different between groups, I did not find evidence that the environmental manipulations acted as a chronic stressor in this situation. It is possible that no significant difference between groups was observed due to the severe winter season already occurring at the site of experiments in London, ON. Experimental manipulations occurred during the 2013-2014 winter season which was dominated by the polar vortex and an altered path of the North American jet stream. Continental polar and continental Arctic air masses dominated southwestern Ontario throughout the winter season, causing unseasonably frigid temperatures and a higher number of severe weather events. Although the birds housed indoors would not experience outdoor cold temperatures, they may have responded to low pressure systems passing through London. Figure 2 shows the ambient conditions experienced at the study site. Birds were already exposed to a higher than average number of low pressure systems thus even my control birds may have had

elevated baseline corticosterone compared to birds that could have had consistently high barometric pressure.

On the other hand, it may be that birds adjust body composition without adjusting baseline corticosterone. Breuner *et al*. (2013) also experimentally altered barometric pressure to simulate storms and found similar results in white-crowned sparrows, a sister species to white-throated sparrows. Levels of corticosterone were not affected by acute changes in barometric pressure, indicating that a short term change in barometric pressure is not significant enough to act as a cumulative stressor. Similarly, a previous study in my lab on white-throated sparrows did not detect a change in baseline corticosterone following acute pressure manipulations (J. Metcalfe, unpublished honours thesis).

In the wild, changes in barometric pressure and temperature are a reliable indicator that a storm is approaching and food sources may soon become sparse or unpredictable. Changes in corticosterone concentration are often associated with the absence of a food source (Pravosudov *et al.* 2001; Boyle *et al.* 2010). In the winter, white-throated sparrows can be faced with snow covering the ground and obscuring their food sources. In my experiment birds were given a fixed amount of food sufficient to maintain body mass. Thus, it is possible that birds in the wild may elevate corticosterone in response to storm cues when they have limited food but that birds in captive studies may limit their stress response when plentiful food is visible. To test this idea a future study should simulate inclement weather cues over a shorter time span and give different amounts of food to each group of birds. It would not be ethical to completely eliminate a food source, but food restriction could occur for a short amount of time. By simulating storms over a

short-term period, one group of birds could be given an unlimited supply of food while other birds are food restricted.

Although baseline glucocorticoids were not significantly different between groups, baseline corticosterone did decrease across time. Glucocorticoid concentrations fluctuate depending on the time of the year. In most small passerines, baseline corticosterone concentrations are relatively low in the winter season and begin to increase at the onset of spring migration and the breeding season at the end of March into mid-May (Romero 2002). Throughout my experiment, birds were kept on natural daylength cycles. Manipulations began at the end of January and ran until mid-March, marking the beginning of spring migration. Birds were likely preparing for spring migration at this time, especially as some individuals began singing towards the end of the experiment. As such, it is surprising that a decline in baseline corticosterone was observed, as the beginning of the breeding season is usually marked with an increase in baseline corticosterone concentration.

These results suggest that one simulated storm per week was not a strong enough frequency to act as a chronic stressor given the severe winter season birds were experiencing in ambient conditions. The environmental manipulations may still have acted as acute stressors to increase circulating glucocorticoid levels while the birds were in the wind tunnel, but I would not have detected this as blood collection occurred 5-6 days following the manipulation. To test this, future studies may look at fecal corticosterone levels to determine if concentrations are changing during manipulations. Additional studies can increase the frequency of simulated inclement weather cues from once per week to two or three additional simulations per week and determine the

threshold of the number of storms required to act as a chronic stressor. Future studies could also lessen the frequency of storm cues to make them less predictable by only subjecting birds to inclement weather cues on alternating weeks, since predictability is often a reason why birds are less stressed (Romero 2002; Romero & Romero 2002).

4.3 Behaviour

4.3.1 Time spent feeding

Since inclement weather can negatively affect successful foraging, I expected that experimental birds would increase their overall feeding duration as barometric pressure and temperature were declining, however, this relationship was not observed. The amount of time birds spent at their food cups was analyzed across the entire duration of the 24 h spent in the wind tunnel, however, I focused on the first 5-6 h of birds entering the wind tunnel as the most important response of birds are predicted to occur as environmental changes are in progress. Constant environmental conditions (i.e. barometric pressure, temperature, humidity, wind) do not act as signals to birds to respond physiologically or behaviourally (Carey & Dawson 1999). For experimental birds, the average time it took barometric pressure to decline to 96.19 kPa and for temperature to drop from 11 °C to 1 °C was 5-6 h. During this time period I did not observe any differences in time at the food cup between groups, even though there was an increase in overall, fat, and lean mass content among birds. It is possible that there were differences in feeding behaviour during other times I did not observe the birds, i.e. the remaining 6 days of the week in their home chambers. A change in metabolism or energy expenditure may also have occurred to account for increased masses. Increasing barometric pressure and temperature, as observed in the final 5-6 hours spent in the wind tunnel, also did not elicit a change in

physiology in behaviour for birds, which was expected. In most cases, a high pressure warm front is dominated by calm, clear weather which does not pose as a threat to the survival or well-being of birds. Metcalfe *et al*. (2013) found that increasing barometric pressure increased the time it took birds to begin feeding, indicating that increasing barometric pressure did not act as a signal to prepare for the onset of poor weather. 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). This effect was not observed in my study, however, both studies mentioned previously were conducted over a much shorter time span. Abrupt changes in barometric pressure and temperature will likely elicit an immediate response, however, once changes in barometric pressure and temperature become consistent across time, birds may be able to respond and adapt better to such changes as environmental changes are becoming more predictable. A predictable stressor allows concentrations of baseline corticosterone to adjust and not elicit any behavioural changes, whereas unpredictable stressors cause sharp changes in baseline corticosterone which activates other physiological and behavioural pathways (Romero 2002).

Increased levels of corticosterone can lead to an increased rate of foraging (Breuner & Hahn 2003), however, since corticosterone levels were not affected by my environmental manipulations, it is perhaps not surprising that there was also no impact on feeding duration. Captive white-crowned sparrows showed little activity around their food cups when food was available ad libitum, but activity at the food cup increased once food was removed (Astheimer, Buttemer & Wingfield 1992). Since food was available to birds at all times, there may not have been a strong response to immediately forage once

environmental changes were detected. Despite the lack of difference in time spent at the food cups in my study, it is possible that birds may have been differentially feeding during these times. Visual observations throughout the duration of the experiment showed that every food cup of experimental birds were nearly, if not completely, empty after the 24 hours spend in the wind tunnel. When control birds finished their 24 hours in the wind tunnel, all food cups still had remaining seed in them. Since this was an experiment spanning over a 2 month period, feeding behaviour may have been altered in a way not observable on the video camera. If feeding behaviour was observed concurrently over the entire duration of the experiment, there may have been changes in the overall, long-term feeding duration. It is difficult to assume that feeding behaviour was not altered by limiting observations to 5 hours per week, even if this was the period that environmental manipulations were occurring. A change in feeding behaviour had to occur at some point during the experiment because I did observe an increase in overall, fat and lean masses between groups. Additional studies branching off from this one should weigh food cups before and after environmental manipulations take place to determine if birds were eating at a faster rate but spending the same amount of time at their food cups.

Although feeding duration was not significantly different between groups, overall mass, fat mass, and lean mass were significantly higher in those birds undergoing manipulations, indicating that winter fattening was still occurring. The higher frequency of storm cues occurring did affect how food was stored and metabolized after ingested, however, it did not affect the overall time birds spent feeding during the manipulations. As seen in Figure 8, it is important to note the significant increase in feeding duration on

weeks 7, 8, and 9 in both groups. This is likely a seasonal change, as week 7 marked the beginning of spring migration. Prior to the onset of migration, birds increase foraging rates and create additional energy stores to prepare for long, energetically taxing migrations.

4.3.2 Distance moved

Interestingly, birds did not increase their overall movement while in the wind tunnel. As mentioned previously, free access to food likely inhibited an increased response. Despite the fact that white-throated sparrows migrate, this ground feeding species still deal with snow in the winter months. 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 & Ramenofsky 1997). Access to food, although limited to a predetermined amount, was still a reliable factor across the duration of the experiment. Increased locomotor activity was likely inhibited due to the constant availability of food. Overall movement may not have been affected between groups because of the higher than average number of storms detected by control and experimental birds at the study site, further indicating that the severe winter season already occurring as ambient conditions significantly impacted this study. In a similarly designed study, Metcalfe *et al*. (2013) found that white-throated sparrows moved more often as barometric pressure was declining. They only observed behavioural changes immediately following dawn and not over a recurrent extended period of time, suggesting further that birds may have adapted to the presence of high frequency, recurrent winter weather cues across the duration of the experiment. Although white-throated sparrows migrate in the fall 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 with the dominance of the polar vortex along the entire eastern seaboard of the United States, closely coinciding with their range. Thus, white-throated sparrows may not induce an increase in their overall movement as alternate strategies are being employed.

A common response to small passerines to inclement winter weather involves hiding in microclimates and taking shelter (Carey & Dawson 1999), assuming significant fat and energy stores are available. It is possible that an escape strategy was not attempted because birds in this study had increased fat and lean mass content, and therefore restlessness (overall movement) was not impacted. As mentioned previously, the storm cues may have become predictable due to the high frequency of storms already present from ambient outdoor conditions.

4.4 Overview

Birds can use changes in barometric pressure and temperature as reliable cues that inclement winter weather is approaching. I report, for the first time to my knowledge, the impacts of experimental recurrent inclement winter weather cues on the behavior and physiology of songbirds. 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 data in this study show that birds may not be as affected by inclement winter weather as previously thought. They also support that certain predictions regarding behaviour and baseline stress levels may not apply under certain scenarios, either indicating a need for further manipulation studies or a different theoretical approach. This study, and continuing those like it, are

important as extreme weather events, including winter storms, are forecasted to increase in frequency and severity across time (NOAA:NCDC 2015). 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. As this study focused on the long-term effects of recurrent inclement cues, I did not determine the effects observed across smaller time scales, i.e. between weeks 1-3. Future studies could focus on the short-term effects and whether birds are habituating to manipulations at specific time scales, as there appeared to be different responses during the course of this long-term experiment. 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.

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modified by urbanization and weather. *The Journal of Animal Ecology*, **80**, 403–413.

Curriculum Vitae

Education:

2013 – Present	Master of Science, Biology: Ecology and Evolution University of Western Ontario, London, ON
2008 – 2013	Bachelor of Science (Honours), Biology University of Windsor, Windsor, ON

Teaching Appointments:

2013-Present	Graduate Teaching Assistant: Centre for Environment & Sustainability: Environmental Science 1021FG – Environmental Issues • Role as lead communication GTA

Academic Associations & Affiliations:

2015 – Present	Society for Conservation Biology Member
2014 – Present	Animal Behavior Society Member
2014	Latornell Conservation Symposium Organizing Committee Member
2012 – 2013	Student Chapter of the American Meteorological Society Member

Contributions to Research:

Apr. 2015	**Boyer, A.** & MacDougall-Shackleton, S. "Effects of recurrent inclement weather cues of white-throated sparrows (*Zonotrichia albicollis*)". Oral Presentation. Earth Day Colloquium, University of Western Ontario, London, ON.
Oct. 2014	**Boyer, A.** & MacDougall-Shackleton, S. "How is climate change impacting avian species?". Oral Presentation. Rotman Institute Conference on Climate Change, University of Western Ontario, London, ON.
Oct. 2014	**Boyer, A.** & MacDougall-Shackleton, S. "Recurrent inclement weather on a songbird species". Poster Presentation. Latornell Conservation Symposium, Alliston, ON.
Oct. 2014	**Boyer, A.** & MacDougall-Shackleton, S. "Effects of recurrent inclement weather cues on the stress response and feeding behaviour of white-throated sparrows (*Zonotrichia albicollis*)". Oral Presentation. Biology Graduate Research Forum, University of Western Ontario, London, ON.

Aug. 2014 **Boyer, A.** & MacDougall-Shackleton, S. "Effects of recurrent inclement winter weather cues on white-throated sparrows' *(Zonotrichia albicollis)* stress response and behaviour*".* Oral Presentation. Animal Behavior Society Conference, Princeton University, Princeton, NJ.

May 2014 **Boyer, A.** & MacDougall-Shackleton, S. "Effects of recurrent inclement weather cues on the stress response and feeding behaviour of white-throated sparrows *(Zonotrichia albicollis)"*. Oral Presentation. Ontario Ecology, Ethology, and Evolution Colloquium, University of Guelph, Guelph, ON.

April 2014 **Boyer, A.** & MacDougall-Shackleton, S. "Inclement weather cues and a songbird species". Oral Presentation. Earth Day Colloquium, University of Western Ontario, London, ON.

Academic Awards & Scholarships

May 2015 Western Science Entrance Scholarship, University of Western Ontario, London, ON

April 2015 Best Oral Presentation – Earth Day Colloquium, University of Western Ontario, London, ON.

Oct. 2014 Best Poster Presentation – Latornall Conservation Symposium, Allison, ON.

Internship Programs:

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

- Assessed statistical meteorological data (temperature, pressure, humidity) to create accurate weather forecasts
- Analyzed several computer models of atmospheric stability values to predict approaching storm and pressure systems

2009 – 2011 Volunteer Internship Program – University of Windsor
Windsor Regional Hospital

- Assisted patients with discharge paperwork

Volunteer Work:

2014 – Present UWO Department of Biology Social Committee

- Organize and carry out social events within and outside of the department

2014 Latornell Conservation Symposium Student Moderator

- Responsible for organizing and running multiple sessions throughout the symposium
- Aided in successfully setting up the symposium program and special events

2014	Biology Graduate Research Forum Organizer • Assisted with registering guests and overall setup of the forum
2013 – Present	Let's Talk Science: University of Western Ontario • Travel to different elementary schools and classrooms to encourage elementary children to be excited about pursuing science