

**INTERACTIONS AMONG
CLIMATE, STRESS, AND AVIAN INFLUENZA VIRUS INFECTION,
AND THEIR IMPACTS ON SURVIVAL IN MIGRATORY WATERFOWL**

A thesis submitted to the
College of Graduate and Postdoctoral Studies
in partial fulfillment of the requirements for the
Degree of Masters of Science
in the Department of Veterinary Pathology
University of Saskatchewan
Saskatoon

By

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ABSTRACT

Wildlife are increasingly faced with the need to adapt or respond to climate change, altered habitats, and emerging infectious diseases. In birds, responses to stressors are mediated by corticosterone (CORT). Though beneficial in life-threatening situations, chronic stress can be energetically costly, negatively impacting disease susceptibility, condition, reproduction, and survival. Waterfowl are natural, asymptomatic reservoirs of low pathogenic avian influenza viruses (LPAIVs), and few studies have demonstrated a cost to infection, showing impacts on body condition and timing of migration. I examined relationships among climate, stress, body condition, and AIV infection, and how they interact to influence survival in migratory waterfowl. Data subsets were selected from >7000 Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairies prior to fall migration, from 2007-2018. Feather CORT (CORT_f) an integrated measure of energy expenditure during the moulting period increased in response to increasing mean daily standard deviation of temperature during feather growth (early July), which carried over to impact subsequent body condition index (BCI) and mass in August. Carry-over effects on BCI were more prominent in females compared to males, and females had a higher mortality rate, based on mark-recapture analysis using band recovery data. Mortality was not, however, associated with CORT_f, BCI, or mass. Males with higher CORT_f were less likely to be hunted within the first year, suggesting CORT_f provided an advantage to males by helping them avoid being hunted, or a lower proportion of males with high CORT_f were present in the population, resulting from increased mortality or failure/delay in migration prior to subsequent hunting seasons. AIV did not appear to pose a cost to Blue-winged Teal, as it was not associated with CORT_f, BCI, mass, or survival. The study demonstrated a complex, non-linear relationship between AIV infection and climate; the probability of infection was negatively associated with mean daily minimum temperatures 3-10 days prior to sampling up to ~10°C, and was positively associated with mean daily minimum temperatures above 12°C. This relationship is likely a reflection of temperature on environmental AIV survival, as well as on waterfowl behaviour, distribution, and movement, affecting local population densities and opportunities for transmission. My results provide insight into complex relationships among climate, stress, condition, AIV infection, and survival in migratory waterfowl.

ACKNOWLEDGEMENTS

I would first like to express deepest sense of gratitude towards my graduate supervisor Dr Catherine Soos for guiding through completion of this research and thesis work. She has been instrumental in developing my professional skills, technical knowledge and progressive attitude. This beautiful journey could not have been possible without her valuable comments and critique. I also want to thank her for believing in me to be able to complete this mammoth task and for being a valuable support in a foreign land that I knew so little about.

I would also like to thank my committee member, Dr Karen Machin for her support and help in completion of this thesis, and encouragement during uncertain times. Am grateful to Drs. Bruce Wobeser (Graduate chair) and Elemir Simko (former graduate chair) for their directions to move ahead. Very special thanks to Jamille McLeod and Landon McPhee, at Environment and Climate Change Canada for fieldwork, lab analysis and teaching me the lab techniques essential for completion of this research work. Very grateful to Dr Yohannes Berhane, Matthew Suderman, Janice Koziuk and Tamiko Hisanaga, at CFIA/ACIA for analysis of AIV samples and teaching me the lab skills required for AIV diagnostics. Am very thankful to Dr Ray Alisaukas for his help with mark-recapture analysis, Drs. Eric Lamb and Kirsty Gurney for their guidance in statistical work whenever needed, and Dr Graham Fairhurst for his earlier contribution to this work. I also truly appreciate and recognize the love and support I have received from Angela Turner, Tyler Moss, and Drs. Fabienne Uehlinger and Sherry Myers throughout my degree. Additionally, I thank all the office and finance staff responsible for smooth functioning of my research work.

I would like to acknowledge the funding sources and partners that supported this research including Alberta Conservation Association, Canada's Inter-agency Wild Bird Influenza Survey, Canadian Wildlife Health Cooperative, CFIA-NCFAD, Ducks Unlimited Canada's Institute for Wetland and Waterfowl Research, Environment and Climate Change Canada, USDA-APHIS, and USFWS.

A vote of thanks to all the USFWS, CWS crew members and volunteers particularly Anne Le Gac, Fiona Moser, Karen Gesy, Mariana Villegas, and Toni Moritz for data collection during the tiring field seasons. Being associated with Environment and Climate Change Canada and Department of Veterinary Pathology, gave me an opportunity to meet some inspirational and

lovely people at both the institutes. Special regards to my work associates and dear friends at Environment and Climate Change Canada, Asha Perera, Christina Desnoyers, and Shathi Akhter. Am also forever grateful to friends at the Western College of Veterinary Medicine including Arefeh Ravanbakhsh, Breanne Murray, Dawn Abbot, Divya Jose, Megan Baker, Mengying Liu, Melanie Fetterly, and Veronique Dufour. In addition to all the students in Department of Veterinary Pathology, sincerest thanks to the faculty members who have always been motivational support throughout these years.

My heartfelt thanks to friends who have acted as my second family in Canada, Mandeep Sagi, Mehak Bath, and Kushnoor Bath, and encouraged me throughout my degree. My profound thanks to dearest friend Gwen Roy for her ever-inspiring words to keep pushing my limits and making me realise what I was capable of doing. I also thank Alisha Chhabra, Ana Guintard, Caroline May, Gurminder Mandhar, Harmanjot Benipal, Kaitlin Tagg and Mercy Harris, for reassuring that I never felt low in life, continued to work hard and have positive attitude all through my stay in Canada. At last, I fall short of words to thank my lovely, optimistic and ever encouraging parents Sardar Satnam Singh and Sardarni Lakhwinderpal Kaur. I cannot imagine success without prayers and blessings of my parents. Their unbreakable trust has made me finish massive tasks confidently and with ease. I would also like to thank my elder brother Gurbir Kahlon, who had faith in me and taught me how harsh life can be.

I may have failed to mention many but I am indebted to every single soul that has been instrumental in my life and especially in the last three years of my master's degree.

DEDICATION

To everyone who fights discrimination on basis of their colour, physical appearance, religion,
gender, sexuality, background, profession, etc.

To my motherland Panjab.

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LIST OF ABBREVIATIONS

ACTH	adrenocorticotrophic hormone
AHY	after hatch year
AIV	avian influenza virus
BCI	body condition index
BWTE	Blue-winged Teal
CORT	corticosterone
CORTf	feather corticosterone
CRH	corticotrophin releasing hormone
CV	coefficient of variation
CWS	Canadian Wildlife Service
ECCC	Environment and Climate Change Canada
ELHS	emergency life history stage
ELISA	enzyme linked immunosorbent assay
GC	glucocorticoid
HA	hemagglutinin
HPA	hypothalamic-pituitary-adrenal
HPAIV	highly pathogenic avian influenza virus
HY	hatch year
LHS	life history stage
LPAIV	low pathogenic avian influenza virus
NA	neuraminidase
NCDIA	National Climate Data and Information Archive
NCFAD	National Centre for Foreign Animal Disease
PCR	polymerase chain reaction
PPR	prairie pothole region
RT-PCR	real time polymerase chain reaction
SAM	sympathetic-adrenal-medullary
USFWS	United States fish and wildlife service

PREFACE

This thesis is organized as a manuscript-style thesis and formatted to follow the guidelines of College of Graduate Studies and Research, University of Saskatchewan. Chapter 1 is a general introduction and literature review, including project goals and objectives. Chapter 2 is organised as manuscript for publication in peer-reviewed scientific journals. Chapter 3 is organised in a similar format and there is some repetition in methodology because of the way this thesis is formatted. Chapter 4 is a general discussion and overall conclusion. References are listed in the References section of the thesis for all the chapters combined. Supporting information associated with the research chapters are presented in the Appendix section.

CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 Climate - A potentially important factor in the ecology of avian stress and avian

Influenza infection in migratory birds

“Scientific evidence for warming of the climate system is unequivocal” (Intergovernmental Panel on Climate Change, 2013). An average increase of 0.74 degree Celsius in earth’s surface temperature has been observed throughout the 20th century (European Environment Agency, 2008), and the last three decades were recorded to be warmer than any other decade (Blunden et al., 2018). Transformation in the earth’s climate not only impacts the global economy but also impacts human health, as well as domestic and free-ranging animals. Although, many animal species may be able to adjust to gradual changes in climate, increasing variations in climatic conditions can jeopardize wildlife health, ultimately impacting survival and reproduction affecting wildlife populations and conservation (Mayhew et al., 2008; Pöysä and Väänänen, 2014). Shrinkage of the planet’s biodiversity, and increased rate of extinction are believed to be some of the dire consequences of climate change and global warming (Twitchett, 2006). Therefore, it is increasingly important to assess the impacts and role that climate may have in affecting wildlife health at the individual and population levels.

Migratory bird population declines are highest in those species that fail to respond to climate change (Both et al., 2006; Møller et al., 2008). Compared to other avian species, due to their dependence on waterbodies, waterbirds have been shown to be more responsive to climate change (Brommer, 2008; Bussière et al., 2015). Climate change can affect birds by triggering physiological responses associated with stress or energetic management, and by altering or disrupting normal physiological and behavioural processes important in their annual cycle, including growth, reproduction, and migration, and can result in impacts on population sizes and distributions (Wingfield, 1983; Maclean et al., 2008; Elmberg et al., 2014; Pöysä and Väänänen, 2014; Lehikoinen et al., 2017). Over the past few decades, a number of bird species have shifted their geographical ranges north globally (Parmesan and Yohe, 2003; Hitch and Leberg, 2007; Melles et al., 2011). Alarmingly, the rate of northward shifting trends per decade in Canada are above the global averages (Parmesan and Yohe, 2003). These shifts increase migratory distances between breeding and non-breeding grounds (Howard et al., 2018) potentially adding additional costs to migration. These changes to migratory patterns may also lead to increased migrant

densities at new, favourable breeding grounds, potentially increasing competition for food sources and/or reducing food availability. Further, as a result of shifts to newer grounds, birds may also face novel predatory or infectious disease risks, requiring additional energy to escape from predators or mount immune responses. Higher energetic demands related to increased predation risk, potential starvation, and unpredictable food supply are known to cause mortality in birds (Berthold, 2001; Sillett and Holmes, 2002; Alerstam et al., 2003; Newton, 2006; Hewson et al., 2016).

Some species of long distance migrant songbirds have advanced their arrival at breeding grounds with warmer regional temperatures (van Buskirk et al., 2009), suggesting changes in timing of spring migration. Studies conducted over the past 63 years indicate that 27 of 96 migratory species have altered their arrival dates to breeding grounds significantly (Heather et al., 2005). Birds arriving early on the breeding grounds may be naïve to hostile local weather resulting in increased energetic demand, and decreased overall fitness through impacts on survival and/or reproduction (Newton, 2008). A mismatch between timing of arrival and food availability, can result in insufficient energy for reproduction and offspring survival (Newton, 2008). A number of species have been severely impacted including the Pied Flycatcher (*Ficedula hypoleuca*) which have experienced a 90% decline in population in the past two decades (Both et al., 2006).

In addition to direct impacts on avian species, climate plays a key role in determining animal health, distribution of vector-borne and other pathogens (Mondet et al., 2005; Anyamba et al., 2009), as well as the pathogenicity of diseases (Chirico et al., 1997). For instance, avian influenza virus (AIV) studies worldwide have demonstrated that climate is an important factor in the ecology of AIVs (Stallknecht et al., 1990; Papp et al., 2017; Morin et al., 2018; Ramey et al., 2020). Further, climate can play a role in affecting waterfowl distribution and population densities through diverting birds to other favourable habitats (Guillemain et al., 2005; Maclean et al., 2008). Increased population densities of waterfowl are also associated with increased risk of AIV infection (Nallar et al., 2016; Papp et al., 2017). In addition, overwinter persistence of AIV has been suggested as a source of exposure for migratory waterfowl returning to breeding areas in the spring, and the virus has been shown to remain viable following freeze-thaw cycles (Shoham et al., 2012; Ramey et al., 2020). Comparative studies have demonstrated that some AIV strains remain infectious for longer periods of time at lower temperatures (4°C) than at

higher temperatures (17°C; Stallknecht et al., 1990). In eastern Canada, lower temperatures have been associated with higher probability of AIV infection in migratory waterfowl (Papp et al., 2017), thus implying the importance of climate in AIV ecology.

1.2 The ecology of stress in migratory birds

1.2.1 Overview of stress physiology in birds

Birds respond to challenges they experience in their environment (e.g., climatic variation, predator avoidance, etc.) through the process of homeostasis. Homeostasis can be defined as the maintenance of physiological systems that are essential for life (Cannon, 1932). Stress is a response to any stimulus (i.e., stressor) that challenges homeostasis, causes an emergency response to perturbations, or produces a chronic state of imbalance following over-activation of the adrenocortical axis (Romero, 2012). Restoration of homeostasis is dependent on two essential physiological pathways: 1) activation of the sympathetic nervous system and 2) stimulation of the hypothalamic-pituitary-adrenal (HPA) axis (Figure 1.1.). In response to a stressor, the sympathetic-adrenal-medullary (SAM) axis stimulates the release of catecholamines, which produce a cardiovascular response resulting in elevated heart rate and blood pressure, and the diversion of blood to muscle tissues to aid in an immediate flight or fight response (Sapolsky et al., 2000; Wingfield and Romero, 2000; Reeder and Kramer, 2005). The hypothalamus releases corticotrophin releasing hormone (CRH) which stimulates the pituitary to secrete adrenocorticotrophic hormone (ACTH) into circulation. Unlike the SAM axis, the HPA operates on a longer time scale by releasing glucocorticoids (GCs) which remain in circulation for a longer period of time compared to catecholamines (Sapolsky et al., 2000; Reeder and Kramer, 2005). Glucocorticoids, including cortisol in mammals and corticosterone (CORT) in birds, are regulated through negative feedback at various levels of the HPA axis (Figure 1.1.) to limit prolonged exposure to their effects (Herman et al., 2016).

Corticosterone and its daily fluctuations are responsible for energy management (Sapolsky et al., 2000; Landys et al., 2006), regulating daily metabolism, locomotor activity (Landys et al., 2006), and mediating short-term physiological and behavioural changes in response to perturbations or stressors (Dallman et al., 1993). Predictable changes in CORT levels, whether daily (circadian rhythm) or seasonally, have evolved to optimize survival and, ultimately, overall fitness in individuals. In response to a stressor the release of CORT increases

gluconeogenesis, suppresses reproduction and immune function, and alters behaviour further facilitating increased survival (Blas and Baos, 2009). Though the immediate short-term elevation in CORT concentrations allows individuals to avoid life-threatening circumstances, persistent elevation of CORT can have deleterious effects on reproduction, immune function, development, metabolism, survival, and, hence, overall fitness (Boonstra et al., 1998; Bruijnzeel et al., 2001; Jovani and Blas, 2004, Sheriff et al., 2009). Negative impacts mediated by prolonged or repeated elevations of CORT may arise from the reallocation of resources necessary to deal with the stressors, at the expense of these normal functions (Padgett and Glaser, 2003).

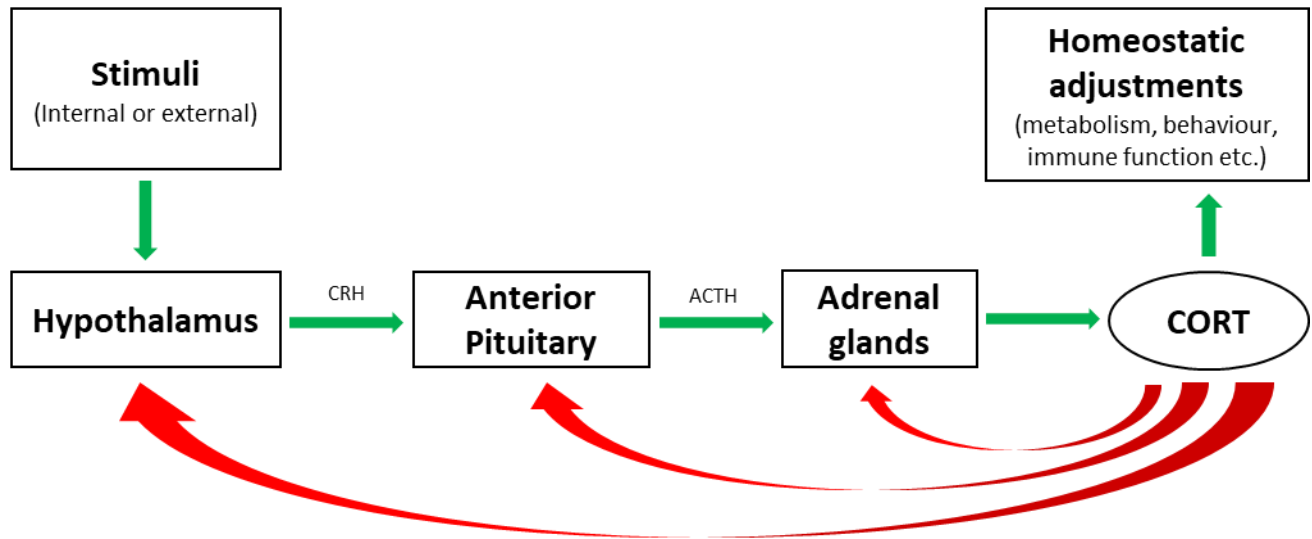


Figure 1.1. The adrenocortical response to a stressor in birds. CRH = Corticotropin releasing hormone, ACTH = Adrenocorticotropic hormone, CORT = Corticosterone. Green arrows indicate the normal progression, whereas red arrows indicate negative feedback mechanisms.

1.2.2 *Modelling stress ecology in migratory birds*

To have a better understanding of stress physiology in birds, it is important to understand the process of homeostasis, and how it is maintained under stressful conditions. Different models proposed by McEwen and Wingfield (2003) help enhance the predictability of stressful conditions that might occur at different times of year and/or when an animal should switch to an emergency life history stage (ELHS; depicted as Type 1 Allostatic Overload, Figure 1.2.) from a normal life history stage (LHS; depicted as homeostatic or allostatic state, Figure 1.2.).

Allotaxis is the process of maintaining homeostasis through physiological changes allowing an individual to respond to or overcome a stressor (Sterling and Eyer, 1988; McEwen and Wingfield, 2010). The Allotaxis Model (Figure 1.2.) incorporates homeostasis in the context of individual's life cycle, experience, and/or response to its dynamic social-physical environment. Energy requirements and energy available in the environment are an important part of this model in maintaining homeostasis. If energy derived from food is sufficient and not limiting, but a perturbation or stressor lasts for a longer period of time (e.g., permanent habitat disturbance or climate change), birds will remain in an allostatic state. Allostatic load represents the cumulative energy requirement for daily and seasonal routines, and the energy required to overcome unpredictable events or stressors without facing deleterious effects (McEwen and Wingfield, 2010). The response to stressors of the same magnitude can vary during different times of the year/life cycle. For example, a response to a stressor during reproduction (i.e., a period of increased energetic demand) will elicit different responses compared to that same stressor during feeding on the wintering grounds (i.e., a period of lower energetic demand). A more energetically costly event may require a greater energy trade-off between essential components of survival or overall fitness, compared to events that are less energetically costly. Thus, depending on its current state or stage of annual cycle, an animal may cope with stressors by diverting resources from normal physiological (e.g., thermoregulation, metabolism, etc.) or behavioural processes (e.g., breeding, incubation, foraging, migration, etc.). When birds are undergoing energetically costly processes, additional stressors may push birds to trade off energy resources in favour of survival. Whereas a stressor of similar magnitude during a less energetically costly phase of the life cycle has a different effect on energy management and subsequent outcomes. Type 1 Allostatic Overload or ELHS (Figure 1.2.; red circle) describes a situation where energy demand surpasses the energy gained from the local environment that may

have negative impacts such as loss of body mass and suppression of reproduction (Wingfield et al., 1983). If responses to a stressor are overly costly, they have the potential to lead to pathological effects and potentially death. This increased energy demand has been termed as Type 2 Allostatic Overload.

The Reactive Scope Model is an extension of the Allostasis Model (Figure 1.2.), and incorporates the concept of “wear and tear” in addition to CORT variations related to predictable daily and seasonal changes (Romero et al., 2009). This model helps elaborate concepts of Predictive Homeostasis (CORT fluctuations in a predictable environment) and Reactive Homeostasis (CORT elevation in response to unpredictable changes or stressors). The balance of Predictive and Reactive Homeostasis is the Reactive Scope of an individual (Figure 1.2.). When an individual is no longer able to maintain its Reactive Scope, the model helps predict occurrence of deleterious effects such as suppression of the immune system and reproduction, and potentially decreased survival. If a bird moves beyond its normal Reactive Scope into the Homeostatic Overload Range (Allostatic Overload in the Allostasis Model) physiological changes to suppress nonessential functions are elicited for survival. However, energy reserves may not be sufficient for survival. In predictable environments, CORT levels usually do not elevate into Reactive Homeostasis ranges (Cherel et al., 1988; Dawson et al., 1991). “Wear and tear” in the Reactive Scope Model represents the cost of maintaining and mediating the allostatic state or maintaining CORT levels within the Reactive Homeostasis range (Romero et al., 2009). As a result of the cost of wear and tear, the threshold for Homeostatic Overload decreases and an individual becomes susceptible to deleterious effects even though the intensity of stressor might still be within normal Reactive Scope of an individual.

1.2.3 Energetic costs of avian migration

Migration is an important phase in the life cycle of many birds, and is equally fascinating to researchers, hunters, wildlife specialists, and bird enthusiasts globally. Migration is a predicted seasonal movement of birds between winter and breeding grounds along a flyway in response to changes in resources, habitats, and/or predatory risk (Loehle, 1995; Dingle, 1996; Bowlin et al., 2010; McKinnon et al., 2010). While birds such as Wallcreepers (*Tichodroma muraria*) and White-throated Dippers (*Cinclus cinclus*) change their altitude of habitat to escape cold weather, other species like Swainson's Thrush (*Catharus ustulatus*) and Blue-winged Teal (*Spatula discors*) are known to migrate up to 10,000 kilometres annually between breeding grounds in Canada to overwintering grounds in Central and South America (Alerstam, 1990; Rohwer et al., 2020). It is estimated that over two-thirds of birds breeding in favourable temperate regions of North America migrate to Mexico, Central and South America and the islands of the Caribbean for their non-breeding period (Keast and Morton, 1980; Rappole, 1995). In North America, there are four key flyways, Central, Mississippi, Pacific and Atlantic, representing the routes followed by avian migrants (USFWS, 2014).

Avian migration is dependent on important navigational cues such as environment and topography. Navigational cues such as magnetic field, positioning of stars, and major landmarks such as rivers, mountains, lakes, and coastlines allow birds to make decisions during one of the most energetic phases of their life cycle (Schummer et al., 2010). However, cues for the initiation of seasonal migration remain unclear and vary among species. Some of the important cues responsible for migration in dabbling ducks are photo-period, food availability, and weather severity, followed by other factors such as feeding ecology, competition, and predatory escape (Nichols et al., 1983; McKinnon et al., 2010; Schummer et al., 2010; Guillemain et al., 2013; 2015). To maximize survival and reproduction, birds breed in food rich conditions and winter in favourable warmer environments (Greenberg, 1980). However, migration carries an enormous level of risk and energetic cost (Alerstam, 1990; Newton, 2008).

Flight is a physiologically and energy demanding activity, and energy requirements vary for different flight patterns (e.g., soaring versus flapping; Hedenström, 1993; Videler, 2005). In preparation for migration, avian species undergo several physiological changes, including amassing vast energy reserves in the form of fat stores and gonadal suppression to decrease unnecessary weight of internal organs (Newton, 2008; Mayntz, 2018). During migration,

additive effects such as severe storms, rainfalls, predation escape may require additional energy to survive. Increased competition during migration, as a result of climate mediated increases in population density and reduced food availability, incurs additional energetic costs. Energy demand can exceed energy availability, requiring the bird to trade off energy reserves in order to protect themselves. In situations where immune function has been used as a trade-off, a low magnitude stressor, not normally harmful, may result in increased susceptibility to disease (Spencer et al., 2001). This is a consequence of lowering the threshold of Homeostatic Overload range, as indicated by wear and tear in the Reactive Scope Model (Figure 1.2.). High energy demand in the face of limited energy stores will ultimately result in adverse effects of Homeostatic Overload (Romero et al., 2009). Hence, both predictable and unpredictable events experienced during an energetically costly phase such as migration, breeding or moulting have the potential to initiate ELHS or Reactive Homeostasis processes in order to promote survival. As a result, the additive energy requirements and unpredictability in food supply during migration often result in higher mortalities (Berthold, 2001; Sillett and Holmes, 2002; Alerstam et al., 2003; Newton, 2006; Hewson et al., 2016).

1.2.4 Adrenocortical responses to environmental changes

Generally, CORT levels fluctuate within baseline or Predictive Homeostasis during various life history stages (Figure 1.2.). Upon activation of the HPA axis during predictable environmental changes such as rainfall and wind gusts, CORT levels do not elevate into Reactive Homeostasis ranges (Cherel et al., 1988; Dawson et al., 1991). Short and longer term environmental changes can produce CORT elevations into Reactive Homeostasis ranges but the degree of response can vary. In response to short term stressors, individuals have evolved to enter ELHS or Homeostatic Overload Range, and return back to normal LHS once stressor has been eliminated. These short term or transient stressors can lead to increased heart rate, arterial dilation in skeletal muscles, bronchiolar relaxation, pupillary dilation, piloerection and mobilization of liver glycogen and free fatty acids (Axelrod and Reisine, 1984; Romero et al., 2009). These changes are well supported by experimental studies where a rapid elevation in metabolism was observed in domestic fowl (Saadoun et al., 1987) and a rapid increase in locomotor activity and foraging was seen in White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*) in response to CORT increase (Breuner et al., 1998). However, these perturbations

can only be considered transient if homeostasis is achieved soon after the response(s). Short term perturbations experienced early in the breeding season and within Predictive Homeostatic range may result in physiological adaptations such as alteration of gonadal development (Wingfield, 1984), resulting in a temporary delay of breeding. For example, delayed onset of egg laying has been observed in White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*) in response to severe weather conditions but without elevation in CORT (Wingfield et al, 1983).

In contrast to highly adaptive CORT responses for short term stressors, chronic CORT elevations lack adaptive value (Blas and Baos, 2009). While negative feedback mechanisms are important in terminating the stress response after the stressor abates, chronic stress can alter normal functioning of the HPA axis producing chronic increases in basal CORT secretion, altered stress responses or even adrenal exhaustion (Herman et al., 2016). Impacts on critical physiological processes include delays in reproductive development or maturation (inhibition of gonadotropin secretion), stress induced dwarfism (growth hormone suppression), impairment of flight capabilities (breakdown of skeletal muscles), and immune suppression (Boonstra et al., 1998; Bruijnzeel et al., 2001; Jovani and Blas, 2004; Sheriff et al., 2009). As discussed in the previous section, chronic CORT elevation leads to Allostatic Overload type 2, and if deleterious effects persist for longer periods they can result in death.

1.3 Feather corticosterone: Usefulness and limitations

Although plasma concentrations can be used to measure CORT levels at the time of sampling, the results can be influenced by the time it takes to acquire the sample and concentrations represent only one time point (Ouyang et al., 2011). Feather CORT (CORTf) is a non-invasive tool (Bortolotti et al., 2008) that can estimate HPA activity during feather growth thus representing a longer window of time (Bortolotti et al., 2008). Measurement of CORTf from opportunistically collected feathers can be very helpful in investigations of species that are impossible to capture during non-breeding periods (Kouwenberg et al., 2013). Studies have demonstrated that CORTf concentrations are not repeatable within individuals from year to year (Legagneux et al., 2013). In addition, CORTf variation is less influenced by intrinsic parameters such as body size, and more associated with environmental parameters such as temperature and precipitation, demonstrating that CORTf is an important tool in understanding avian stress physiology (Bortolotti et al., 2008; Legagneux et al., 2013).

In Common Eiders (*Somateria mollissima*), annual variation of CORTf can be explained by average temperatures during the period of moult (Legagneux et al., 2013). In the same species, CORTf was used to study carry over effects (COEs) of energy expended during the post-breeding moulting period and their effects on the subsequent breeding period (Harms et al., 2015). Using path analysis, CORTf, an index of energy expenditure in the previous August-September, was directly associated with subsequent pre-breeding body condition and arrival dates of birds returning to the breeding colony, and indirectly negatively associated with reproductive success and survival of the subsequent breeding period (Harms et al., 2015). In a study conducted by Carrete et al. (2012), high CORTf levels in response to declining conditions and reduced food availability on wintering grounds in Africa, were associated with declines in western European populations of Egyptian Vultures (*Neophron percnopterus*). Furthermore, in Atlantic Puffins (*Fratercula arctica*), increased CORTf in feathers grown months prior to egg-laying were positively associated with egg mass, indicating increased foraging effort during moult in response to CORT (Kouwenberg et al., 2013). Rector et al. (2012) determined that plasma CORT was higher in years with favourable conditions (as measured by food availability) compared to years with less favourable conditions potentially due to increased feeding efforts in response to food availability.

Care must be taken in the interpretation of CORTf results. During the process of extraction, steroidal hormones and metabolites can cross-react with CORT, and can vary among kit manufacturers (Koren et al., 2012). Experimental studies have demonstrated lower feather growth and quality in CORT-implanted birds (Romero and Reed, 2005; DesRochers et al., 2009), which may influence interpretation of results. Uptake of CORT in feathers can also be influenced by hormones or pigments like melanin (Lattin et al., 2011; Jenni-Eirmann et al., 2015), potentially altering results. Thus, for reliability and accuracy of results, validation of techniques used for CORTf extraction and analysis are recommended for each species being studied.

1.4 The ecology of avian influenza viruses in migratory birds

1.4.1 Avian influenza viruses

Avian influenza viruses (AIVs) are segmented, negative-stranded RNA viruses belonging to the family Orthomyxoviridae. This family is further subdivided into three genera: Influenza

virus A, B, and C (Webster et al, 1992). Influenza viruses can further be classified into various subtypes based on the presence of surface glycoproteins, hemagglutinin (HA) and neuraminidase (NA). The antigenicity of influenza viruses depend on surface glycoproteins (Webster et al., 1992). Glycoprotein subtypes (16 HA and 9 NA) and their combination have been isolated from a wide range of hosts including wild birds, captive caged birds, and domestic poultry (Fouchier et al., 2005).

Avian influenza viruses are classified as low pathogenic (LPAIVs) or highly pathogenic (HPAIVs) based on lethality in poultry and amino acid sequencing (OIE, 2012). Infection with most subtypes of LPAIVs generally result in no overt signs of disease or mortality. Avian influenza viruses have been reported in over 100 wild bird species, and most of them have been reported as LPAIVs (Kawaoka, et al., 1988; Stallknecht and Shane, 1988). All known influenza A virus subtypes have been found in wild birds of the order Anseriformes (particularly ducks, geese, and swans) and Charadriiformes (particularly gulls, terns, and shorebirds), which are thought to be reservoir host species for AIVs (Webster et al., 1992; Alexander et al., 2000; Krauss et al., 2004; Fouchier et al., 2005; Olsen et al., 2006). Amongst wild waterfowl, dabbling duck species like Mallard ducks (*Anas platyrhynchos*) and Teal (*Spatula discors*, *A. crecca carolinensis*) are generally reported to have higher prevalences than other waterfowl species (Jonassen and Handeland, 2005; Papp et al., 2017), and Mallards have been shown to harbour the highest diversity of HA and NA subtypes (Hinshaw et al., 1980; Alexander, 1986; Olsen et al., 2006). In addition to wild birds of the orders Anseriformes and Charadriiformes, AIVs have also been recovered from ratites, cranes, songbirds and raptors (Becker, 1966; Hinshaw et al., 1982a; Hinshaw et al., 1982b; Stallknecht and Shane, 1988; Verhagen et al., 2012).

Low pathogenic AIVs replicate in cells lining the intestinal tract of birds, and are shed in high concentrations in feces, often into water (Webster et al., 1978). LPAIVs generally cause asymptomatic infection in the natural hosts with no development of clinical disease (Webster et al., 1992; Takekawa et al., 2010). However, mortality can be as high as 100 percent in poultry flocks infected with HPAIVs of subtypes H5 or H7 (Webster et al., 1992). In addition to causing large scale mortality in poultry, HPAIVs can impact the economy locally, nationally, and internationally, through implementation of trading restrictions and other limitations imposed on the infected areas.

Most H5 and H7 subtypes found in wild birds have low pathogenic properties, however they have the potential to become high pathogenic strains, particularly in domestic poultry which are less adapted to LPAIVs and are in high density environments. Low pathogenic AIVs of subtypes H5 and H7 may become highly pathogenic through the insertion of extra basic amino acids in the cleavage site and substitutions of non-basic amino acid (Perdue et al., 1996). Lesions associated with HPAIV infection can be either localized or systemic, affecting respiratory and intestinal tracts (Kuiken et al., 2006). Clinical signs due to HPAIVs can vary from being an asymptomatic infection to mortality. Although domestic poultry can exhibit a variety of signs such as head tremors, torticollis, opisthotonus, depression, rales, sneezing etc. (Swayne 2003), similar neurological signs have been seen in both free-flying and experimentally infected wild birds including goose and gulls (Lui et al., 2005). Generally, there are no pathognomonic lesions of AIVs in birds and the respiratory lesions can be invaded and complicated by other secondary pathogens.

Although HPAIVs generally do not persist or circulate in wild bird populations, sporadic mortality has been observed in multiple species of wild birds. Wild bird mortalities caused by HPAIV H5N1 (Goose/Guangdong lineage) were observed in numerous species and countries in Asia, Europe, and Africa, shortly after the turn of the millennium, beginning in 2002 (Lebarbenchon et al., 2010; Ramey et al., 2018).

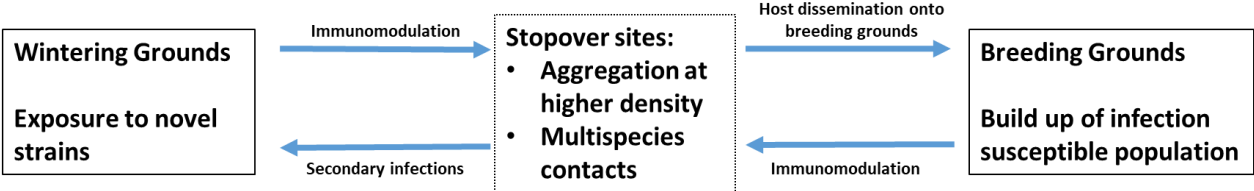
1.4.2 The ecology of avian influenza viruses in migratory waterfowl and other wild birds

During migration, most species of migratory birds will make temporary stops at stopover sites (Figure 1.3.) to rest, feed, and “refuel” prior to continuing their journey. High energetic demands of migration may compromise host immunity, and can increase the susceptibility of birds to infections (Wilcove, 2008), and increase the rate of transmission and exposure. At breeding, moulting, or stopover sites, migratory birds may come in contact with high densities of birds originating from multiple populations or flyways. As a consequence, these sites can act as potential hot spots for infectious agents, with a potential for increased transmission and spread among multiple bird populations (Krauss, 2010; Altizer et al., 2011). Response to pathogens, such as AIV induces physiological changes that incur additional costs in order to promote survival. Lower energy reserves associated with AIV infection have been shown to delay migration for as long as a month, and also reduce migratory distance of infected birds (van Gils et al., 2007).

Stopover sites along migratory pathways can serve as hotspots for transmission, exposure, and the generation of new strains of AIVs given that they may have high densities of birds from multiple different flyways (Hinshaw et al., 1985; Krauss et al., 2004; Wallensten et al., 2007) (Figure 1.3.). Risk of LPAIV infection has been shown to be positively associated with population density, (Nallar et al., 2015; Papp et al., 2017) with the highest prevalence observed in late summer or early fall, just after the breeding season, with the recent recruitment of large numbers of naïve and susceptible hatch year birds, and prior to fall migration (Hinshaw, 1985; Kraus, 2004; Nallar et al., 2015; Papp et al., 2017). Hatch year (HY) birds are less likely to have antibodies to AIV nucleoproteins, and more likely to be infected with LPAIV compared to adults because of the absence of prior exposure (Nallar et al., 2016; Papp et al., 2017). Higher densities of birds, particularly with increasing human encroachment and industrial development, may also impact availability of food resources and habitats suitable for breeding, staging, or stopping over. Additionally, in response to variations in climate, densities of birds might increase markedly at forage rich sites. Hence, birds migrating to favourable grounds as a result of habitat loss or reduced food availability may be faced with an increased cost of migration. Thus, spending energy on migration and dealing with new, unpredictable challenges such as predation can further contribute to increased susceptibility to AIV infection (Hinshaw et al., 1980; Okazaki et al., 2000; Munster et al., 2007; Wallensten et al., 2007).

Given that LPAIVs generally do not appear to affect the health status of migratory waterfowl, it is possible that viruses are distributed along migratory routes, possibly between countries and continents (Hoyo et al., 1996). During the 2006 outbreaks of HPAI (H5N1) from Asia to Europe, wild birds, particularly aquatic birds, were suggested to be inter-continental virus vectors owing to the fact that the virus presence was seen in areas with no history of virus incidence but corresponded to the fall migration of the birds in those areas (Gilbert et al., 2006; Bragstad et al., 2007; Palmai et al., 2007). The ability of some AIVs, particularly highly pathogenic strains, to cross from birds to infect and cause diseases in mammals, including humans, remains a global threat to human and animal health, and the global economy.

Spring Migration



Fall migration

Figure 1.3. Annual avian migratory cycle where key processes can increase or decrease pathogen exposure or transmission (modified from Altizer et al., 2011).

1.5 Study species – The Blue-winged Teal

Blue-winged Teal are the second most predominant duck species in North America, after Mallards. They are one of the most common migratory birds that travel to the Canadian prairies in spring for the breeding season. The breeding range is extensive and stretches from the southern high-plains of New Mexico and Texas in the United States (U.S.) in south, to the boreal forest of Canada and Alaska in the north, and from the Pacific to the Atlantic coast above approximately 40°N (Bennett, 1938, Bellrose, 1980, Rohwer et al., 2020). However, the north-central U.S. and the prairies in Canada are primary breeding ranges with approximately >85% of all Blue-winged Teal breeding pairs (USFWS, 2009). The prairie pothole region (PPR) in North America is one of the most important areas for waterfowl reproduction and ecology. The PPR is comprised of the Canadian provinces of Alberta, Saskatchewan and Manitoba, and the states of Montana, North Dakota and South Dakota in the United States. The region is known to provide habitat to more than 60% of breeding population of important waterfowl species like Mallard, Blue-winged Teal, Northern Shoveler (*Spatula clypeata*), Northern Pintail (*Anas acuta*) (Smith, 1995).

In their primary breeding range, Blue-winged Teal largely use marshes, vegetated wetlands around lakes, and rice fields which can be sources of AIV, especially when duck population density is high. Breeding and moulting are energetically costly events that may increase the susceptibility of adults to AIV infection, in addition to producing offspring naïve to AIV. Although Teal along with Mallards are known to have higher prevalence rates (Munster et al., 2007), no species differentiation with respect to AIV prevalence was observed in the prairies (Papp et al., 2017). Conversely, Teal had slightly lower prevalences of AIV compared to Mallards in eastern Canada and British Columbia (Papp et al., 2017). In the prairie provinces, AIV status increased with increasing population density and a complex interaction was observed between age and sex of bird. Hatch year (HY) birds were more likely to be infected with AIV compared to after hatch year (AHY) birds overall and amongst AHY birds, females were more likely to be infected than males (Papp et al., 2017).

1.6 Rationale and importance

The current rate of climate change in the Canadian prairies can be a threat to wild waterfowl health. Climate change can influence AIV ecology in migratory birds through its impacts on stress responses, population ecology, migratory pathways, and on AIV transmission and spread. The relationships among climate, stress responses, and AIV infection are likely to be complex, and are yet to be investigated. The role of stress in relation to climate and AIV infection, and how they interact to impact body condition in wild waterfowl are currently unknown. In this thesis, I used CORTf as an integrated measure of HPA activity to establish links between energetically costly responses to climatic conditions during the period of feather growth (July), and subsequent carry over effects on body condition and AIV infection following the breeding season and prior to fall migration (August), and how climate, stress, body condition, and AIV infection may interact to impact survival in migratory Blue-winged Teal. Given our rapidly changing environment, understanding the relationships among climate, stress, condition, and AIV infection in waterfowl will be increasingly important to understand the role that climate change will have on waterfowl health and AIV ecology in waterfowl populations.

1.7 Thesis summary

1.7.1 Thesis topics and hypothesis

See figure 4.1., which illustrates an overview of the predictions investigated in this thesis.

Relationships among Climate, Stress, Body Condition and Avian Influenza Virus Infection in Blue-winged Teal (*Spatula discors*) in the Canadian Prairies.

Hypothesis: Climatic variation will affect stress responses and/or the level of energy required for wildlife to respond or adapt to changes in climate.

Prediction: CORTf, an index of stress responses or energy expenditure, will vary in response to climatic parameters during the period of feather growth in Blue-winged Teal.

Hypothesis: Stress responses/or increased energy expenditure will have an influence on body condition, and avian influenza virus (AIV) status.

Prediction: Increased energy expenditure or stress responses during the moulting period (as measured by CORTf) will be associated with reduced body condition and increased likelihood of infection with avian influenza virus.

Impacts of Stress, Body Condition, and Avian Influenza Virus Infection on Survival of Blue-Winged Teal (*Spatula discors*).

Hypothesis: Stress responses/or increased energy expenditure, reduced body condition, and avian influenza virus infection will influence the probability of ducks being hunted (i.e., shot).

Prediction: Increased CORTf levels, reduced body condition, and avian influenza infection will increase the likelihood of Blue-winged Teal being hunted.

Hypothesis: Stress responses/or increased energy expenditure, reduced body condition, and avian influenza virus infection will influence survival in waterfowl.

Prediction: Increased CORTf levels, reduced body condition, and avian influenza virus infection will reduce the probability of survival in Blue-winged Teal.

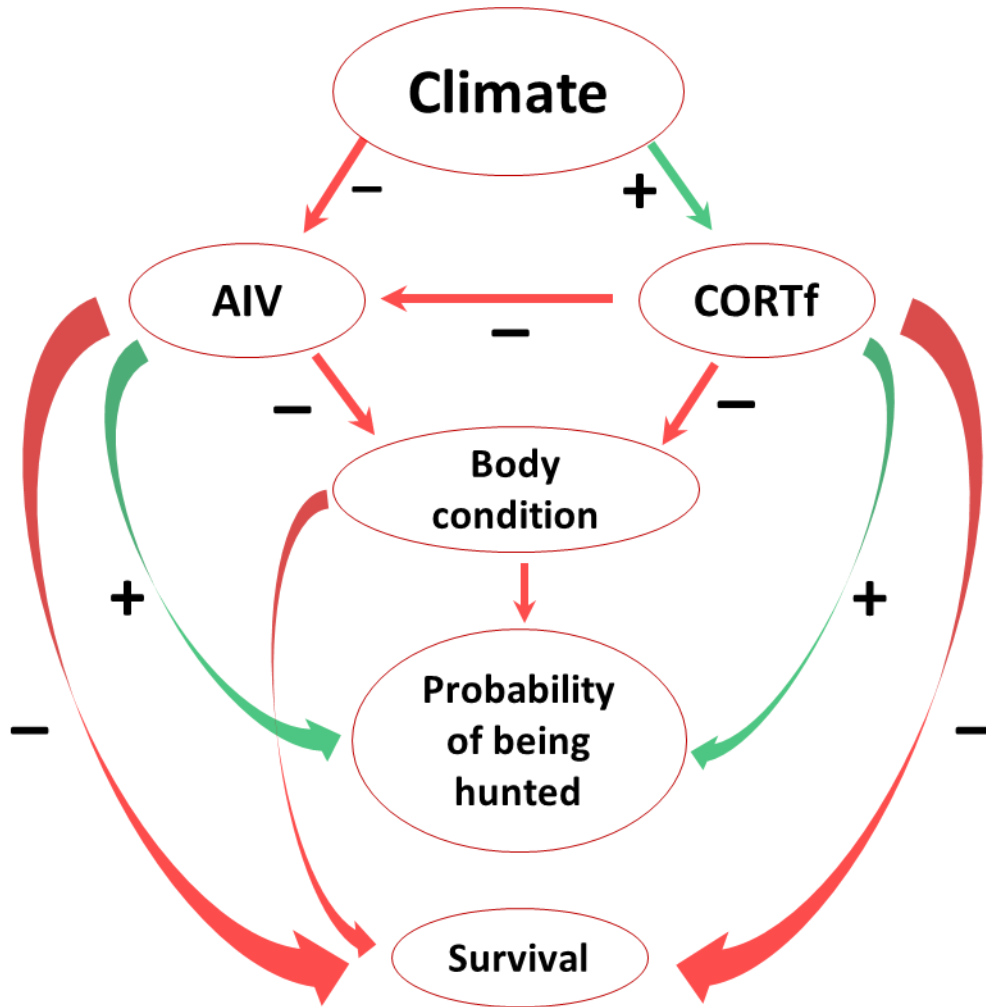


Figure 1.4. Overview of the associations among climate, stress response/energy expenditure (represented by CORTf), avian influenza virus (AIV) infection, and body condition, and their impacts on the probability of being hunted, and overall survival in Blue-winged Teal (*Spatula discors*) in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba), from 2007-18. A priori predictions are represented by + and – symbols, which indicate predicted positive and negative relationships, respectively. Green and red arrows also indicate predicted positive and negative relationships, respectively. Abbreviations: AIV = Avian influenza virus infection and CORTf = Feather corticosterone.

CHAPTER 2: ASSOCIATIONS AMONG CLIMATE, STRESS, AND AVIAN INFLUENZA VIRUS INFECTION IN MIGRATORY WATERFOWL

ABSTRACT

Wildlife are increasingly faced with the need to adapt or respond to a rapidly changing environment associated with a changing climate, altered habitats, and increasing emerging infectious diseases. Appropriate responses to stressors, mediated by the hormone corticosterone (CORT) can be beneficial in life threatening situations, however, chronic stress can be energetically costly and have deleterious effects on metabolism, disease susceptibility, condition, reproduction, or survival. Waterfowl are natural reservoirs for low pathogenic avian influenza viruses (LPAIVs), and generally show no overt signs of disease. Studies have demonstrated associations between infection and body condition, timing of migration, or resighting rates, implying a potential cost to infection. I examined relationships between climate and stress responses, and how they interact to influence body condition and probability of AIV infection. Over 7000 Blue-winged Teal (*Spatula discors*) were sampled in the Canadian prairies prior to fall migration from 2007-2018. Feather CORT (CORT_f), an integrated measure of energy expenditure during the period of feather growth, was measured using commercial ELISAs. Oral and cloacal swabs were tested for AIV using established RT-PCR methods. Using information theoretic approaches to model selection, I found that waterfowl experienced higher energetic costs in response to increased variation in daily temperatures during the period of feather growth, and this cost subsequently resulted in reduced body condition index and mass. Study demonstrated a complex, non-linear relationship between AIV infection and climate 3-10 days prior to sampling. The likelihood of AIV infection decreased with mean daily minimum temperatures ranging between 7 and 10°C, and increased when mean daily minimum temperatures exceeded 12°C. Existence of this complex relationship is likely a reflection of the impacts of temperature on environmental survival of AIV, as well as on the behaviour, distribution, or movement of birds, affecting local population densities and opportunities for transmission and exposure. The results demonstrate an existence of complex relationships among climate, stress, condition, and AIV infection in migratory waterfowl, and provide evidence of impacts of climate change on stress physiology and AIV dynamics in migratory waterfowl.

2.1 Introduction

Our world is experiencing rapid large scale environmental changes associated with a changing climate, altered habitats, intensified agricultural practices, natural resource extraction, and increasing emerging infectious diseases (Millennium Ecosystem Assessment, 2011). Changes in global climate have potentiated over the mid-20th century (European Environment Agency, 2008; IPCC, 2013), with the last few decades recorded as the warmest since the 1800s (Blunden et al., 2017). While fluctuating weather patterns such as increasing temperatures, and precipitation are some of the primary and recurrent effects of global climate change, changes in sea levels, local water levels, air and food quality, vector and disease ecology and pathogenicity, and the health of animals and ecosystems are secondary effects of climate change (Chirico et al., 1997; Mondet et al., 2005; Anyamba et al., 2009; Lubroth, 2012).

Climate change has direct and indirect impacts on the health of wild animals in multiple, interacting ways, impacting individuals at the sub-cellular, physiological, and behavioural levels, and across a range of geographic scales from local to global scales (Black and Butler, 2014; Stephen and Soos, 2021). Stressors associated with a changing climate will require birds to expend additional energy to adapt to a constantly changed environment. Direct costs may be associated with thermoregulation, and an increase in coping with severe, unpredictable weather conditions (e.g., storms) and recovering from injuries in their aftermath. Indirect impacts of climate change on migratory bird health can be just as costly, and include significant alterations to habitats or food webs, forcing significant shifts in habitat choice (Nature Canada), and altered migratory patterns which can involve increased migratory distances (Howard et al., 2018) and increased migrant densities. Thus, increased competition for food resources and risk of exposure to new predators or pathogens at staging or stopover sites (Berthold, 2001; Sillett and Holmes, 2002; Alerstam et al., 2003; Newton, 2006; Hewson et al., 2016), and phenological mismatches between timing of arrival and food availability required for reproduction, offspring development, and survival (Newton, 2008; Zhang et al., 2013). All of the above scenarios present additional energetically costly challenges that migratory birds must cope with, in addition to meeting their physiological and behavioural requirements essential for normal growth, development, reproduction, immune function, and survival (Spencer et al., 2001; reviewed in Zera and Harshman, 2001; Stephen and Soos, 2021). When energy demands exceed availability of energy resources, animals can be forced to trade off energy reserves by diverting resources away from

these key activities to cope with the increased challenges associated with climate change or other stressors (Spencer et al., 2001; reviewed in Zera and Harshman, 2001; Cox et al. 2010; Crespi et al., 2013).

To meet the energetic demands and resource allocation trade-offs associated with responding to variable or unpredictable environmental changes, the stress response activates the hypothalamic-pituitary-adrenal (HPA) axis and increases circulating glucocorticoids (GCs) to mobilize energy stores. The stress response has evolved to allow animals to deal with stressors such as reduced food availability, contaminants, predators, and social interactions (Romero, 2004). After exposure to a stressor, the body responds through activation of sympathetic-adrenal-medullary (SAM) axis, facilitating in flight or fight response (Sapolsky et al., 2000; Wingfield and Romero, 2000). Stressors may also stimulate the release of GCs through activation of the HPA axis (Sapolsky et al., 2000, Wingfield and Romero, 2000; Herman et al., 2016). These GCs are responsible for mediating physiological and behavioural changes in the body facilitating increased survival through changes like increased arousal and alertness, and mobilization of energy in order to deal with the stressor (Dallman et al., 1993; Blas and Baos, 2009). Appropriate responses to stressors can be beneficial in life threatening situations, but chronic stress and persistent elevation of GCs can have deleterious effects on reproduction, development, metabolism, and survival (Bruijnzeel et al., 2001; Jovani et al., 2004). Furthermore, chronic elevations of GCs can lower the immune response, and predispose animals to diseases that they would normally be able to overcome (Padgett and Glaser, 2003).

Climate change can affect the distribution, transmission, and severity of infectious pathogens of wildlife (Chirico et al., 1997; Purse et al., 2005; Rohr and Raffel, 2010). Numerous studies exist that demonstrate existing and projected impacts of climate on host-pathogen interactions, and the emergence and spread of wildlife diseases (Lafferty, 2009; Lindgren et al., 2012; Public Health Agency of Canada). For example, the dynamics of avian influenza viruses (AIVs) have the potential to be impacted by climate change through multiple direct and indirect routes (Morin et al, 2018). Highly pathogenic or zoonotic AIVs remain a concern globally, given that they have the potential to threaten human health, food security, and wildlife populations (Ito et al., 1999; Magalhães et al., 2012; Harder et al., 2016). Waterfowl of the order Anseriformes act as natural reservoirs for most subtypes of low pathogenic AIVs, generally show no overt signs of disease or mortality (Webster et al., 1992; Takekawa et al., 2010), and may act as

potential agents in dispersing the virus along migratory flyways (Gilbert et al., 2006). Low pathogenic H5 and H7 subtypes have the potential to evolve into highly pathogenic viruses, which can cause large scale mortality in poultry and, occasionally, in wild birds, and some strains have the potential to cause illness and mortality in humans (Webster et al., 1992; Subbarao and Katz, 2000; Ellis et al., 2002; Munster et al., 2005; Chen et al., 2006; Hill et al., 2015; Verhagen et al., 2015). Climate has been shown to be an important factor in the ecology of AIVs. Avian influenza viruses can persist and remain infectious for longer periods at low temperatures compared to higher temperatures under experimental conditions (Stallknecht et al., 1990), and lower environmental temperatures prior to sampling have also been associated with a higher probability of AIV infection in waterfowl sampled in eastern Canada (Papp et al., 2017). Northern wetlands and subarctic regions are suggested to be important for overwintering transmission and maintenance of AIV's after being shed from the alimentary tract of migratory waterfowl during summer breeding (Zhang et al., 2006; Ramey et al., 2020). Thus, rising environmental temperatures in association with climate change may reduce the survival of virus in the environment (Brown et al., 2009), however, impacts on distribution, density, range, migratory pathways, and length of breeding seasons of migratory waterfowl may increase opportunities for transmission, viral reassortment, emergence of novel strains, and spread (Altizer et al., 2011; Tian et al., 2015; Morin et al., 2018).

Although waterfowl generally show no overt signs of disease or mortality, infection with LPAIV may still pose a cost to migratory waterfowl. A few studies have demonstrated relationships between AIV infection, body condition and migration in birds. Although van Dijk et al. (2015a) found no relationship between AIV infection and body mass in Mallards (*Anas platyrhynchos*), Mallards experimentally infected with AIV were shown to have lower body mass compared to ducks that were not infected (Latorre-Margalef et al., 2009a; Kleijn et al., 2010). Additionally, free-ranging Bewick's Swan (*Cygnus columbianus bewickii*) infected with AIV experienced delayed timing of spring migration by one month (van Gils et al., 2007). The results of these studies imply that there may be a cost to responding to AIV infection, despite the lack of clinical signs.

Given the above, climate change will impact AIV ecology in migratory birds through its impacts on stress responses, population ecology, migratory pathways, and on AIV transmission and spread. The relationships among climate, stress responses, and AIV infection are likely to be

complex, and have yet to be investigated. The role of stress in relation to climate and AIV infection, and how they interact to impact body condition in wild waterfowl are currently unknown. In this study, I investigated the relationships among climate, stress, AIV infection, and body condition in Blue-winged Teal (*Spatula discors*) sampled prior to fall migration in the Canadian prairies. Feather corticosterone (CORTf) was used as an integrated measure of HPA activity during the period of feather growth, representing an index of the stress responses and energy expended during that period (Bortolotti et al., 2008). Feather CORT has been successfully used to reveal possible links between energetically costly responses to environmental conditions during the moulting period, and subsequent carry over effects on reproductive success and survival in the subsequent breeding period in migratory birds (Harms et al., 2015). I predicted that CORTf would vary in response to climatic parameters measured during the period of feather growth. Further, I examined CORTf in relation to body condition at time of sampling, and predicted that measures of body condition would decrease in response to increasing CORTf levels (which reflect increased energetic demand during moult). In addition, I predicted that the likelihood of AIV infection would vary with climatic variables measured prior to sampling, would increase in response to higher CORTf levels, and that AIV infection would also reduce body condition. Blue-winged teal is an ideal species in which to examine these relationships because it has one of the most extensive migratory ranges amongst waterfowl species and they are abundant in prairie wetlands prior to fall migration, which is when they have the highest prevalence of AIV infection throughout their annual cycle (Nallar et al., 2015; Rohwer et al., 2020).

2.2 Methodology

2.2.1 Archived data and feather samples

This study made use of archived and newly collected field and AIV data obtained from over 7000 Blue-winged Teal in Alberta, Saskatchewan, and Manitoba, from 2007 to 2018, as part of ongoing investigations on the ecology of AIV infection in the Canadian prairie provinces (Appendix A). All birds ($n = 7549$) with available AIV real-time polymerase chain reaction (RT-PCR) result were used for apparent AIV prevalence in Blue-winged Teal. For CORTf analysis, archived and newly collected feather samples were randomly selected for a subset of 40-50 birds per year with a total target sample size of 595 birds for 12 year period. Available data for each

bird included band ID, location, date of sampling, age, sex, province, mass, head-to-bill length, CORTf and AIV RT-PCR result (of the matrix gene), however body mass was available for only 557 of these birds.

2.2.2 *Field methods*

Sampling of Blue-winged Teal occurred in mid to late August, prior to fall migration, in collaboration with Canadian Wildlife Service (CWS) and United States Fish and Wildlife Service (USFWS) field crews during annual waterfowl banding programs. Field methods were followed as outlined in Nallar et al. (2016). Briefly, ducks were captured using standard bait traps (USFWS; CWS). Each duck was banded with a uniquely numbered USFWS leg band, and information on band ID, location, latitude, longitude, date of sampling, age, sex, mass, and head-to-bill length was recorded. Age and sex were determined by experienced USFWS or CWS waterfowl biologists, by assessing wing plumage (Pearse et al., 2014), and examining bills for the presence of numerous small spots which are present in females, and lacking in males (Mouronval, 2016). Each bird was weighed in a cloth bag using a Pesola spring scale to nearest 1-5 grams, and head-to-bill length was measured from the tip of the beak to the back of the head using callipers to nearest 0.1 millimetre.

To assess AIV infection status, oral and cloacal swabs were collected and placed in a cryovial containing modified Hanks buffer, and stored as described in Parmley et al. (2011). One tail feather (second outermost rectrix from the right) was plucked and stored at room temperature, in a paper envelope until analyses for CORTf could be done. All field work and procedures including capture, handling, and sampling were approved by the University of Saskatchewan's Animal Research Ethics Board (protocol 20070039) and adhered to the Canadian Council on Animal Care guidelines for humane animal use.

2.2.3 *Laboratory analysis*

2.2.3.1 *Feather corticosterone*

Feather corticosterone of tail feathers was used in this study to represent an integrated measure of HPA activity during the period of feather growth, which generally occurs throughout July and early August in Blue-winged Teal in the prairies (Rohwer et al., 2020). A total of 595 tail feathers were measured, weighed, and processed following a methanol-based protocol for

CORT extraction described by Bortolotti et al. (2008). These methods have been previously successfully used for CORTf analysis of numerous avian species including nestling Tree Swallows (Harms et al., 2010), Clark's Nutcrackers (Fairhurst et al., 2011), Cory's Shearwaters (Fairhurst et al., 2012), and Common Eiders (Legagneux et al., 2013). Briefly, for each feather, after measuring mass and length, the calamus was removed and the length of the remaining feather was measured (to the nearest mm) and weighed (to the nearest mg). The sample was then cut into pieces (less than 5 mm) using scissors, and pieces were placed into glass scintillation vials. Methanol (10 ml) was then added to the sample vials, which were then placed in a sonicating water bath for 30 minutes, followed by overnight incubation at 50°C and 100rpm in a shaking water bath. Contents of each sample vial were vacuum filtered and rinsed with 5 ml methanol to remove feather material from the methanol solution. The filtration funnel was rinsed with 5ml of methanol and dried to prevent cross-contamination between samples. Methanol was then evaporated, either by placing vials in a fume hood until complete evaporation (first 13 batches) for 48-72 hours, or by using a vacuum concentrate evaporator (CentriVap, Labconco, Kansas City, Missouri) to standardize and reduce the amount of time required, 6-8 hours, for complete evaporation of samples (latter 7 extraction batches; see below).

Feather samples collected in 2007-15 (n = 474) were extracted in 13 batches without counterbalancing years and sites across all extraction batches as they were analysed chronologically and by site. Feather samples collected in 2015-2018 (n = 121) were extracted randomized and blind, counterbalancing year and site across 7 extraction batches. For the latter 7 extraction batches, a slight modification of extraction technique was used to reduce variation in data associated with the extraction process. Changes included the use of an evaporator to standardize and reduce the amount of time required for the evaporation of samples, and the use of larger round bottom glass tubes for the evaporation process, rather than smaller vials with flat bottoms.

Feather extracts were reconstituted in 500ul ELISA buffer using commercially available ELISA kits (Cayman Chemical Company, MI, USA) following manufacturer instructions. Reconstituted feather extracts were then stored at -20°C until analysis. All extracts were measured for CORT in triplicate, using a plate reader set at 412 nm (BMG SPECTROstar Omega, Mandel Scientific, Guelph, Canada), and quantified in pg/mm of feather (Bortolotti et al., 2008). Intra-assay variability, the percent coefficient of variation (CV) within ELISA plates,

was calculated using sample CORTf concentrates run in triplicate. The inter-assay variability, the percent coefficient of variation (CV) between ELISA plates, was calculated using internal CORT standards run across all plates. Intra and inter-assay variability were 6.31% and 16.28% respectively, for all 595 samples analysed using 43 ELISA plates. Intra-assay CVs were similar between the first 13 extraction batches (CV = 6.20%) and the last 7 batches (6.71%), but inter-assay variation was lower for the last 7 batches (12.15%, 18 ELISA plates) compared to the first 13 batches (20.40%, 25 plates), possibly because of improvement in pipetting, technique, and assay setup in the latter part of the experiment. Serial dilutions of pooled and individual feather sample extracts produced displacement curves that were parallel to the standard curve (Appendix B). Feather corticosterone analyses were performed at the Prairie and Northern Wildlife Research Centre, Environment and Climate Change Canada (ECCC), Saskatchewan, Canada.

2.2.3.2 Avian influenza virus screening

Avian influenza virus samples collected in 2007-10 were analysed as part of Canada's Inter-agency Wild Bird Influenza Survey. For the latter years, (2011-18), swab samples were analysed at National Centre for Foreign Animal Disease (NCFAD), Canadian Food Inspection Agency (CFIA), in Winnipeg, Manitoba. The samples were analysed using a RT-PCR analysis targeting the matrix 1 gene, as described by Spackman et al. (2002), and by using standardized methods in all participating labs (Parmley et al., 2008). Cycle threshold values of equal to or less than 35 were considered positive.

2.2.4 Climate data

For each year, temperature and precipitation data was obtained from ECCC's National Climate Data and Information Archive (NCDIA) (https://climate.weather.gc.ca/historical_data/search_historic_data_e.html) for time periods (July and August) and regions where birds likely moulted (Rohwer et al., 2020). Weather data was obtained from weather stations located within 25 kilometres of each sampling site. If data was missing for a given weather station, information from the next closest weather station was used (<50 km from the sampling site). Daily minimum (min), maximum (max), and average temperatures for each site were used to estimate the average daily min, max, average and standard deviation of temperatures for the month of July, as well as for July 1-16, and July 17-

31. These time periods were selected as covariates to explore sources of variation in CORTf, given that Blue-winged Teal generally moult their primary flight and tail feathers, throughout July and early August in the Canadian prairies (Rohwer et al., 2020), and birds were being sampled in early to mid-August. Temperature covariates used for examining variation in probability of AIV infection were similar to Hall et al. (2019); I used temperature covariates experienced by birds before the day of sampling (lag times), ranging from 0 to 14 days prior to sampling, where 0 day indicates the temperature on the day of sampling. This data was then also used to calculate mean daily minimum, maximum, and mean temperatures for time periods between 0-7 days, 3-10 days, and 7-14 days prior to sampling date. These daily lag temperatures and their ranges in relationship to AIV infection were based on experimental findings of Hall et al. (2015) in sea ducks. Total daily precipitation data was used to calculate average total precipitation for the same time periods described above.

2.2.5 Migratory waterfowl population and pond density data

I obtained estimates of spring waterfowl breeding population density and pond density for each region in which ducks were sampled from 2007-2018, from the Waterfowl Breeding Population and Habitat Survey, an ongoing annual program led by the USFWS and CWS since 1955 (Smith, 1995). Spring pond density and breeding population density for Blue-winged Teal and for all dabbling duck species were estimated from aerial transects, and defined as the number of ducks or standing water bodies counted per km² of transects within each stratum surveyed in May each year (USFWS). As previously described by Nallar et al. (2016) and Papp et al. (2017), estimates of spring breeding population density were used as a proxy for population density during moulting or sampling periods, with the assumption that a positive correlation exists between population densities in the spring and July/August. This assumption is supported by evidence that spring pond and breeding density are positively correlated (Johnson and Grier, 1988; Nallar et al., 2015), and result in higher reproductive success, and hence higher population densities, in late summer (Howerter et al., 2014).

2.2.6 Statistical analysis

Descriptive analyses were completed using the program R (R Development Core Team, 2016 version 3.4.2) and Microsoft Excel. Statistical analysis were conducted in R using information theoretic approaches to model selection.

CORTf: Prior to analysing the *CORTf* data, I examined whether extraction batch confounded the effects of year and site, given that the first 13 batches of feather samples were processed in chronological order (2007-15) without randomizing year or province across extraction batches. A two way-ANOVA was conducted (including batch and province-year as categorical variables) to examine the effects of both extraction batch and province-year. The results demonstrated that the variation in *CORTf* observed in batches 1-13 and batch 14-20 was not associated with extraction batch (Batches 1-13: $F_{\text{batches}}(11, 474) = 0.82, p = 0.62$; Batches 14-20: $F_{\text{batches}}(6, 121) = 1.68, p = 0.13$), but was associated with province-year (Batches 1-13: $F_{\text{province-year}}(22, 474) = 7.24, p = 0.0001$; Batches 14-20: $F_{\text{province-year}}(21, 121) = 2.1, p = 0.06$). This result suggests that extraction batch was not a confounding variable nor a source of significant variation in my *CORTf* data.

I investigated the influence of climatic factors during the period of feather growth, and other environmental and demographic factors (listed in Table 2.1.), on *CORTf*, using generalized linear mixed models (GLMER), with year as a random term (Package 'lme4', Bates et al., 2015). To account for skewedness in the distribution of *CORTf* data, family Gamma and link identity were used to construct models (Bengtsson et al., 2016).

AIV: I used GLMER with year as a random term, and binomial distribution, using a logit link function based on maximum likelihood estimation, to examine whether *CORTf* and other environmental variables were associated with the probability of AIV infection. To explore effects of temperature on AIV infection at the time of exposure, multiple measures of lag temperature prior to the date of sampling were explored to approximate the time period when positive birds were most likely exposed, using similar lag temperature ranges as described in Hall et al. (2019) and Papp et al. (2017). Temperature has been shown to be important for survival of AIVs in the environment, and hence, AIV transmission (Stallknecht et al., 1990). Other variables previously shown to influence AIV infection in waterfowl were also included as covariates (e.g., age, sex, Blue-winged Teal population density, and province) (Table 2.2.).

Body condition and mass: Body condition index (BCI) was estimated for each bird, using a method described by Peig and Green (2009), incorporating mass and body size to define the energy capital accumulated in the body. Linear mixed models (LMER) with year as a random term were explored to examine the role of CORTf and AIV infection in explaining variation in body condition. Age, sex, and province were also included in the analyses. Similar models were constructed to examine the role of CORTf and AIV infection on body mass, given that body mass has been shown to be an important indicator of condition in other waterfowl species (Thompson, 1961; Bêty et al., 2003; Klaassen et al., 2006; Dannemiller et al., 2017).

Model selection strategy: Explanatory variables with an initial association with the outcome variable in univariate models were selected and further explored in models containing multiple variables that were not collinear (Murray and Conner, 2009). Biologically meaningful two-way interactions were also explored. Models containing only informative variables were ranked using Akaike's information criterion (AICc) adjusted for sample size (Anderson, 2007), using the MuMIn package (Barton, 2012). Explanatory variables were deemed uninformative or redundant if their ΔAICc were >2 units relative to the null model in univariate models, if their addition to models with existing variables did not further reduce AICc, and if their 95% confidence intervals spanned zero (Akaike, 1974; Burnham and Anderson, 2004; Arnold, 2010). Error distribution and model assumptions (model diagnostics) were checked using residual plots in DHARMA package (Hartig, 2017).

Table 2.1. List of explanatory variables used in models for explaining environmental and demographic factors affecting variation in corticosterone levels of the tail feather (CORTf, pg/mm) in Blue-winged Teal (*Spatula discors*; BWTE) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in 2007 to 2018.

Variable	Type	Description	Categories/Units/Range
Year	Random term	Year of sampling	2007 – 2018
Age	Categorical	Age at capture	Hatch Year (< 1 year old)/ After Hatch Year (> 1 year old)
Sex	Categorical	Sex	Female/ Male
Province	Categorical	Province where duck was sampled	Alberta/ Saskatchewan/ Manitoba
Mean daily minimum temperature during the period of feather growth	Continuous	Mean daily minimum temperatures for July 1-31, July 1-16, and July 17-31	July 1-16 = 7.3 – 17.2 °C July 17-31 = 9.3 – 16.9 °C July 1-31 = 8.3 – 16.9 °C
Mean daily maximum temperature during the period of feather growth	Continuous	Mean daily maximum temperatures estimated for the period of feather growth for July 1-31, July 1-16, and July 17-31	July 1-16 = 18.6 – 30.0 °C July 17-31 = 22.7 – 30.9 °C July 1-31 = 20.8 – 29.6 °C
Mean daily temperature during the period of feather growth	Continuous	Mean daily temperatures for July 1-31, July 1-16, and July 17-31	July 1-16 = 12.9 – 23.3 °C July 17-31 = 16.2 – 23.3 °C July 1-31 = 14.6 – 23.2 °C
Mean daily standard deviation in temperature during the period of feather growth	Continuous	Mean daily standard deviation in temperatures for July 1-31, July 1-16, and July 17-31	July 1-16 = 1.4 – 5.0 °C July 17-31 = 1.3 – 3.2 °C July 1-31 = 1.8 – 4.9 °C
Mean total daily precipitation during the period of feather growth	Continuous	Mean daily total precipitation for July 1-31, July 1-16, and July 17-31	July 1-16 = 0.1 – 6.9 mm July 17-31 = 0 – 5.8 mm July 1-31 = 0.03 – 4.9 mm
Population density	Continuous	Total dabbling duck breeding population density, estimated by aerial surveys in spring	2.3 – 17.9 ducks/km ²

Blue-winged Teal density	Continuous	Total BWTE breeding population density estimated by aerial surveys in spring	0.4 – 6.7 BWTE/km ²
Pond density	Continuous	Total number of ponds estimated by aerial surveys in spring	0.9 – 6.9 ponds/km ²

Table 2.2. List of explanatory variables used in models for explaining factors influencing the probability of avian influenza virus (AIV) infection in Blue-winged Teal (*Spatula discors*; BWTE) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in 2007 to 2018.

Variable	Type	Description	Categories/Units/Range
Feather corticosterone (CORTf)	Continuous	Feather corticosterone levels	Pg/mm
Year	Random term	Year of sampling	2007 – 2018
Age	Categorical	Age at capture	Hatch Year (< 1 year old)/ After Hatch Year (> 1 year old)
Sex	Categorical	Sex	Female/ Male
Province	Categorical	Province where duck was sampled	Alberta/ Saskatchewan/ Manitoba
Mean daily minimum lag temperature	Continuous	Mean daily minimum temperatures for time period* prior to the date of sampling	0-7 days = 6.4 – 15.7°C 3-10 days = 7.3 – 15.9°C 7-14 days = 6.9 – 15.6°C
Mean daily maximum lag temperature	Continuous	Mean daily maximum temperatures for time period* prior to the date of sampling	0-7 days = 19.5 – 30.8 °C 3-10 days = 20.0 – 31.2 °C 7-14 days = 19.5 – 30.7 °C
Mean daily lag temperature	Continuous	Mean daily temperatures for time period* prior to the date of sampling	0-7 days = 13.3 – 21.5 °C 3-10 days = 13.7 – 21.5 °C 7-14 days = 13.4 – 21.5 °C
Population density	Continuous	Total dabbling duck breeding population density, estimated by aerial surveys in spring	2.3 – 17.9 ducks/km ²
Blue-winged Teal density	Continuous	Total BWTE breeding population density estimated by aerial surveys in spring	0.4 – 6.7 BWTE/km ²
Pond density	Continuous	Total number of ponds estimated by aerial surveys in spring	0.9 – 6.9 ponds/km ²

*Variables for lag minimum, maximum and mean temperatures were estimated for 0-7 days, 3-10 days, and 7-14 days prior to sampling.

2.3 Results

2.3.1 Factors affecting variation in feather corticosterone in Blue-winged Teal

Of the 7549 Blue-winged Teal sampled in Alberta, Saskatchewan, and Manitoba from 2007 to 2018, CORTf was measured in a subset of 595 individuals.

Descriptive statistics: CORTf ranged from 0.002pg/mm to 15.83 pg/mm, and means for age, sex, and province are presented in Supplementary Information (Appendix C). Manitoba ($2.21 \text{ pg/mm} \pm 0.31$) had higher mean CORTf levels in comparison to Alberta ($1.4 \text{ pg/mm} \pm 0.11$) and Saskatchewan ($1.48 \text{ pg/mm} \pm 0.1$; Appendix C). CORTf levels were similar among females and males, but after hatch year (AHY) birds had higher CORTf ($1.68 \text{ pg/mm} \pm 0.11$) compared to hatch year (HY) birds ($1.37 \text{ pg/mm} \pm 0.1$; Appendix C).

Model results: Based on my top model (Table 2.3.; Appendix D.1. and Appendix D.2.), the mean daily standard deviation of temperature during the period of feather growth in the first half of July (July 1-16) explained most of the variation in CORTf ($wAICc = 0.985$). CORTf increased with increased variation in daily temperatures ($\beta = 0.81 \pm 0.15$; Table 2.3.; Figure 2.1.), which suggests there is an energetic cost for Blue-winged Teal to respond to increased variation and ranges of temperatures. Mean daily standard deviation of temperature during the latter half of July (July 17-31) was also a competitive model in relation to the null (Appendix D.1.), with a similar positive association (Appendix D.1.), however it was outcompeted by the same variable for the time period within the first half of July, and explained a negligible amount of additional variation ($wAICc = 0.001$; Appendix D.1.). The second ranked model showed a positive association between CORTf and mean daily minimum temperatures for the latter half of July ($\beta = 0.22$; 95% CI = 0.13, 0.31), however it was out-ranked by the top model, and explained only an additional 1.4% of the variation in CORTf (Appendix D.1.). Univariate models containing age and province improved the null model when examined alone (Appendix D.2.), however they ranked low in my candidate set of models, and explained no additional variation in CORTf beyond that explained by the top model (Appendix D.1.), and were not informative when combined with the top ranking temperature variables (Appendix D.2.).

Table 2.3. Best supported generalized linear mixed model using year as a random term and family Gamma, and link Identity explaining variation in feather corticosterone in Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba), in August (2007-2018) prior to fall migration (n = 595).

Variables	β	SE	P
Intercept	-0.70	0.45	0.12
SD Temp. July 1-16	0.81	0.15	<0.0001

Intraclass Correlation Coefficient for Random term (Year) = 0.35

Abbreviations: β = Coefficient estimate; SE = Standard error; P = p-value; and SD Temp. July 1-16 = Mean daily standard deviation in temperatures for July 1-16.

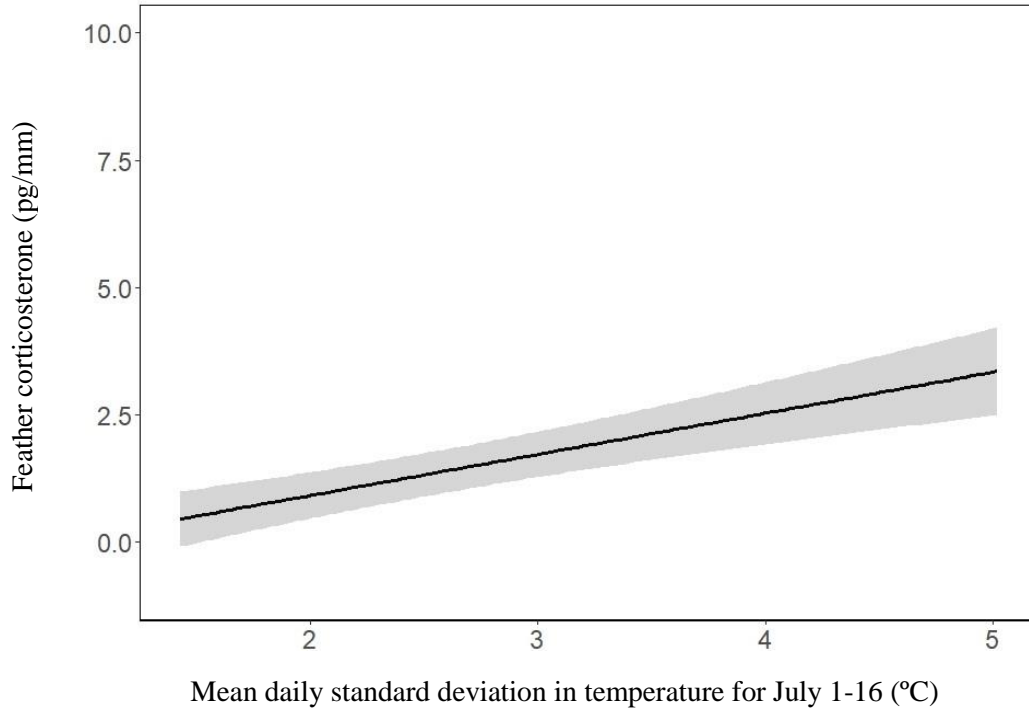


Figure 2.1. Model-estimated effects of mean daily standard deviation in temperature in the first half of July (July 1-16) (95% CI, grey zone) on feather corticosterone levels in Blue-winged Teal (*Spatula discors*) sampled in Alberta, Saskatchewan, and Manitoba in 2007-18. Estimates are based on the best-supported generalized linear mixed model in Table 2.3.

2.3.2 Overview of AIV in Blue-winged teal from 2007 to 2018

Descriptive statistics: From 2007 to 2018, 7549 Blue-winged Teal were sampled in the Canadian Prairies during annual waterfowl banding programs. The overall apparent prevalence of AIV infection in Blue-winged Teal during this period was 12.45% (95% CI = 11.71, 13.22; Table 2.4.). Annual variation in apparent prevalence ranged from as high as 31.13 % in 2010 (95% CI = 27.5, 34.94) to as low as 0.45 % in 2008 (95% CI = 0.05, 1.62; Figure 2.2.). Considerable variation in apparent prevalence of AIV was also observed among provinces, ranging from 7.74% in Alberta to 25.71% in Manitoba (Table 2.4.). HY birds showed a significantly higher apparent prevalence (19.14 %, 95% CI = 17.89, 20.43) compared to AHY birds (5.8 %, 95% CI = 5.07, 6.57). Females (16.9 %, 95% CI = 15.53, 18.34) appeared to have a slightly higher apparent prevalence compared to males (10.59 %, 95% CI = 9.72, 11.5), however this trend was likely driven by that fact that a large proportion of females sampled were HY birds, while a larger proportion of males sampled were AHY birds (Table 2.4.).

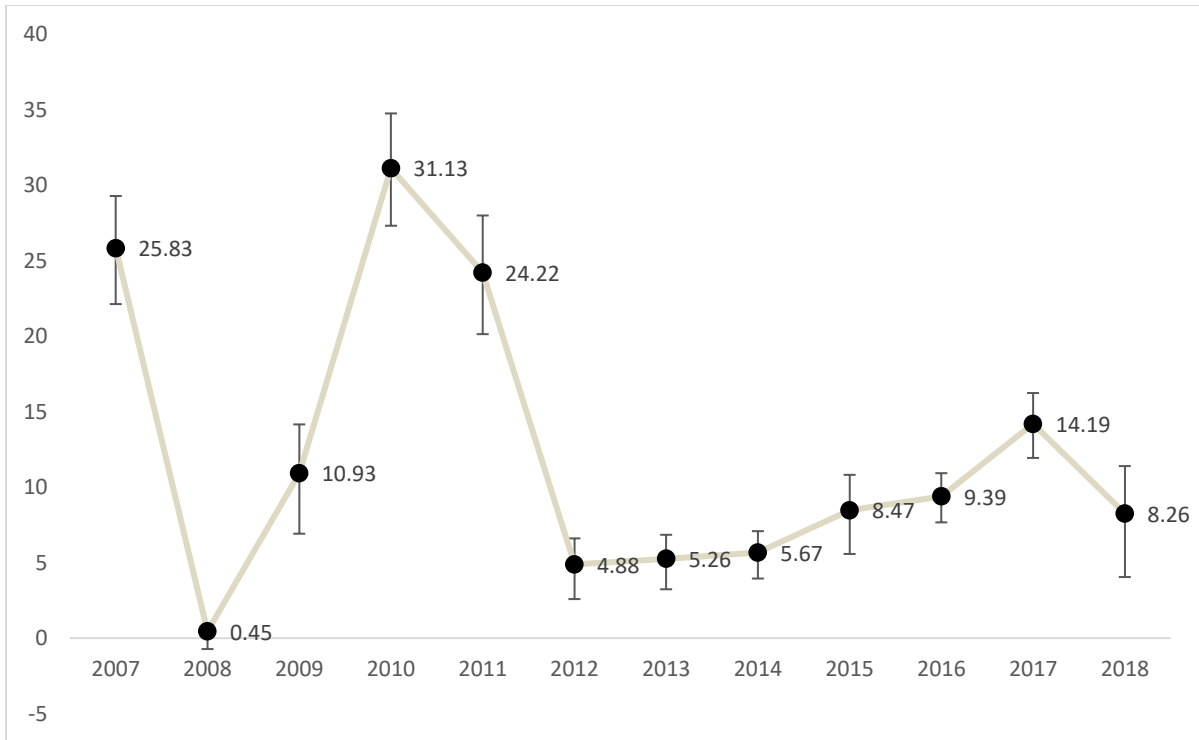


Figure 2.2. Annual apparent prevalence of Avian Influenza Virus (AIV) in Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in 2007-18 (n = 7549).

Table 2.4. Apparent prevalence of Avian influenza virus infection in Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in 2007-18 by year, age (Hatch Year: HY; After Hatch Year: AHY), sex and provinces (n = 7549).

	N	Apparent prevalence	95% CI
Overall	7549	12.45	11.71, 13.22
By Age			
HY	3751	19.14	17.89, 20.43
AHY	3834	5.79	5.07, 6.57
By Sex			
Female	2798	16.9	15.53, 18.34
Male	4751	10.59	9.72, 11.5
By Age-Sex			
HY- Female	1783	20.19	18.35, 22.13
AHY- Female	1015	7.59	6.03, 9.4
HY- Male	1932	18.53	16.82, 20.34
AHY-Male	2819	5.14	4.36, 6.02
By Province			
Alberta	2261	7.74	6.67, 8.92
Manitoba	840	25.71	22.79, 28.81
Saskatchewan	4448	12.34	11.39, 13.34

Abbreviations: N = Total number of birds; 95% CI = 95% confidence intervals; HY = Hatch years; and AHY = After hatch years.

2.3.3 *The role of feather corticosterone and environmental variables in explaining variation in AIV infection*

Model results: For this analysis, 557 Blue-winged Teal had complete data on AIV status, CORTf, mass or BCI, age, and sex. My best-supported model (Table 2.5.; Appendix E), showed that age and mean daily minimum temperatures 3-10 days prior to sampling explained most of the variation in the probability of AIV infection, and outranked all other candidate models (Appendix E, E.1., and E.2.). As in previous studies, the probability of AIV infection was higher in hatch year birds compared to after hatch year birds ($\beta = 1.79 \pm 0.40$). The addition of the quadratic term for mean daily minimum temperatures significantly improved the model by reducing AICc by an additional 14 units (Appendix E.2.), showing a non-linear association of AIV infection in relation to this lag temperature variable (Figure 2.3.; Table 2.5.). These results indicate that the probability of AIV infection decreased with increasing mean minimum daily temperatures up to about 10°C, after which the relationship levelled off, and became a positive relationship at mean minimum daily temperatures above 12°C (Figure 2.3.). The second best model exhibited a similar trend, using mean daily minimum temperatures 7-14 days prior to sampling, however, it was well outranked by the 3-10 day variable, and explained an additional 2% of the variation in probability of AIV infection (Appendix E.1.). The third best model in my competitive model set contained age and province, however it was outcompeted by the top model, and explained no additional variation in the probability of AIV infection (Appendix E.1.; Appendix E.2.). Mean minimum daily temperatures 0-7 days prior to sampling also improved the null model when examined on its own, but was well outranked by the 3-10 day and 7-14 day lag variables (Appendix E.2.). Models exploring other lag temperature variables such as mean daily maximum temperature and mean daily temperatures for time period 3-10 days, as well as temperature variables for lag periods at 0-7 days and 7-14 days either did not improve the null, or were outcompeted, and were thus dropped from modeling (Appendix E.2.). In contrast to previous studies, population density of Blue-winged Teal was not informative when examined alone or in combination with other variables (Appendix E.2.). However, total dabbling duck population density was marginally informative in relation to the null, but explained no additional variation in probability of AIV infection when combined with age and mean daily temperatures

prior to sampling, which explained most of the variation in AIV (Appendix E.2.). Furthermore, the probability of AIV infection was not associated with CORTf or sex (Appendix E.2.).

Table 2.5. Best supported generalised linear model using year as a random term and family Binomial, and link Logit with coefficient estimates and standard errors, fitted to estimate probability of avian influenza virus infection in Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in 2007-18. The feather samples and oral and cloacal swab samples were collected in August (2007-2018) prior to fall migration of birds (n = 557).

Variables	β	SE	P
Intercept	14.01	5.13	0.006
Age (Ref= HY)	1.79	0.40	<0.0001
Lag Mean Daily Min Temp_{3-10d}	-3.30	0.87	0.0002
(Lag Mean Daily Min Temp_{3-10d})²	0.15	0.04	<0.0001

Intraclass Correlation Coefficient for Random term (Year) = 0.16

Abbreviations: β = Coefficient estimate; SE = Standard error; P = p-value; Ref = Reference; HY = Hatch year; and Lag Mean Daily Min Temp_{3-10d} = Mean daily minimum lag temperature 3-10 days prior to sampling day.

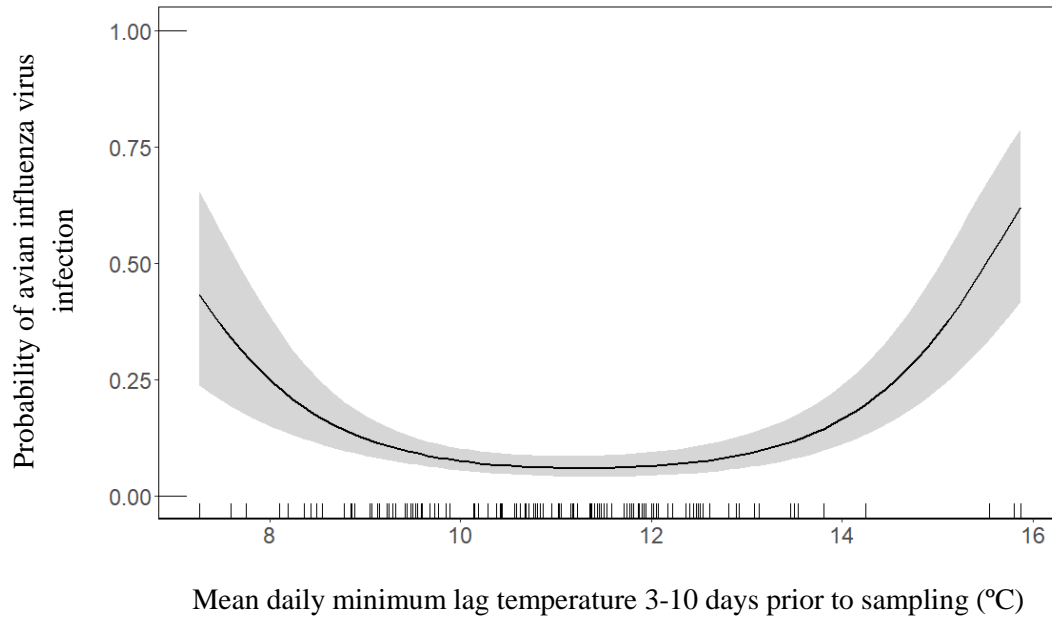


Figure 2.3. Predicted probability of avian influenza virus infection (95% CI, grey zone) in Blue-winged Teal (*Spatula discors*) as a function of mean daily minimum lag temperature 3-10 days prior to sampling. Predicted probability was estimated based on the best-supported generalized linear mixed model shown in Table 2.5., with Age set at hatch year.

2.3.4 *The role of feather corticosterone in explaining variation in mass and body condition index*

Descriptive statistics: AHY birds had higher mean body mass, but lower mean BCIs compared to HY birds (Appendix F). Males were heavier than females, but females had higher mean BCIs compared to males (Appendix F). Amongst the three prairie provinces, birds sampled in Saskatchewan had relatively higher mean body mass compared to ducks in Alberta and Manitoba, and ducks in Manitoba appeared to have the lowest BCIs compared to birds in Saskatchewan and Alberta (Appendix F).

Model results: The best-supported model examining factors influencing BCI demonstrated an interaction with $CORT_f$ and sex (Tables 2.6., Appendix H, and Appendix H.1.). The BCI decreased with increasing levels of $CORT_f$, and the magnitude of the effect was significantly more prominent in females compared to males (Figure 2.4.; Table 2.6.). Although age was informative compared to the null model when examined on its own, it was determined to be an uninformative variable when added to the top model, given that its 95% CI spanned zero ($\beta = -3.55$; 95% CI = -18.5, 11.6; Appendix H.2.). AIV infection status was determined to be uninformative when combined with the top model ($\beta = 11.39$; 95% CI = -12.10, 35.01; Appendix H.2.), as was province (MB: $\beta = -10.41$, 95% CI = -34.66, 13.58; SK: $\beta = 1.70$, 95% CI = -13.38, 16.82). The best-supported model examining factors influencing body mass demonstrated that, similar to BCI, mass decreased with increasing levels of $CORT_f$ (Table 2.7., Appendix G.1., and Appendix G.2.; Figure 2.5.). However, there was no interaction between sex and $CORT_f$, and males were significantly heavier compared to females (Figure 2.5.). Furthermore, AHY birds were significantly heavier compared to HY birds, and ducks sampled in Saskatchewan and Manitoba were heavier than ducks in Alberta (Table 2.7.).

Table 2.6. Best supported linear mixed models using year as a random term with coefficient estimates and standard errors, fitted to estimate probability of body condition index in Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba). Samples were collected in August (2007-2018) prior to fall migration of birds (n = 557).

Variables	β	SE	P
Intercept	435.61	10.54	<0.0001
Sex (Ref= Male)	76.33	9.84	<0.0001
CORTf	-8.62	3.22	0.01
Sex * CORTf	8.34	3.97	0.04

Intraclass Correlation Coefficient for Random term (Year) = 0.08

Abbreviations: β = Coefficient estimate; SE = Standard error; P = p-value; Ref = Reference; and CORTf = Feather corticosterone.

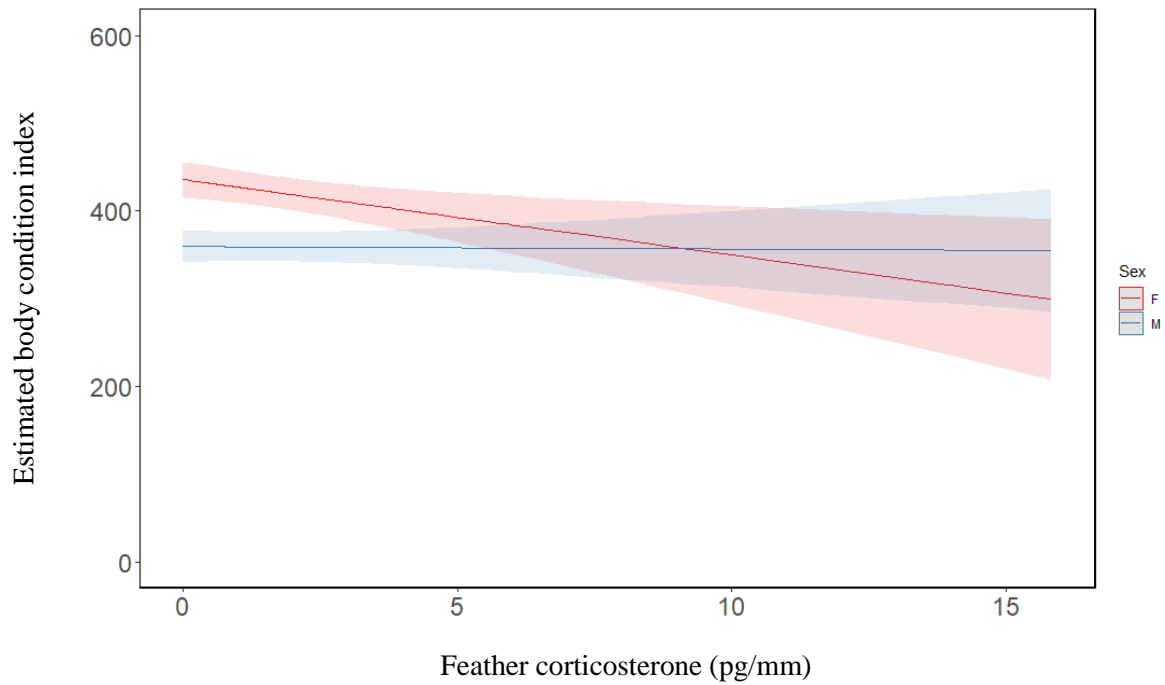


Figure 2.4. Estimated body condition index (95% CI, coloured zone) as a function feather corticosterone in male and female in Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in 2007-18. Estimates were based on the best-supported linear mixed model (Table 2.7.) using year as a random term. Red line = females and Blue line = males.

Table 2.7. Best supported linear mixed models using year as a random term with coefficient estimates and standard errors, fitted to estimate probability of body mass (grams) in Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba). The samples were collected in August (2007-2018) prior to fall migration of birds (n = 557).

Variables	β	SE	P
Intercept	363.41	5.05	<0.0001
Province (Ref = Alberta)			
Manitoba	16.19	6.24	0.01
Saskatchewan	13.57	3.80	0.0004
Age (Ref = AHY)	-36.45	3.92	<0.0001
Sex (Ref= Male)	-31.01	3.80	<0.0001
CORTf	-1.53	0.98	0.12

Intraclass Correlation Coefficient for Random term (Year) = 0.04

Abbreviations: β = Coefficient estimate; SE = Standard error; P = p-value; Ref = Reference; AHY = After Hatch Year; and CORTf = Feather corticosterone.

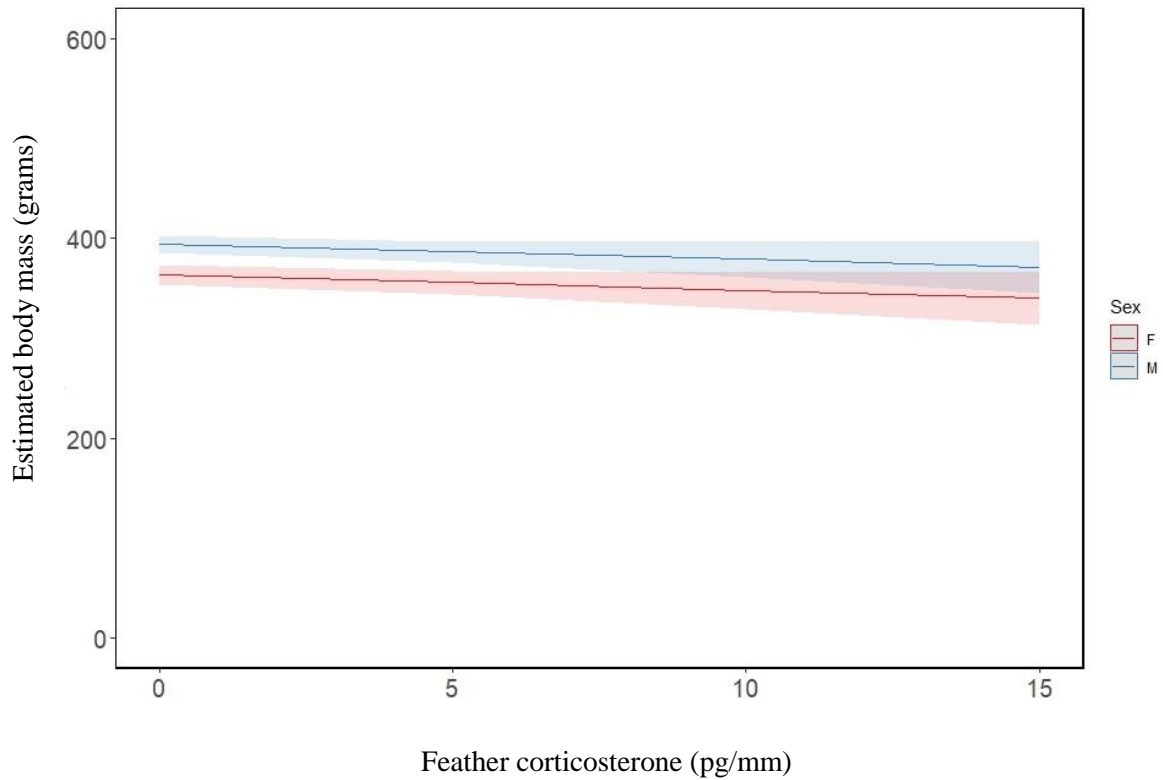


Figure 2.5. Model-estimated body mass (grams) (95% CI, coloured zone) as a function feather corticosterone in male and female Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in 2007-18. Estimates were based on the best-supported linear mixed model (Table 2.6.) using year as a random term, with explanatory variables set at Female (Sex), After hatch year (Age) and Alberta (Province). Red line = females and Blue line = males.

2.4 Discussion

In this study, I examined relationships among climate, stress, AIV, and body condition in wild waterfowl sampled in the Canadian prairie provinces from 2007 to 2018.

2.4.1 Relationships among climate, stress, and body condition

The study demonstrated that waterfowl experience energetic costs in response to increased variation in daily temperatures during the period of feather growth, and that this cost resulted in reduced body condition. These results showed that CORTf effectively linked climatic conditions experienced during the moulting period to subsequent downstream effects on multiple measures of body condition in Blue-winged Teal.

Mean daily standard deviation of temperature in the first half of July explained almost all of the variation in CORTf compared to all other climatic variables and time periods examined. The mean daily minimum temperatures, as well as the daily standard deviation of daily temperatures in the latter half of July were both positively associated with CORTf, but ranked well below the top model, and collectively explained less than an additional 2% of the variation in CORTf compared to the top model. This result suggests that birds must mobilize more CORT, and hence expend more energy in order to maintain homeostasis, by physiologically responding to higher variability and ranges of temperature during the period of moult. Similarly, Treen et al. (2015) found elevated CORTf levels among birds in areas with higher temperature variations in House Sparrows (*Passer domesticus*). Nestling Tree Swallows (*Tachycineta bicolor*) were also shown to have higher CORTf levels in relation to increased temperature variations in nest boxes (Fairhurst et al., 2012). Legagneux et al. (2013) also found an association between CORTf levels and climatic variables in arctic-nesting Common Eiders (*Somateria mollissima*), however they found that average temperatures during the period of moult (August-September) explained most of the variation in CORTf, compared to standard deviation of temperature in that same time period, which explained an additional 10% of the variation in CORTf. Other studies which have demonstrated relationships between CORTf levels and average temperatures, have revealed positive associations (Fairhurst et al., 2012; Treen et al., 2015), as well as negative associations (López-Jiménez et al., 2016), and Treen et al. (2015) demonstrated a negative association with precipitation.

Climatic variations may also indirectly increase $CORT_f$ by contributing to behavioural and physiological responses to reductions in food availability or quality (Kitaysky et al., 2007; Doody et al., 2008; Sears and Hatch, 2008; Kitaysky et al., 2010; Dorresteijn et al., 2012). However, in my study, there was no evidence to suggest that increased standard deviations in temperature in July were associated with reduced food availability or quality, and temperatures were still within the normal ranges expected in the prairies in July (average July temperatures were 18.6°C, ranging from 14.6 to 23.2°C). The increased energy expended in response to more variable daily temperatures during the period of feather growth resulted in a trade-off with body condition, as measured with both mass and BCI. Thus, if ducks expended more energy and resources to adapt to more variable daily temperatures or larger temperatures ranges in the first half of July, this resulted in lower mass as well as BCI in August, just before fall migration. This suggests that responding and adapting to higher daily temperature variations during an already energetically costly period (i.e., moulting) resulted in a carry-over effect on body condition, as measured by both mass and body condition index. During the moulting period, fluctuations in body mass were observed in multiple waterfowl species in Africa, beginning with an initial decrease in mass at the start of the moulting period, and a return back to normal or higher body mass upon completion of the moulting period (Ndlovu et al., 2017). Thus, it is possible that the energy and resources required for the recovery of mass lost during feather growth may have been diverted to enable ducks to respond to the increased energetic costs associated with higher variations in daily temperatures. Furthermore, my results demonstrate that the magnitude of the impact of increased energy expenditure on BCI was significantly more prominent in females, possibly because adult females experience a higher depletion of energy reserves and loss of condition from the associated with additional energetically costly processes of egg-laying and incubation just prior to the moulting period (Harris, 1970; Rohwer, 1986; Gabrielsen et al., 1991).

Impacts on body condition, particularly just prior to migration, can have significant fitness consequences, as multiple measures of condition have been associated with delayed migration, reduced survival, and reduced reproduction in waterfowl (Anteau and Afton 2009; Harms et al., 2015; Hughes et al., 2019), and in other avian species, such as American Redstarts (*Setophaga ruticilla*; Cooper et al., 2015). In Green-winged Teal (*Anas carolinensis*), late spring migrants had significantly lower lipid reserves, compared to early spring migrants (Klimas et al.,

2019). Migration carries an enormous energetic cost (Alerstam, 1990; Newton, 2008), hence decreased body condition prior to migration can potentially have detrimental effects on migratory performance and/or survival during migration. Devries et al. (2008) found that female Mallards in better condition commenced nesting earlier, and had larger clutch sizes compared to females in poorer body condition. In a declining population of Greater White-fronted Geese (*Anser albifrons frontalis*), Schmutz and Ely, (1999) found that body condition of female geese measured during the breeding period was positively associated with survival during the subsequent fall and spring migration. Harms et al. (2015) determined that increased energetic expenses (as measured by CORTf), in response to higher temperatures during the moulting period not only resulted in a decrease in subsequent pre-breeding body condition and late arrival dates, but also indirectly impacted subsequent survival and reproduction in arctic-nesting Common Eiders. Additionally, the rapid decline of Lesser Scaup (*Aythya affinis*) population sizes during the 1970s-2000s has also been linked to reduced body condition during spring migration, resulting in a carry-over effect on subsequent reproduction (Austin et al., 2000; Anteau and Afton, 2004; 2006; 2009). Furthermore, body condition has also been associated with disease susceptibility in migrating Lesser Scaup (Merrill et al., 2018) and Mallards (Arsnoe et al., 2011).

2.4.2 *AIV infection in relation to climate, stress, and body condition*

My study revealed a complex relationship between climate and AIV infection in the Canadian prairies. The probability of AIV infection was associated with mean daily minimum temperatures 3-10 days prior to sampling, which is the period of time that an infected and actively shedding duck may have first been exposed to the virus (Hall et al., 2019). The association was non-linear, such that the probability of AIV infection decreased with increasing mean minimum daily temperatures ranging from approximately 7.3 to 10°C. As mean minimum daily temperatures increased beyond 10°C, the relationship tapered off, and became a positive association at minimum daily temperature ranges of approximately 12 to 15.9°C. Hall et al. (2019) also found a non-linear association between AIV infection and minimum sea temperatures 11 days prior to sampling in wild sea ducks in the marine environment. The range of minimum sea temperatures reported were colder compared to my study, ranging from 2 to 12°C overall, and optimal AIV infection rates occurred at approximately 5-8°C, above or below

which the probability of infection declined. Hence, similar to my study, they observed a decreasing probability of AIV infection with increasing minimum daily temperatures within ranges of 7-12°C. This negative association between AIV infection and minimum temperature was expected, based on previous studies demonstrating increased viral persistence at lower water temperatures (Stallknecht et al., 1990; Brown et al., 2009; Davidson et al., 2010; Domanska-Blicharz et al., 2010; Hall et al., 2019). For example, viability of AIV in saline water was longer at constant temperatures of 4°C (3 weeks), compared to 8°C (2 weeks; Hall et al., 2019). Furthermore, in eastern Canada, the probability of AIV infection was negatively associated with average daily temperatures from 0-14 days prior to sampling, with average temperatures ranging from 1.9-23.1°C (daily minimum temperatures were not reported in this study; Papp et al., 2017).

The positive association between probability of AIV infection and mean daily minimum temperatures ranging between 12 and 16°C may have been more associated with effects of higher temperatures on host behaviour predisposing birds to becoming exposed, rather than on impacts on viral survival in the environment. For instance, satellite-imaging studies revealed that higher temperatures restricted the distribution of migratory waterfowl during the breeding season, resulting in increased population densities, and potentially increased rates of AIV transmission (Tian et al., 2015). In response to increasing temperatures, many bird species have been shown to advance the timing of their migration (Jonzén et al., 2006), which may potentially increase the prevalence of LPAIV infection (van Dijk et al., 2014). Interestingly, ducks fitted with Global Positioning System (GPS) loggers that were infected with LPAIVs exhibited lower regional movements particularly during inclement weather, and lower local movements during warmer temperatures (van Dijk et al., 2015b), which may potentially contribute to increases in local transmission and spread within a given wetland. Even though, water temperature is a key determinant, the viability of virus is also affected by factors such as neutral/basic pH (Davidson et al., 2010; Keeler et al., 2014), low ammonia concentration (Keeler et al., 2014), low salinity (Brown et al., 2009), and lesser biological material in the water (Domanska-Blicharz et al., 2010). The pH of wetlands in the prairie pothole regions (PPR) are typically slightly acidic to alkaline (Driver and Peden, 1977; Detenbeck et al., 2002), and are known to turn alkaline to acidic from July to August (Brunet, 2011). It is unknown how temperature may interact with the above physio-chemical parameters of water in affecting the viability of AIV in wetlands of the PPR, and this was beyond the scope of my study.

Although my study determined that energy expenditure in response to climatic variation during the time of moult had a carry-over effect on subsequent condition as measured using mass and BCI, no carry-over effect was found on subsequent AIV infection. Furthermore, AIV infection had no impact on either mass or BCI, which suggests that responding to an AIV infection poses little cost to infected Blue-winged Teal. A few studies have shown that waterfowl and geese naturally infected with AIV infection had lower body mass than uninfected birds (Latorre-Margalef et al., 2009a; Kleijn et al., 2010), while others found no association (van Dijk et al., 2015a; Dannemiller et al., 2017). Nutritional condition of birds has been shown to be important in immune function (Brunner et al., 2014; Forbes et al., 2016), and birds in poorer body condition are generally more susceptible to infection and severity of disease (Beldomenico and Begon, 2010). Additionally, it has been hypothesized that the maintenance and spread of AIV through migrating waterfowl may be influenced by host body condition (Flint and Franson, 2009; Arsnoe et al., 2011). My results suggest that susceptibility or responses to LPAIV infection in Blue-winged Teal are not condition-dependent, most likely because the cost to responding to LPAIV infections is not large enough to require a trade off with condition. In contrast, Arsnoe et al. (2011) found increased susceptibility to AIV infection, and higher viral loads shed from wild Mallards in normal body condition, compared to birds in poorer body condition. Thus, given the inconsistent findings among studies examining associations between condition and AIV infections in waterfowl, it is possible that the condition-dependent hypothesis for infection or disease susceptibility does not apply for LPAIVs in their reservoir hosts which are well-adapted to these viruses, or have had prior exposure and, hence, some level of immunity to them (Latorre-Margalef et al., 2009b).

As expected, the probability of AIV infection was significantly higher in HY birds compared to AHY birds, as seen in numerous studies (Parmley et al., 2008; Hoye et al., 2010; Huang et al., 2013; Nallar et al., 2015; Papp et al., 2017), likely because immunologically naïve juveniles are at higher risk of AIV infection when exposed, and shed for longer periods when infected (van Dijk et al., 2014). Another factor contributing to higher prevalence rates in HY birds might be the ratio of susceptible HY with respect to AHY birds (Papp et al., 2017; Rohwer et al., 2020) shortly after the breeding period and prior to fall migration. Increase in population density with the influx of susceptible HY birds may result in rapid transmission among birds in the population. Although population density has been previously found to influence AIV

infection in waterfowl due to density-dependent transmission (Nallar et al., 2016, Papp et al., 2017), it explained no additional variation in the probability of AIV infection when added to my top model containing mean daily minimum temperatures and age.

2.5 Conclusions

This study demonstrated that climatic variation affected stress responses and/or the level of energy required for free-ranging migratory birds to respond or adapt to changes in climate. Furthermore, the increased energetic cost in response to increasing temperature variations resulted in a carry-over effect on both mass and body condition index of migratory waterfowl, which may have significant fitness consequences. To understand the ultimate implications of these findings, further investigations are required to assess the potential downstream effects on subsequent migration, survival, and reproduction.

My study also showed climate to be important in affecting AIV infection in migratory waterfowl in the Canadian prairies, just prior to fall migration. The study demonstrated a complex, non-linear relationship between the probability of AIV infection and mean daily minimum temperatures 3-10 days prior to sampling. The likelihood of AIV infection decreased with mean daily minimum temperatures ranging between 7 and 10°C, and increased when mean daily minimum temperatures exceeded 12°C. Existence of this complex relationship between temperature and AIV infection is likely a reflection of the impacts of temperature not just on the survival of AIV in water at time of exposure, but also on the behaviour, distribution, or movement of birds, affecting local population densities and opportunities for transmission and exposure among birds.

Canada is warming at more than twice the rate of average global warming, and mean temperatures in the Canadian prairies and northern Canada have increased at higher rates than the entire country across all seasons (Government of Canada, 2019). According to Canada's Changing Climate Report (Government of Canada, 2019), both annual temperatures and precipitation are projected to keep rising in decades ahead, causing an increase in warmer extremes and a decrease in cold extremes, impacting both human-inhabited and natural ecosystems. Hence, based on my findings, these projected exacerbations of temperature extremes, ranges, and fluctuations will have the potential to increase the energetic costs required by migratory birds to physiologically respond or adapt to maintain homeostasis, forcing them to

redirect valuable energy and resources from body condition, survival, or other costly activities depending on the stage of their annual cycle (e.g., migration, reproduction, immune function). Wetland dynamics in the PPR are rapidly changing with climate, becoming drier in the western PPR, but wetter in the eastern PPR (Niemuth et al., 2014). Furthermore, the Canadian prairies are projected to become hotter and drier in the summer and early fall months (Government of Canada, 2019), which may increase the prevalence of AIV infection just prior to fall migration, when AIV prevalences are at the highest during the annual cycle of migratory waterfowl (Kraus et al., 2004; Wallensten et al., 2007; Wilcox et al., 2011; Nallar et al., 2015). Increasing minimum temperatures during these periods of high AIV prevalence can further impact AIV infection and dynamics, by influencing the host behaviour, distribution and increased local population densities, increasing the likelihood of transmission among migratory waterfowl. In comparison to changes in annual temperature and precipitation in Canadian prairies, increasing temperature and precipitation over a longer period of time can markedly impact the abundance of birds and aquatic insects in prairies (Mantyka-Pringle et al., 2019).

The projected changes in climate can affect migratory birds via incurring higher energetic costs in order to physiologically adapt to the fluctuations. Further, AIV prevalence among these migratory hosts can also be affected due to changing climate, potentially causing an additional burden on the host physiology. Increasing daily minimum temperatures above 12°C in my study were shown to increase the probability of AIV infection among migratory waterfowl in August prior to energetically costly fall migration. Although, in my study I did not find a cost to infection with AIV, if birds are forced to respond to increasing variations in climate and extreme temperatures, they may diminish their energy reserves and show additional costs to AIV infection such as decreased local movements (van Dijk et al., 2015b).

It will increasingly be more important to understand how carry-over effects of stress responses and increased energy expenditure will impact migratory bird ecology and health in response to a rapidly changing climate, through impacts on survival and reproduction, as well as migration, immune function, and other key activities important for survival and reproduction. Furthermore, it is critical to understand how future scenarios of a warmer and drier climate in the Canadian Prairies in autumn (when AIV prevalence is highest in migratory waterfowl) will affect the prevalence, distribution, and impacts of AIV infection in migratory waterfowl. Understanding the impacts of climate change on AIVs in waterfowl populations is essential for

predicting how future climatic conditions will affect AIV dynamics in waterfowl, and the associated risk of spill-over into poultry or humans.

CHAPTER 3: IMPACT OF STRESS AND AVIAN INFLUENZA INFECTION ON SURVIVAL OF BLUE-WINGED TEAL (*SPATULA DISCORS*)

ABSTRACT

Anthropogenic challenges including habitat destruction, pollution, and direct and indirect effects of climate change can act as stressors and impact wildlife health. Responding to environmental stressors may impact or trade off with other costly activities, such as reproduction, migration, and immune function, and have direct or indirect impacts on survival. I used long term band recovery data to examine whether energy expenditure during moulting (as measured by feather corticosterone; CORT_f), body condition and avian influenza virus (AIV) infection influenced overall survival (n = 688) and probability of being hunted (n = 637), in migratory Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairies just prior to fall migration, in 2007-2018. Waterfowl are natural reservoirs for low pathogenic avian influenza viruses (LPAIVs), and show no overt signs of disease. Similar to other waterfowl species, female Blue-winged Teal had higher mortality rates (52%) compared to males (38%), likely due to increased energetic costs and risks to predation during the breeding period, compared to males which do not contribute to incubation or brood rearing. Mortality did not appear to be directly mediated by CORT_f or body condition. However, a weak interaction was found between sex and CORT_f on the probability of being hunted within the first year. In male Blue-winged Teal, lower levels of CORT_f were associated with a higher probability of being hunted, suggesting that higher CORT_f may have provided males with an advantage, making them less vulnerable to being hunted. Alternatively, males with higher CORT_f may have died shortly following banding, or may have delayed migration, such that fewer males with high CORT_f were available in the population during subsequent hunting seasons. Study also determined that, in addition to having no association with body condition or CORT_f, AIV infection prior to fall migration did not influence survival or probability of being hunted in Blue-winged Teal, and thus does not appear to pose a cost in this reservoir host species which is well-adapted to LPAIVs. This study provides important information about energetic costs, survival, and the ecology of AIV in migratory waterfowl. Given the role that climate may play in affecting energetic costs and stress responses in wild waterfowl, understanding associations among stress, condition, infection, and

survival is critical to predicting how climate may affect the dynamics, spread, and impacts of AIV infections in wild waterfowl populations.

3.1 Introduction

Marked increases in human populations have resulted in diminished wildlife populations due to anthropogenic challenges including habitat destruction, pollution, and direct and indirect effects of climate change (Milligan et al., 2009). Climate change has been linked with shrinkage in the planet's biodiversity through negative effects on survival and reproduction (Twitchett, 2006). Some of the most dramatic population declines have been seen in avian species that fail to adapt to climate change (Both et al., 2006; Møller et al., 2008). Physiological response to stressors associated with environmental changes plays a key role in survival of migratory birds. The stress response has evolved to allow animals to deal with stressors such as reduced food availability, contaminants, predators, and social interactions (Romero, 2004). Birds respond to a stressor through the sympathetic-adrenal-medullary (SAM) axis, releasing catecholamines, eliciting an immediate fight and flight response in order to escape (Reeder and Kramer, 2005). The hypothalamic-pituitary-adrenal (HPA) axis is activated releasing glucocorticoids (GCs) which remain in circulation for longer than catecholamines, facilitating survival and a return to homeostasis (Sapolsky et al., 2000; Reeder and Kramer, 2005). Appropriate reactions to stressors, mediated by corticosterone (CORT; primary avian GC) can be beneficial in life threatening situations (Bruijnzeel et al., 2001), but persistent CORT elevations can have deleterious effects (Bonier et al., 2009). Elevations in CORT leads to redistribution of energy away from systems that are not essential for immediate survival (Blas and Baos, 2009; Bonier et al., 2009). Chronic reallocation of energy can result in decreased body condition and reduced reproduction (Bonier et al., 2009; Harms et al., 2015; Latta et al., 2016). Increased CORT has been associated with lower survival rates (Romero and Wikelski, 2001) and decreased likelihood of successful breeding in subsequent years (Blas et al., 2007; MacDougall-Shackleton et al., 2013), implying that chronic stress or increased energy expenditure can result in carry-over effects with significant fitness consequences.

Chronic stress has been linked to decreased immune response and increased disease susceptibility, through diverting resources away from immune function to deal with the costs associated with increased stress or energy expenditure, but also through direct immunopathology (Spencer et al., 2001; Aguanta et al., 2018). When pathogens do not affect immediate survival, reallocation of energy toward fighting the disease leaves less energy for foraging or locomotor activity thus reducing body condition and growth, impacting the host's fitness through impacts

on reproduction and survival (Bradley and Altizer, 2005; de Crespigny and Wedell, 2006; Venesky et al., 2009). Concurrently, individuals in poorer body condition have higher disease susceptibility and experience greater disease intensities (Beldomenico and Begon, 2010). In migratory waterfowl, low pathogenic avian influenza virus (LPAIV) infections generally show no overt signs of disease or mortality (Webster et al., 1992, Takekawa et al., 2010), but infection may carry an energetic cost (Gilbert et al., 2006). Therefore, it is important to assess the interacting roles that stress, body condition, and infectious diseases might play in affecting survival, and in understanding the ecology of LPAIVs in migratory waterfowl.

In free-living species such as migratory waterfowl, it can be challenging to study stress physiology and energy management. Measurement of GCs like CORT have long been suggested as key indicators in monitoring health of individuals (Busch and Hayward 2009; Angelier et al., 2010). However, it is difficult to interpret stress responsive GCs because circulating levels of GCs quickly rise in response to capture and handling stress (Romero and Reed, 2005). Feather CORT (CORTf) can provide an integrated measurement of HPA activity deposited during feather growth (Bortolotti et al., 2008), reflecting baseline plus the stress response or energy expenditure during this time period (Legagneux et al., 2013). Capture and handling does not alter CORTf and feathers can be collected opportunistically. This is particularly advantageous for species that are not accessible during non-breeding periods (Kouwenberg et al., 2013; Harms et al., 2015). Other studies have utilized CORTf to examine how historical stress influences future fitness. Elevated CORTf has been linked to decreased body condition in waterfowl species including arctic-nesting Common Eiders (*Somateria mollissima*; Harms et al., 2015) and Blue-winged Teal (Chapter 2). Furthermore, CORTf was indirectly associated with a decline in reproductive success and survival during the subsequent breeding season in Common Eiders, demonstrating carry over effects of increased energetic expenditure during the moulting period (Harms et al., 2015).

In this study, I built on limited studies examining stress in relation to AIV infection and body condition, and how they may interact to influence survival. My overall goal was to investigate impacts of stress, body condition, and AIV infection on survival of Blue-winged Teal (*Spatula discors*) sampled during fall migration in Canadian prairies. In Chapter 2, I determined that climatic variation (mean daily standard deviation in temperature in the first half of July (July 1-16)) was positively associated with CORTf. This increased energetic cost was further found to

have carry-over effects on the body condition of the Blue-winged Teal. Given this, I predicted that survival would be negatively associated with CORTf, and positively associated with body condition. In Chapter 2, I also determined that AIV was not associated with body condition or CORTf, and I interpreted the results to mean that AIV infection does not pose a significant cost to Blue-winged Teal, a reservoir host for AIVs. However, as birds were sampled just prior to fall migration, the additional cost of dealing with an infection during migration could potentially impact migratory performance and may reduce the probability of survival. I also investigated associations between CORTf, AIV infection, body condition, and probability of Blue-winged Teal being hunted within first year after banding in order to assess the immediate effects of reallocated energy expenditure (i.e., condition and infection). I predicted that AIV infection, higher CORTf levels, and lower body condition would increase the likelihood of being hunted within the first year after banding. These relationships were investigated utilizing band recovery and archived data collected from Blue-winged Teal in Canadian prairie provinces from 2007 to 2018. Blue-winged Teal are an ideal species in which to examine these relationships, as they have the most extensive migratory ranges amongst waterfowl species, are abundant and in high densities in Canadian prairie wetlands prior to fall migration, and they generally have high prevalences of AIV, particularly just prior to fall migration when AIV prevalences are highest (Nallar et al., 2016; Rohwer et al., 2020).

3.2 Methodology

3.2.1 Archived data, feather samples, and encounter data

As per Chapter 2, this chapter used a subset selected from archived and newly collected data and samples from over 7000 Blue-winged Teal sampled in Alberta, Saskatchewan, and Manitoba, from 2007 to 2018, as part of ongoing investigations of the ecology of AIV infection in the Canadian prairie provinces (Appendix I). All birds selected for the subset had data on band identification, location and date of sampling, age, sex, province, mass, body condition index (BCI), head-to-bill length, and AIV infection status. To obtain data on CORTf, archived and newly collected feather samples were randomly selected for 40-50 birds per year, resulting in an initial selection of 557 birds for the 12 year period. Of the 557 birds, only 23 (4.1%) were reported to the Canadian Wildlife Service Bird Banding Office as “hunted” or “dead” after banding and release. Thus, to improve my ability to evaluate differences between ducks that died

or survived, or ducks that were hunted or not hunted, I included an additional 131 birds with encounter data to my subset, for a total sample size of 688 birds used for this analysis. Given that this dataset was no longer a random subset of the larger dataset, it was only used to compare differences among birds that were hunted or not hunted within the first year after banding and sampling, and among birds that survived and died. No inferences were made about overall prevalences or overall means with this data subset.

3.2.2 Field methods

Sampling of Blue-winged Teal occurred in mid to late August, prior to fall migration, in collaboration with the Canadian Wildlife Service (CWS) and United States Fish and Wildlife Service (USFWS) field crews during annual waterfowl banding programs. Field methods were followed as outlined in Nallar et al. (2016). Briefly, ducks were captured using standard bait traps (USFWS; CWS). Each duck was banded with a uniquely numbered USFWS leg band, and information on band identification, location, latitude, longitude, date of sampling, age, sex, mass, and head-to-bill length was recorded. Age and sex were determined by experienced USFWS or CWS waterfowl biologists, by assessing wing plumage (Pearse et al., 2014), and examining bills for the presence of numerous small spots which are present in females, and lacking in males (Mouronval, 2016). Each bird was weighed in a cloth bag using a Pesola spring scale to the nearest 1-5 grams, and head-to-bill length was measured from the tip of the beak to the back of the head using callipers to nearest 0.1 millimetre. As in Chapter 2, body condition was assessed using mass and BCI, which was estimated using mass and head-to-bill length, using methods described in Peig and Green (2009).

To assess AIV infection status, oral and cloacal swabs were collected and placed in a single cryovial containing modified Hanks buffer, and stored as described by Parmley et al. (2011). One tail feather (second outermost rectrix from the right) was plucked and stored at room temperature, in a paper envelope until CORTf analyses could be done. All field work and procedures including capture, handling, and sampling were approved by the University of Saskatchewan's Animal Research Ethics Board (protocol 20070039) and adhered to the Canadian Council on Animal Care guidelines for humane animal use.

3.2.3 *Laboratory analysis*

3.2.3.1 *Feather corticosterone*

Feather corticosterone of tail feathers was used in this study to represent an integrated measure of HPA activity during the period of feather growth, which generally occurs throughout July and early August in Blue-winged Teal in the prairies (Rohwer et al., 2020). All 688 feathers selected for this study were measured, weighed, and processed following a methanol-based protocol for CORT extraction described by Bortolotti et al., 2008. These methods have been successfully used for CORT analysis of numerous avian species including nestling Tree Swallows (Harms et al., 2010), Clark's Nutcrackers (Fairhurst et al., 2011), Cory's Shearwaters (Fairhurst et al., 2012), and Common Eiders (Legagneux et al., 2013). Briefly, for each feather, after measuring mass and length, the calamus was removed and the length of the remaining feather was measured (to the nearest mm) and weighed (to the nearest mg). Each sample was then cut into pieces (less than 5 mm) using scissors, and pieces were placed into glass scintillation vials. Methanol (10 ml) was added to the sample vials, which were then placed in a sonicating water bath for 30 minutes, followed by overnight incubation at 50°C and 100 rpm in a shaking water bath. Contents of each vial were vacuum filtered and rinsed with 5 ml methanol to remove feather material from the methanol solution. The filtration funnel was rinsed with 5ml of methanol and dried between samples to prevent cross-contamination. Methanol was then evaporated, either by placing vials in a fume hood until complete evaporation (first 13 batches) for 48-72 hours, or by using a vacuum concentrate evaporator (CentriVap, Labconco, Kansas City, Missouri) to standardize and reduce the amount of time required, 6-8 hours, for complete evaporation of samples (latter 7 extraction batches).

Feather samples collected in 2007-15 (n = 474) were extracted in 13 batches without counterbalancing years and sites across all extraction batches as they were analysed chronologically and by site. Feather samples collected in 2015-2018 (n = 214) were extracted randomized and blind, counterbalancing year and site across 7 extraction batches. For the latter 7 extraction batches, a slight modification of extraction technique was used to reduce variation in data associated with the extraction process. Changes included the use of an evaporator to standardize and reduced time required for the evaporation of samples as described above, and the

use of larger round bottom glass tubes for the evaporation process, rather than smaller vials with flat bottoms.

Feather extracts were reconstituted in 500ul ELISA buffer from commercially available ELISA kits (Cayman Chemical Company, MI, USA) following manufacturer instructions. Reconstituted feather extracts were then stored at -20°C until analysis. All extracts were measured for CORT in triplicate, using a plate reader set at 412 nm (BMG SPECTROstar Omega, Mandel Scientific, Guelph, Canada), and quantified in pg/mm of feather (Bortolotti et al., 2008). Intra-assay variability, the percent coefficient of variation (CV) within ELISA plates, was calculated using sample CORTf concentrates run in triplicate. The inter-assay variability, the percent coefficient of variation between ELISA plates, was calculated using internal CORT standards run across all plates. Intra and inter-assay CVs were 6.25% and 16.28% respectively, for all 688 samples analysed using 43 ELISA plates. Intra-assay CVs were similar between the first 13 extraction batches (CV = 6.16%) and the last 7 batches (6.46%), but inter-assay variation was lower for the last 7 batches (12.15%, 18 ELISA plates) compared to the first 13 batches (20.40%, 25 plates), possibly because of the improvement in pipetting, technique, and assay setup in the latter part of the study. Serial dilutions of pooled and individual feather extracts produced displacement curves that were parallel to the standard curve (Appendix B). Furthermore, using the same approach as in Chapter 2, I determined that extraction batch was not a confounding variable, nor a significant source of variation in my CORTf data when controlling for province and year (Batches 1-13: $F_{\text{batches}}(11, 474) = 0.82, p = 0.62$; $F_{\text{province-year}}(22, 474) = 7.24, p = 0.0001$, Batches 14-20: $F_{\text{batches}}(6, 214) = 1.75, p = 0.11$); $F_{\text{province-year}}(22, 214) = 2.5, p = 0.0004$). Feather corticosterone analyses were performed at the Prairie and Northern Wildlife Research Centre, Environment and Climate Change Canada (ECCC), Saskatchewan, Canada.

3.2.3.2 Avian influenza virus screening

Avian influenza virus samples collected in 2007-10 were analysed as part of Canada's Inter-agency Wild Bird Influenza Survey (Parmley et al., 2008). For the latter years, (2011-18), swab samples were analysed at National Centre for Foreign Animal Disease (NCFAD), Canadian Food Inspection Agency (CFIA), in Winnipeg, Manitoba. For all years of this study, samples were analysed using a RT-PCR analysis targeting the matrix 1 gene, as described by

Spackman et al. (2002), and by using standardized methods in all participating labs (Parmley et al., 2008). Cycle threshold values of equal to or less than 35 were considered positive.

3.2.4 *Statistical analysis*

Descriptive analyses were completed using R (R Development Core Team. 2016 version 3.4.2) and Microsoft Excel. Statistical analysis were conducted in R and program MARK (White and Burnham 1999), using information theoretic approaches to model selection.

Probability of Blue-winged Teal being hunted: To analyse whether CORTf, AIV infection, and body condition (as measured by mass and BCI) were associated with the probability of ducks being hunted within the first year following capture and sampling, I used generalized linear mixed models (GLMER), with year as a random term and family Binomial, link Logit function based on maximum likelihood estimation. The 51 birds that were hunted after one year following sampling (Appendix J) were excluded from this analysis (total n = 637). Variables such as age, sex, and province were also included in these analyses (Table 3.1.), and relevant interactions were examined. Error distribution and model assumptions (model diagnostics) for all analyses were checked using residual plots in DHARMA package (Hartig, 2017).

Survival of Blue-winged Teal: Mark-recapture analysis was conducted using Brownie parameterization to estimate the influence of CORTf, AIV infection, and body condition (as measured by mass and BCI) on overall survival (S) and recovery rate (f), using program MARK (White and Burnham, 1999). Survival rate indicates the probability of birds surviving over time, whereas recovery rate indicates the probability of birds being shot, and then being retrieved and reported (Brownie et al., 1985). The advantage of this parameterization is that a single marked individual can potentially have multiple encounters and be seen or recaptured on more than one occasion, and it efficiently accounts for the probability of an individual being captured in the long term, and its temporary absence from the study area, thus providing a less biased estimator of adult survival (Lebreton et al., 1992). Hence, all Blue-winged Teal reported as encountered, including those reported beyond one year following sampling, were included in this analysis (n = 688). Age and sex were also included as covariates, and relevant interactions were examined (Table 3.1.).

Model selection strategy: Explanatory variables were explored in univariate models and in models containing multiple variables that were not collinear (Murray and Conner, 2009). Models containing only informative variables were ranked using Akaike's information criterion (AICc) adjusted for sample size (Anderson, 2007), using the MuMIn package (Barton, 2012). Explanatory variables were deemed uninformative or redundant, if their ΔAICc were >2 units relative to the null model in univariate models, if their addition to models with existing variables did not further reduce AICc, and if their 95% confidence intervals spanned zero (Akaike, 1974; Burnham and Anderson, 2004; Arnold, 2010).

Table 3.1. List of explanatory variables used to investigate impacts of stress, body condition, and AIV infection on the probability of being hunted within the first year following banding (using generalized linear mixed models), and the probability of survival (using mark-recapture analysis) in Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in 2007 to 2018.

Variable	Type	Description	Categories/Units
Year	Random term	Year of sampling	2007-2018
Avian influenza virus infection (AIV) status	Categorical	Current infection status, as determined using RT-PCR of the matrix gene	Positive/ Negative
Feather corticosterone (CORTf)	Continuous	Feather corticosterone levels	0.15 – 15.83 pg/mm
Body mass	Continuous	Mass at sampling	220 – 649 grams
Body Condition Index (BCI)	Continuous	Measure incorporating mass and body size to define the energy capital accumulated in the body (Peig & Green, 2009).	172.14 – 859.22
Age	Categorical	Age at capture	Hatch Year (< 1 year old)/ After Hatch Year (> 1 year old)
Sex	Categorical	Sex	Female/ Male
Province	Categorical	Province where duck was sampled	Alberta/ Saskatchewan/ Manitoba

3.3 Results

Descriptive statistics: Of the 7549 Blue-winged Teal sampled from 2007 to 2018, 370 (4.9%) were reported to the Canadian Wildlife Service Bird Banding Office as encountered. Encountered birds included those that were reported as hunted, found dead, or resighted alive. Of those 370 banded ducks, 277 were hunted within the first year of being banded, which was 3.7% of all ducks banded (Appendix I). More than half of the ducks hunted within the first year after banding were hunted in September, and almost all were hunted within the first five months (Appendix L). Ducks that were hunted within the first year were reported from Canada, USA, Mexico, Nicaragua, and Colombia, but most were reported from the southern USA, in Louisiana and Texas (Appendix M).

Of the 277 ducks hunted within the first year, 168 (60.6%) were male, and 109 (39.4%) were female (Appendix J). Although there appeared to be a male bias among hunted ducks, 63% of the ducks not hunted within the first year were also male (4583/7272), and 37% were female (2689/7272; Appendix J). A similar proportion of age classes were found among ducks hunted within the first year (e.g., HY birds 130/277, 46.9%), and those not hunted (e.g., HY birds 3621/7272, 49.8%; Table 3.2.). Similar proportions were also observed in my subset of 688 birds (Table 3.2.). Body mass and BCI were similar between birds hunted and not hunted within the first year following banding, and CORT_f appeared to be slightly higher in ducks not hunted within the first year (Table 3.2.). The proportion of birds that were positive for AIV was similar among birds that were hunted within the first year following capture and sampling (14/103, 13.6%), and those that were not hunted (68/585, 11.62%; Table 3.2.).

Table 3.2. Overview of the apparent prevalence of AIV, mean body mass, estimated body condition index (BCI), and feather corticosterone (CORTf), in Blue-winged Teal (*Spatula discors*) that were hunted and not hunted within first year following banding and sampling in Alberta, Saskatchewan, and Manitoba, from 2007 to 2018 (n = 688). Birds not hunted within the first year also included those that had been reported as hunted after the first year.

Variable	Hunted within first year	Not hunted in first year
N	103	585
Age: HY	45 (43.7%)	261 (44.6%)
AHY	58 (56.3%)	324 (55.4%)
Sex: M	70 (68.0%)	374 (63.9%)
F	33 (32.0%)	212 (36.2%)
Mass (SE)	375.9 (13.4) g	373.4 (5.5) g
BCI (SE)	380.4 (22.0)	381.2 (8.0)
CORTf (SE)	1.44 (0.14) pg/mm	1.62 (0.15) pg/mm
AIV (% positive)	14/103 (13.6%)	68/585 (11.62%)

Abbreviations: N = Total number of birds; SE = Standard errors; HY = Hatch years; AHY = After hatch years; M = Males; F = Females.

3.3.1 *Impact of CORTf, body condition, and AIV infection on the probability of Blue-winged Teal being hunted within the first year*

Model results: Based on my best supported model, the probability of being hunted within the first year of sampling was explained by province and an interaction between CORTf and sex (Table 3.3.). When examined alone, neither CORTf nor sex were informative, and did not improve the null, however, when added to the model containing province, the interaction between CORTf and sex was informative, and improved model weight (Appendix N.1.). Males were more likely to be hunted compared to females ($\beta = 0.66$, 95% CI = 0.0, 1.33, $p = 0.05$, Table 3.3.). The interaction between CORTf and sex suggested that as CORTf increased, the probability of being hunted within the first year decreased for males only ($\beta = -0.29$, 95% CI = -0.65, 0.01, $p = 0.08$; Figure 3.1.; Table 3.3.). Although, the opposite trend may be true for females but the high confidence intervals of CORTf suggests that the trend was not informative in females. Blue-winged teal banded in Manitoba (MB) and Saskatchewan (SK) were more likely to be hunted in comparison to those banded in Alberta (AB) (MB: $\beta = 0.84$; 95% CI= 0.17, 1.50, SK: $\beta = 0.62$; 95% CI = 0.13, 1.13, Table 3.3.). The probability of being hunted in the first year following banding and sampling was not associated with BCI ($\beta = 0.0003$; 95% CI = -0.003, 0.002), body mass ($\beta = 0.001$; 95% CI = -0.002, 0.006), AIV infection, ($\beta = 0.20$; 95% CI = -0.46, 0.80, or age at time of sampling ($\beta = -0.06$; 95% CI = -0.51, 0.36) (Appendix N.2.).

Table 3.3. Best supported generalised linear mixed model using year as a random term and family Binomial, link Logit explaining the probability of Blue-winged Teal (*Spatula discors*) being hunted within the first year following banding of birds in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in August (2007-2018) prior to fall migration of birds (n = 637).

Variables	β	SE	P
Intercept	-2.32	0.30	<0.001
Sex (Ref = Male)	-0.66	0.33	0.05
CORTf	0.04	0.09	0.68
Sex * CORTf	0.29	0.17	0.08
Province (Ref = Alberta)			
Manitoba	0.84	0.34	0.01
Saskatchewan	0.62	0.25	0.01

Abbreviations: β = Coefficient estimate, SE = Standard error, P = p-value, Ref = Reference, CORTf = Feather corticosterone.

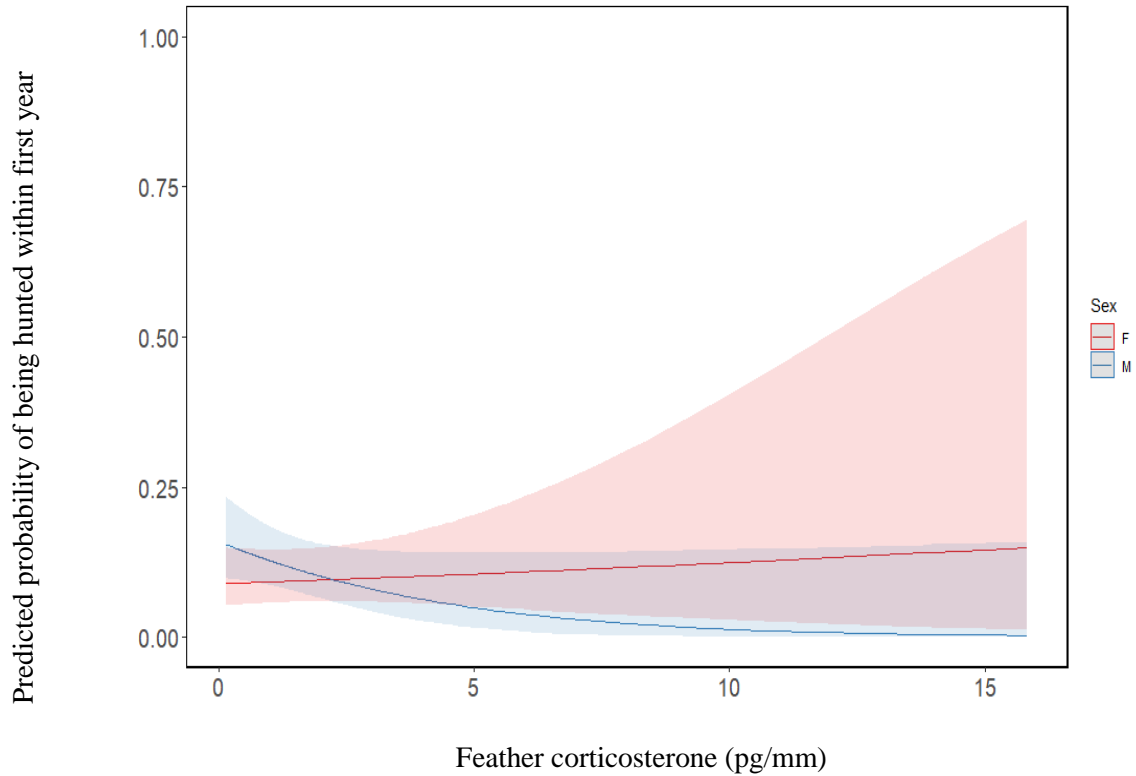


Figure 3.1. Predicted probability of male (M) and female (F) Blue-winged Teal (*Spatula discors*) being hunted within first year following sampling in August as a function of feather corticosterone (95% CI, coloured zone). Probability was estimated based on the best-supported generalised linear mixed model. The birds were banded in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in August (2007-18) prior to fall migration of birds (n = 637). Blue zone = males and red zone = females.

3.3.2 *Impact of CORTf, body condition, and AIV infection on survival of Blue-winged Teal*

Mark-recapture modelling techniques: Using Brownie models, survival of Blue-winged Teal was not associated with BCI ($\beta = -0.001$, 95% CI = -0.003, 0.001), mass ($\beta = 0.002$, 95% CI = -0.002, 0.006), CORTf ($\beta = -0.07$, 95% CI = -0.19, 0.06), or AIV infection status ($\beta = 0.12$, 95% CI = -0.36, 0.61), whether examined alone, or in combination with other variables (Appendix O). The best supported model included sex, which revealed that males were more likely to survive than females ($\beta = 0.62$, 95% CI = 0.55, 0.68; Table 3.4.; Appendix O). Model-estimated survival rates were 0.48 for females (95% CI = 0.36, 0.60) and 0.62 for males (95% CI = 0.55, 0.70; Appendix O), and no difference in survival was found between hatch year and after hatch year birds (Appendix O).

Table 3.4. Best supported Brownie model using mark recapture analysis explaining the probability of survival and recovery in Blue-winged Teal (*Spatula discors*) banded in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in August (2007-2018) prior to fall migration (n = 688).

Variables	β	SE	95% CI
Intercept (Survival)	-0.07	0.21	-0.49, 0.34
Sex (Ref = Male)	-0.58	0.22	0.14, 1.02
Intercept (Recovery)	-2.22	0.11	-2.42, -2.01

Abbreviations: β = Coefficient estimate, SE = Standard error, 95% CI = Confidence Intervals, and Ref = Reference.

3.4 Discussion

Study results demonstrated that, similar to other waterfowl species, male Blue-winged Teal had a higher survival rate compared to females. Furthermore, a weak interaction was found between sex and CORTf on the probability of being hunted within the first year, in that lower levels of CORTf were associated with an increased probability of being hunted in males, but not in females.

In my study, survival estimates for males and females were 62% and 48%, respectively. Female waterfowl have lower survival rates compared to males in many species of dabbling ducks, including Mallards (Smith and Reynolds, 1992; Promislow et al., 1994; Arnold and Clark, 1996), Northern Pintails (*Anas acuta*; Rice et al., 2010; Bartzen and Dufour, 2017) and Blue-winged Teal (Johnson et al., 1992; Arnold and Clark, 1996). Although males were more likely to be hunted compared to females (i.e., 4.6% for males and 4% for females), females had a higher overall mortality rate of 52% compared to 38% for males (based on model-estimated survival rates). Females spend vast amounts of energy on egg formation and incubation, potentially depleting significant energy reserves (Harris, 1970; Rohwer, 1986; Johnson et al., 1992; Sargeant and Raveling, 1992). Females thus are more vulnerable to mortality because of significant investment of energy and resources into nesting and brood rearing (Johnson et al., 1992). As a result of carrying the burden of egg-laying, incubation, and brood-rearing, females are significantly more vulnerable to predation compared to males (Arnold et al., 2012), and may also be more vulnerable to risks and costs associated with subsequent fall migration, especially if the costs of reproduction and the subsequent moulting period are not recovered (Lonsdorf et al., 2016). Conversely, males generally abandon females shortly after egg laying and incubation initiation and do not contribute to either incubation or rearing offspring (Rohwer and Anderson, 1988) although some males may continue to accompany females on incubation breaks, or accompany young broods early in the season prior to departing (Miller, 1976; Rohwer et al., 2020).

In Chapter 2, I demonstrated that increased energy expenditure during feather growth resulted in reduced mass and BCI for both sexes, and the impact on BCI was more severe in females compared to males (Chapter 2). Given this, I hypothesized that one potential physiological mechanism explaining increased mortality particularly for females following banding and sampling prior to migration, would be via increased energy expenditure during the

moulting period. This is evidenced by higher CORTf levels and/or through reduced mass or body condition, increasing susceptibility to mortality during the subsequent fall migration period. However, neither mass nor BCI were associated with Blue-winged Teal survival, or the probability of being hunted within the first year following banding. Furthermore, CORTf was also not associated with overall survival in Blue-winged Teal, however, males with lower CORTf levels were more likely to be hunted within the first year of banding, which was opposite to what I had predicted. There are two ways in which this result can be interpreted. One is that the increased energy expenditure during the moulting period may have provided males with an advantage and made them less vulnerable to being hunted. Distribution and management of energy, regulation of daily metabolism, and locomotor activities facilitating foraging are governed by CORT, and can mediate physiological and behavioural changes leading to increased survival (Dallman et al., 1993; Sapolsky et al., 2000; Landys et al., 2006; Blas and Baos, 2009). It is possible that higher energy expenditure during the moulting period in males was beneficial if, for example, it may be related to increased efforts to forage, gain weight or increase energy reserves prior to fall migration (Boves et al., 2016), thus improving the ability of males to avoid hunting pressures en route. Another possibility is that males with higher CORTf may have died shortly following banding, or may have delayed migration, such that fewer males with high CORTf were available to harvest along migratory routes, during the hunting seasons in Canada and the USA, where most recoveries were reported. Similar suggestions were made by Hill et al. (2003), in goshawks where birds in good condition were more likely to be hunted, not because they were more susceptible to being hunted, but because the birds in poorer condition had likely died before or early in migration, prior to the onset of hunting seasons.

Although there was an association between CORTf and the probability of being hunted in males, I did not find an association between CORTf and overall survival. It is possible that had I examined only first year survival in mark-recovery analysis, rather than overall survival, an association may have been seen. Furthermore, although the original sample size was large, the low band recovery rate of 4.9% reduces the power of analysis, thus higher sample sizes or increased recovery are needed to better evaluate this question. Various studies have shown mixed association between increased GCs with return rates and survival. Common Eiders with higher levels of CORTf were shown to return later to the breeding colony, and in poorer body condition, which subsequently resulted in an increased probability of mortality during avian cholera

outbreaks (Harms et al., 2015). MacDougall-Shackleton et al. (2013), demonstrated that higher stress responses in Song Sparrows (*Melospiza melodia*) were associated with lower return rates to the breeding grounds in subsequent year. Lower return rates were also associated with increased CORT during reproduction in Common Murres (*Uria aalge*; Kitaysky et al., 2007). On the other hand, Cliff Swallows (*Petrochelidon pyrrhonota*) with very low or very high levels of CORT had lower survival compared with birds having intermediate levels of CORT (Brown et al., 2005). Using capture-recapture and mortality data, increased CORT levels in adult male Barn Owls (*Tyto alba*) during breeding were associated with higher annual survival rates (Béziers, et al., 2019). The increased survival may have been related to behavioural and physiological modifications made by birds with elevated CORT levels, e.g., reducing reproductive behaviour or home range size, in order to reduce further energetic costs associated with activities other than self-maintenance and survival.

Given that GCs are responsible for overall energy management during various life stages birds (Sapolsky et al., 2000), the relationship between GCs and survival is complex. Migratory birds have varying energy requirements during normal life history stages, and during unpredictable events (i.e., emergency life history stages). Thus, the inability to standardize factors such as environment, disease exposure, predation risk, and food availability can be a challenge when studying CORT with respect to survival of migratory birds (Jenni-Eiermann et al., 2008; Sheriff et al., 2009; Ouyang et al., 2015; Love et al., 2016).

Similar to most dabbling duck species, male Blue-winged Teal had a higher probability of being hunted compared to females. This may be partially due to the increased availability of males resulting from a male-biased waterfowl population post-breeding (Bellrose et al., 1980). Given the increased vulnerability of females and their higher investment in energy during the breeding season, females may have a higher mortality rate during or shortly after breeding (Armstrong and Robertson, 1988). Male Blue-winged Teal initiate moult-migration well before females or hatch year birds (Bellrose, 1958; Owen, 1968; Rohwer et al., 2020), thus getting a head start on migration, which may alter availability of males during subsequent hunting seasons. There may also exist a bias in hunters choosing to hunt males based on larger body size/target size (Elder, 1955), the colour or plumage pattern (Cooch, 1961), and choosing to hunt bright coloured males even when accompanied by females (Metz and Ankney, 1991). There have

also been lower reporting rates found in females compared to males (Nichols et al., 1995), potentially adding additional bias to the higher male harvest among hunted birds.

I did not detect an effect of body condition or age on survival of Blue winged Teal, or on the probability of being hunted within the first year following banding. A study conducted in southern Saskatchewan concluded that neither age nor body condition were associated with survival in Northern Pintails (Richkus et al., 2005). Similarly, others did not find an association between body condition and survival among Mallards and Northern Pintails in North America (Jeske et al., 1994, Lee et al., 2007; Dooley et al., 2010). Conversely, using band-recovery data in Mallards, Dufour et al. (1993) found birds with better body condition had higher survival and lower recovery rates due to harvesting, suggesting a condition bias among hunter shot waterfowl. Other studies have also demonstrated that poor body condition increased the probability of being harvested in Mallards (Robb, 2002), hence, body condition biases should be considered when examining hunting mortality in relation to other recovery-based parameters. Pace and Afton (1999), demonstrated a positive relationship between body mass of Lesser Scaup (*Aythya affinis*) and probability of recovery. However, Hill et al. (2003), observed that hatch year Canada Geese (*Branta canadensis interior*) in good body condition were more likely to be shot, and suggested that goslings in poor condition may have died prior to fledging. Thus, associations between body condition and survival in waterfowl are inconsistent which may be related to the fact that condition can be affected by several interacting factors including age, sex, stage of the annual cycle, the presence of concurrent diseases or stressors, and how condition is assessed. I did not find interactions between age and body condition or sex and body condition. Associations between age and survival and/or recovery have not been demonstrated in Blue-winged Teal, Mallards, or American Wigeon (*Mareca americana*) banded in Saskatchewan (Arnold and Clark, 1996), or Northern Pintails banded in the prairies (Bartzen and Dufour, 2017). However, others found that HY birds had lower survival rates in Northern Shovelers (*Spatula clypeata*) and Gadwalls (*Mareca strepera*) banded in Saskatchewan (Arnold and Clark, 1996), and Northern Pintails (Rice et al., 2010) and Mallards (Alisauskas et al., 2014) in North America.

I found no association between AIV infection status and survival of Blue-winged Teal, and no impact of AIV infection on the probability of being hunted within the first year after banding. Waterfowl with LPAIVs generally show no overt signs of disease or mortality (Webster et al., 1992, Takekawa et al., 2010). Similarly, a study comparing AIV-infected and uninfected

Ruddy Turnstones (*Arenaria interpres morinella*) also found no effect on survival (Maxted et al., 2012). However, analysis of 4.5 years data of Mallards in north-western Italy found that young birds infected with AIV were less likely to survive than uninfected birds (Giammarino et al., 2014). Despite very little evidence for LPAIV infection to cause mortality in their reservoir hosts, infection and physiological responses to LPAIVs can incur a cost. Delayed migration has been demonstrated in Bewick's Swan (*Cygnus columbianus bewickii*) infected with AIV (van Gils et al., 2007). Infected Bewick's Swans, Mallards and White-fronted Geese (*Anser albifrons albifrons*) have been shown to have lower body mass (van Gils et al., 2007; Latorre-Margalef et al., 2009; Kleijn et al. 2010), indicating that there exists a cost to infection. It is possible that my results showing no association of AIV and survival could be related to a relatively low sample size and low recovery rates. However, given that I determined that AIV infection was not associated with CORTf or body condition in Chapter 2, nor did it affect survival or probability of being hunted, it is likely that infection with low pathogenic strains of AIV does not pose a significant cost to Blue-winged Teal, a common reservoir host.

3.5 Conclusions

Energetically costly processes such as reproduction, moulting, migration, and responding to stressors can trade off on each other, and ultimately have direct or indirect impacts on survival (Nilsson and Svensson, 1996; Dehorter and Tamisier, 1998). In Chapter 2, I found that reduced body condition in Blue-winged Teal was associated with increased energetic expenditure during the period of feather growth, with a more severe impact on body condition in females. In the present chapter, I found that females indeed had higher mortality rates compared to males, however, this did not appear to be mediated by body condition at the time of sampling, as no association was found between body condition and survival. Furthermore CORTf, measure of energy expenditure during the period of feather growth in this study, also did not predict overall survival in Blue-winged Teal. However males with higher CORTf were less likely to be hunted within the first year, which suggests that higher CORTf either provided them with an advantage to avoid or make them less susceptible to being hunted, or that males with higher CORTf died or delayed migration following banding, and prior to the hunting season, and hence fewer males with higher CORTf were in the population during subsequent hunting seasons.

In Chapter 2, I determined that $CORT_f$ increased in response to higher variation in mean daily temperatures, and had subsequent impacts on condition. I determined that AIV infection did not appear to pose a cost to Blue-winged Teal, as it was not associated with $CORT_f$ or body condition in Chapter 2, nor survival or probability of being hunted in this Chapter. Nonetheless, the probability of AIV infection was affected by climate, and had a complex relationship with mean daily minimum temperatures, with increasing probabilities of infection at temperatures above 12°C. Temperatures in the Canadian prairies are changing rapidly in comparison to other parts of Canada and the world (Government of Canada, 2019). Therefore, it is becoming increasingly important to understand the role that a changing climate may play in affecting energetic costs and stress responses in wild waterfowl, and subsequent condition, infection, and ultimately survival. Understanding these interactions and how they impact waterfowl survival are increasingly critical given the rapidly changing climate and projected losses of wetlands important for waterfowl populations, and may also have consequences for the dynamics and spread of LPAIVs.

CHAPTER 4: GENERAL DISCUSSION

This thesis comprises results examining interactions among climate, stress, avian influenza virus (AIV) infection, and body condition, and their impacts on survival in migratory waterfowl.

This research presents:

- The apparent prevalence of AIV infection in the Canadian prairie provinces of Alberta, Saskatchewan, and Manitoba from 2007-2018.
- Relationships between sources of stress or energy expenditure (e.g., climatic factors, population density), and the physiological responses of birds (measured by feather corticosterone; $CORT_f$), AIV infection, and how their interactions might influence individuals (body condition and survival).

4.1 Overview of research approach and findings

As the human population increases globally, industrialization, intensified agricultural practices and natural resource extraction are also on the rise. These changes are associated with rapid and large-scale environmental changes globally (Millennium Ecosystem Assessment, 2011). Although these changes have already been shown to affect human and animal health (Stephen and Soos, 2021), human populations along with their domestic animal population continue to increase over time, while wildlife populations have diminished, and continue to decline (Twitchett, 2006; Milligan et al., 2009). Climate change can affect birds by triggering physiological responses associated with stress or energetic management, and by altering or disrupting normal physiological and behavioural processes important in their annual cycle, including growth, reproduction, and migration, and can result in impacts on population sizes and distributions (Wingfield, 1983; Maclean et al., 2008; Elmberg et al., 2014; Pöysä and Väänänen, 2014; Lehikoinen et al., 2017). In response to a changing climate, birds of many species have shifted their home ranges and/or timing of migration, potentially adding to the costs associated with migration, foraging, or reproduction, and increasing risks to predators or disease exposure (Heather et al., 2005; Newton, 2006; Howard et al., 2018). Shifting habitats and migratory patterns can cause increased population densities at stopover sites, wintering, or breeding grounds, leading to increased risk of exposure, transmission, and spread of infectious diseases

(Papp et al., 2017), and increased competition for food and other resources (Robert and Fletcher, 2007). Climatic variation is also known to play a key role in the ecology of AIV (Papp et al., 2017) by affecting both virus survival in the environment, as well as host populations. Moving forward it will be increasingly important to study how long distance migratory birds interact and respond to these changes, and how associations between climate, AIV and increased stress or energetic costs to wildlife may influence waterfowl populations, as well as the dynamics and spread of AIV in waterfowl populations.

The research conducted in Chapter 2 of this thesis aimed to identify impacts of local weather on stress responses and energy expended during the period of feather growth, in migratory waterfowl sampled in the Canadian prairies just prior to fall migration. I predicted that CORTf, an index of the stress response and energy expenditure, would vary in response to climatic variation during the period of feather growth. The increased energetic demand during moult may result in increased CORTf levels, and cause carry-over effects resulting in loss of subsequent body condition, and increased likelihood of AIV infection. In addition, I predicted that the likelihood of AIV infection would vary with climatic variables measured prior to sampling, and AIV infection would be associated with body condition. To my knowledge, this is the first study to investigate stress responses in relation to climate in dabbling ducks, and how that might impact body condition, and AIV infection.

The research conducted in Chapter 3 focused on impacts of stress/energy expenditure, AIV infection, and body condition on survival of Blue-winged Teal sampled in the Canadian prairie provinces of Alberta, Saskatchewan, and Manitoba, using long term band recovery data from 2007-2019. I predicted that increased energy expended during the period of feather growth may result in carry-over effects affecting body condition, and that these costs have the potential to reduce the probability of subsequent survival, and increase the likelihood of being hunted within the first year. Additionally, if AIV infection poses an increased energetic cost to Blue-winged Teal, AIV infection may also reduce the probability of survival, and increase the likelihood of being hunted within the first year.

4.1.1 Associations among climate, stress, body condition, and survival

In chapter 2, I found that CORTf was influenced by climate experienced by Blue-winged Teal in the Canadian prairies (Figure 4.1.). Birds experienced increased stress or expended more

energy with greater fluctuations in daily temperatures during the period of feather growth (July 1-16). This suggests that alterations in climate can influence energetic demands on migratory birds. Furthermore, increased energetic costs in response to increasing temperature variations resulted in a carry-over effect on both mass and body condition index (BCI) of migratory waterfowl, which may have significant fitness consequences. Both BCI and mass decreased with increasing levels of $CORT_f$. Furthermore, the impact of $CORT_f$ on BCI was significantly more prominent in females compared to males (Figure 4.1.). Adult females undergo energetically costly processes of nesting, egg formation and incubation. The additional cost of escaping predatory risk during the time of incubation and rearing of offspring is also a costly add on to breeding females (Rohwer, 1986; Arnold et al., 2012). In contrast, males play little to no role in parental care and spend more time gaining energy reserves for fall migration (Rohwer, 1986; Boves et al., 2016). Therefore, female birds are expected to be more impacted by increased energetic costs compared to males. Therefore, it is important to consider environmental covariates when examining the role of stress, and its subsequent impacts on body condition and survival in wildlife.

In chapter 3, using mark-recapture analysis I found that females had a higher overall mortality rate (52%) compared to males (38%). The highly energetically costly processes like egg production, incubation, and predation escape while incubating deplete females of their energy reserves and leave less time to replenish the lost reserves before fall migration, unlike males. My results of Chapter 2 support this as BCI in females decreased more prominently than males with increased energy expenditure during the period of feather growth (Figure 4.1.). Despite the impacts of increased energetic expenditure on subsequent body condition, no impact of either energetic expenditure or body condition was found on overall survival of Blue-winged Teal. However, increasing $CORT_f$ was found to be associated with a lower probability of being hunted in males only (Figure 4.1.). A possible explanation for this result is that a smaller proportion of males with higher levels of $CORT_f$ were in the population during the subsequent hunting seasons – i.e., they may have failed to migrate, or experienced higher levels of mortality prior to the hunting season. An alternate explanation is that higher $CORT_f$ could have provided males with an advantage, making them more able to avoid being hunted, particularly if it was associated with increased foraging activity to increase internal energy reserves in preparation for fall migration. Thus, $CORT$ likely plays a complex role in modulating and facilitating

redistribution of energy, regulation of daily metabolism, and modification of behaviour to amass energy reserves prior to fall migration. These modifications in response to elevated CORT further could assist in avoidance of additional energetic costs and higher survival. As for most other waterfowl species, males were more likely to be hunted compared to females, suggesting a male bias in the population post-breeding, and/or that males are more likely to be targeted or reported by hunters.

4.1.2 Associations among climate and AIV infection

The results suggest that AIV infection does not pose a cost to Blue-winged Teal, as I found no association between infection with CORTf, measures of condition, probability of being hunted, or probability of survival. However, I found that there exists a complex, non-linear relationship between temperature and AIV infection. Mean daily minimum temperatures 3-10 days prior to the date of sampling were associated with the probability of AIV infection (Figure 4.1.). Up to about 10°C, the probability of AIV infection decreased with increasing temperature, however, this relationship levelled off between 10-12°C. This relationship of AIV infection at lower ranges of temperature corresponds with previous studies that have demonstrated that survival of the virus increases with lower temperatures (Stallknecht et al., 1990; Ramey et al., 2020). However, my study also showed that when mean daily minimum temperatures 3-10 days prior to sampling exceeded 12°C, the probability of AIV infection increased. This positive association between AIV infection and minimum daily temperatures at higher temperatures may potentially be a result of the influence of temperature on bird movement or behaviour, rather than impacts on the virus itself. For instance, higher temperatures may influence migration patterns, distribution (Tian et al., 2015), or local movement (van Dijk et al., 2015b), resulting in increased bird densities and therefore increased rate of exposure and transmission.

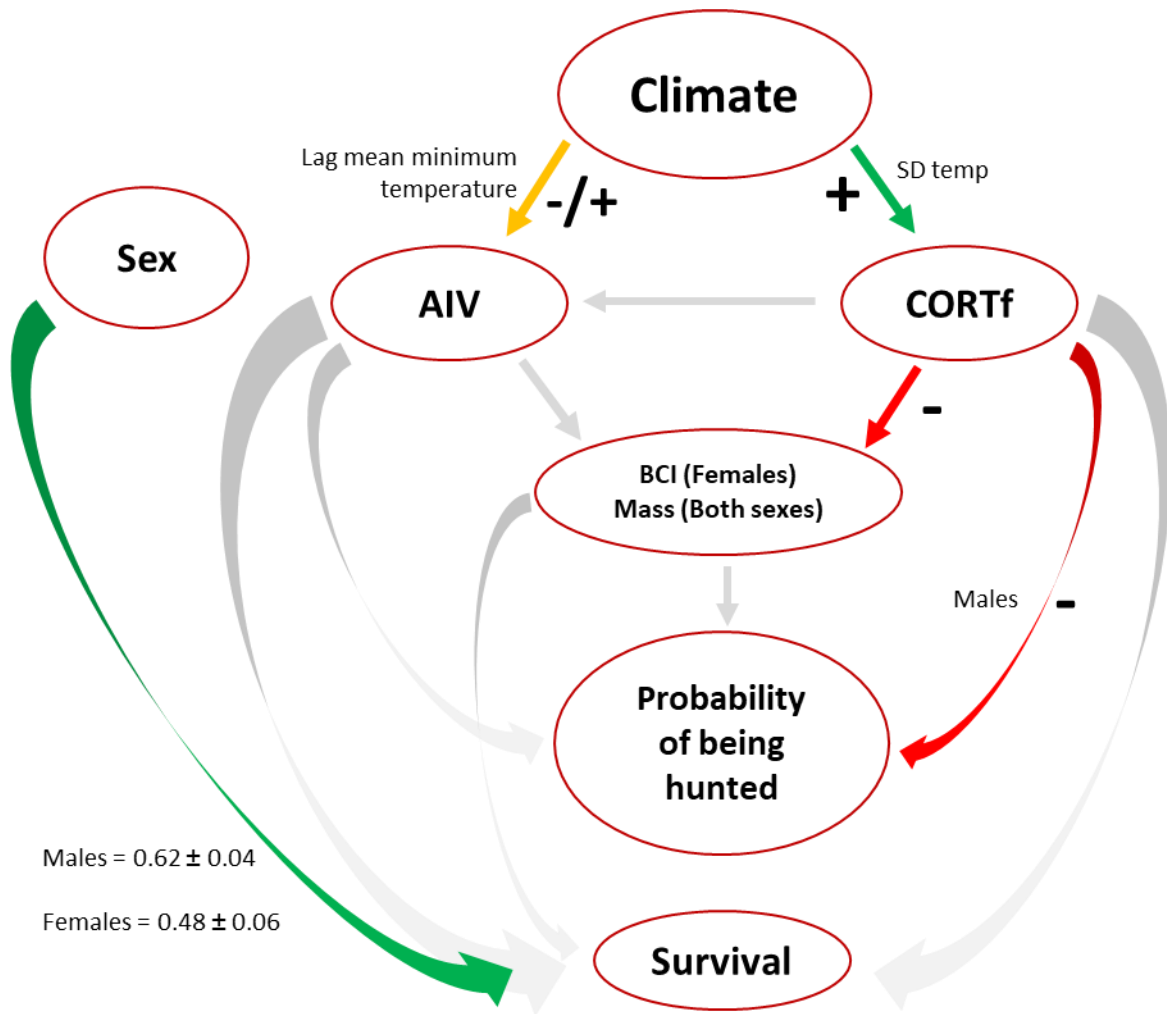


Figure 4.1. Overview of the study results examining relationships among climate, stress, avian influenza virus (AIV) infection, and survival in Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) from 2007-2018. In figure, + = positive relationship and - = negative relationship. Arrows: green = positive relationship, red = negative relationship, yellow = quadratic relationship, and grey = no significant relationship. Abbreviations: SD temp= Mean daily standard deviation in temperature for July 1-16 ($^{\circ}\text{C}$), and Lag mean temperature= mean daily minimum temperature 3-10 days prior to sampling.

4.2 Implications in the face of a changing climate

Global warming has affected, and continues to affect Canada significantly more than it has affected the rest of the world. Temperatures across all seasons throughout the country have risen, and are projected to keep rising in the near future, with most significant impacts seen in the Canadian prairies and northern Canada (Government of Canada, 2019). My study, establishes a bridge between the role of climatic variations and physiological adaptations/energy expenditure of migratory waterfowl in the Canadian prairies. The prairie pothole region is one of the most important areas for waterfowl reproduction and ecology, providing habitat to more than 60% of the breeding population of several waterfowl species (Smith, 1995). Based on my findings, increasing fluctuations in climate will potentially increase energetic costs faced by migratory birds to maintain homeostasis and adapt or respond to a changing climate. These higher energetic costs can result in significant carry-over effects and fitness consequences, by forcing birds to redirect valuable energy and resources from body condition, survival, migration, or other costly activities such as reproduction and immune function.

In addition to potentially increasing energetic costs to migratory waterfowl, climate warming will have significant impacts on the ecology, spread, and evolution of AIVs globally. Warming temperatures have the potential to increase the spread and generation of novel, potentially highly pathogenic AIVs, through impacts on migratory bird breeding seasons, migratory pathways, host range and population densities. (Morin et al., 2018). Increasing northward distributions of migratory bird populations have been observed with increasing temperatures globally (Patterson and Guerin, 2013), which could potentially increase interactions among populations and species converging from different flyways and wintering sites. For example, Northern Pintails (*Anas acuta*) overwintering in California and Japan are suggested to have higher possibilities of pathogen exposure when spending their breeding season in Russia (Flint et al., 2009). Furthermore, Northern Pintails in Alaskan breeding grounds have been shown to have higher prevalences of LPAIVs of Asian lineages (Pearce et al., 2009), and higher prevalence among trans-hemispheric migrants compared to local migrants (Pearce et al., 2011). Hill et al. (2017) showed that LPAIV-infected Mallards with subtypes H5N2 and H1N1 in Alaska shared their ancestries with HPAIV subtypes after the interhemispheric movement of birds from Eurasia. Therefore, these sites of convergence for birds can potentially cause higher

transmission and reassortment of AIVs and pose a threat to wildlife, domestic poultry and humans.

Similar to northern regions of Canada, the prairies are warming at an alarming rate. As shown in this study, these variations in climate are not only costly to birds but the warming temperatures at higher ranges of temperatures can also increase the probability of AIV in the Canadian prairies. Climate change can also diminish wetlands across the prairies, and affect densities of waterfowl populations, which can also affect the ecology of AIVs. Furthermore, the expansion of breeding seasons due to warming temperatures can increase opportunities and risk for transmission, spread, and reassortment of AIVs in waterfowl populations (Cappelle et al., 2014; Morin et al., 2018), potentially increasing the spread of existing and novel strains of AIV in North America and across different flyways (Scotch et al., 2014). The presence of migratory waterfowl has also been shown to be positively associated with outbreaks of AIV in commercial poultry within North America (Humphreys et al., 2020), further emphasizing the role of migration in transmission and spread of AIVs. In other parts of the world where agriculture systems such as rice fields are important for interactions between the wild birds and domestic poultry (Gilbert et al., 2017), the effects of climate change on agriculture can also play a role in AIV transmission, spread, and generation of novel strains of AIV. With projections of warming temperature and increasing human populations in eastern and south-east Asia, prolonged growing seasons and increased rice growth are expected, potentially increasing the interface between wild birds and domestic poultry (Zhang et al., 2017a, 2017b), which increases the risk of emergence and spread of HPAIV of concern to human and animal health, and the global economy. Additionally, the presence of live poultry markets can further contribute to the spread of HPAIV (Artois et al., 2017).

4.3 Management implications and future directions

With rising temperatures, and the positive association between temperatures and probability of AIV infection at mean daily minimum temperatures above 12°C, it will be increasingly important to understand the role of climate change on AIV dynamics in waterfowl. Infectious diseases and increased energetic costs in relation to temperatures have the potential to influence waterfowl populations by affecting survival or reproduction, and can have implications for waterfowl species that are more vulnerable. Management tools to mitigate the effects of some

infectious diseases on waterfowl populations can include the changing of hunting regulations (e.g., reduced bag limits), or closure of affected wetlands or sites to hunters or the general public. Knowing the prevalence of potentially zoonotic AIVs or other infectious diseases in waterfowl also can help inform hunters on risks of infection, and can be used to help educate on methods to avoid infection.

Transmission of AIV infection in waterfowl has been found to be a density-dependent process, with higher AIV prevalences observed at higher waterfowl population densities (Nallar et al., 2016, Papp et al., 2017); however, density variables were not found to be informative in my analyses. Moving forward I recommend examining actual population density at the time of sampling (in lieu of spring population densities as an index of August population density) or average population density per pond, as that might provide a better idea of local population densities by taking into account the water bodies. Given that wetlands are responsive to snow melt, local climatic conditions, human management, and land use (Schertzer et al., 2004; Government of Canada, 2019), it will be important to see if reduction in water bodies increases the population densities of migratory waterfowl, or diverts populations to more favourable locations, which would have implications for transmission and spread of AIV. Reduction of prairie wetlands over time may also indirectly act as additional stressors for migratory birds breeding in the Canadian prairies. Therefore, it will be important to explore relationships between the role of diminishing wetlands in AIV transmission and their interactions causing potential energetic costs.

The use of band recovery data to analyse survival in relation to AIV infection or stress requires a larger dataset is required across many years when encounter rates are as low as they are in Blue-winged Teal. Other species with higher recovery rates such as Mallards can be used to explore these relationships further. In this study, I focused on a subset of Blue-winged Teal with associated CORTf data but I could have possibly explored relationship between AIV, body condition index and survival on a larger dataset, without including the CORTf data. Telemetry studies can also be utilized that could follow birds and assess AIV or CORTf in relation to subsequent flight patterns/speed, length or locations of stopovers, habitat quality, how long it takes to arrive at wintering sites, and more accurate estimates of survival.

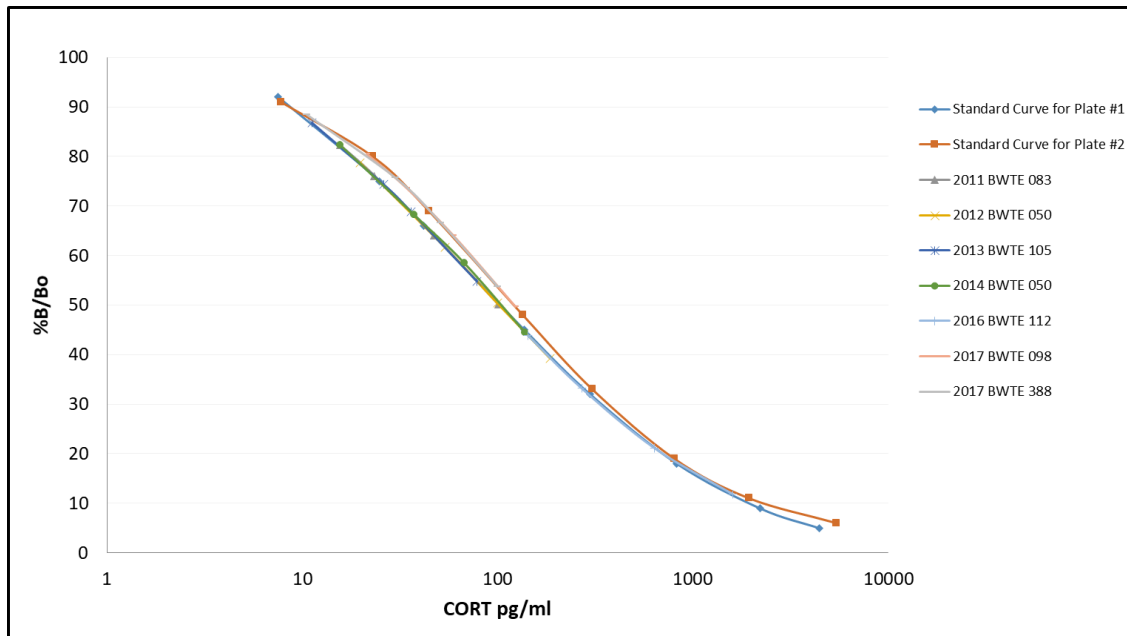
Results of this study have potential to provide a platform for modelling and predicting survival of waterfowl in relation to stress, body condition, and AIV status in migratory

waterfowl. My study provides insight into the stress response and/or energy expenditure in a migratory waterfowl species in response to climatic variation. Further studies are required in order to explore the impacts of a changing climate on stress, AIV infection dynamics, and how those interact to impact body condition, migration and survival in migratory birds. This study also provides surveillance data and epidemiological evidence of factors that contribute to the prevalence of AIV in migratory waterfowl prior to fall migration in the Canadian prairies over a decade (2007-2018). In addition to previously established population parameters such as population density, this research incorporates environmental conditions experienced by waterfowl at their breeding, moulting, or staging grounds. Therefore, it provides further insight on the maintenance of AIV infection in migratory waterfowl population in prairies.

APPENDICES

Appendix A: All sampling sites within three prairie provinces and number of Blue-winged Teal (*Spatula discors*) swab samples used in the on-going investigation on ecology of avian influenza viruses, samples prior to fall migration (2007-18).

Province	Location	Number of Samples
Alberta	Brooks	1760
	Buffalo Lake	302
	Frank Lake	199
Manitoba	Big Grass Marsh	221
	Delta Marsh	612
	Interlake	7
Saskatchewan	Cochin	685
	Last Mountain Lake	2600
	Rice Lake	1143
	Sullivan Lake	20
Total		7549



Appendix B: Displacement curves of serially diluted (1:1, 1:2, 1:4 and 1:8) reconstituted tail feather extracts from 7 Blue-winged Teal sampled (*Spatula discors*) in the Canadian prairie provinces (2007-2018), demonstrating parallelism in relation to the standard curve. %B/B₀ (% Bound/Maximum Bound): ratio of the absorbance of a particular sample or standard well to that of the maximum binding (B₀) well.

Appendix C: Feather corticosterone (CORTf) levels (mean +/- standard error) in tail feathers of Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Saskatchewan, Manitoba, and Alberta) in 2007-18, by age, sex and province (n = 595).

Variable	Location	N	CORTf (pg/mm) Mean (SE)
Age	After Hatch Year birds	319	1.68 (0.11)
	Hatch Year birds	276	1.37 (0.10)
Sex	Females	227	1.53 (0.12)
	Males	368	1.54 (0.10)
Province	Alberta	242	1.40 (0.11)
	Manitoba	75	2.21 (0.31)
	Saskatchewan	278	1.48 (0.10)
Overall		595	1.54 (0.08)

Appendix D: Models explaining variation in corticosterone levels (CORTf) measured in tail feathers of Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba), from 2007 to 2018 (n = 595). Year was included as a random effect term. (1) List of competitive models used for calculating model weights. The table includes models containing only informative variables and excludes nested versions of the top models. Best-supported model is **bolded**. (2) Full list of models explored, and all uninformative variables are displayed in *italics*. The null model includes the random effect of year.

1. Competitive models	<i>k</i>	Log. lik	AICc	ΔAICc	Weight
Mean Daily SD Temp_{July 1-16}	2	-802.26	1612.58	0.00	0.985
Mean Daily Min Temp _{July 17-31}	2	-806.52	1621.11	8.53	0.014
Mean Daily SD Temp _{July 17-31}	2	-809.22	1626.50	13.92	0.001
Mean Daily Temp _{July 17-31}	2	-812.25	1632.57	19.98	0
Mean Daily Min Temp _{July 1-31}	2	-814.68	1637.43	24.85	0
Mean Daily Max Temp _{July 1-16}	2	-814.72	1637.51	24.92	0
Province	3	-816.27	1642.63	30.05	0
Mean Daily Temp _{July 1-16}	2	-817.70	1643.47	30.89	0
Age	2	-817.90	1643.87	31.29	0
Mean Daily Max Temp _{July 1-31}	2	-818.19	1644.46	31.87	0
Null	1	-819.39	1644.83	32.24	0

2. All models explored	<i>k</i>	Log. lik	AICc
Mean Daily SD Temp_{July 1-16}	2	-802.26	1612.58
Mean Daily SD Temp _{July 1-16} + <i>Age</i>	3	-801.34	1612.79
Mean Daily SD Temp _{July 1-16} + <i>Province</i> + <i>Age</i>	5	-800.08	1614.35
Mean Daily SD Temp _{July 1-16} + <i>Province</i>	4	-801.49	1615.12
Mean Daily SD Temp _{July 1-16} + <i>Province</i> + <i>Age</i> + <i>Sex</i>	6	-799.55	1615.34
Mean Daily Min Temp _{July 17-31}	2	-806.52	1621.11
Mean Daily SD Temp _{July 17-31}	2	-809.22	1626.50
Mean Daily Temp _{July 17-31}	2	-812.25	1632.57
Mean Daily Min Temp _{July 1-31}	2	-814.68	1637.43
Mean Daily Max Temp _{July 1-16}	2	-814.72	1637.51
Province	3	-816.27	1642.63
Mean Daily Temp _{July 1-16}	2	-817.70	1643.47
Age	2	-817.90	1643.87
Mean Daily Max Temp _{July 1-31}	2	-818.19	1644.46
<i>Age</i> + <i>Sex</i> + <i>Sex*Age</i>	4	-816.20	1644.55
<i>Age</i> + <i>Sex</i>	3	-817.25	1644.59
Null	1	-819.39	1644.83
<i>Population density</i>	2	-818.48	1645.03

<i>AIV</i>	2	-818.87	1645.46
<i>Mean Daily Min Temp</i> _{July 1-16}	2	-819.10	1646.27
<i>Sex</i>	2	-819.17	1646.41
<i>Mean Total Daily Precipitation</i> _{July 1-16}	2	-819.21	1646.49
<i>Mean Daily Temp</i> _{July 1-131}	2	-819.21	1646.49
<i>Mean Daily Temp</i> _{July 17-31}	2	-819.27	1646.61
<i>Mean Total Daily Precipitation</i> _{July 1-31}	2	-819.35	1646.77

Abbreviations: k = number of parameters; Log lik = Log likelihood; AICc = Akaike's Information Criterion values adjusted for sample size; SD = Standard deviation; Temp = Temperature; Min = Minimum; Max = Maximum; and AIV = Avian influenza virus infection.

Appendix E: Models explaining probability of avian influenza virus (AIV) infection in Blue-winged Teal (*Spatula discors*; BWTE) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba), from 2007 to 2018 (n = 557). Year was included as a random effect term. (1) List of competitive models used for calculating model weights. The table includes models containing only informative variables and excludes nested versions of the top models. Best-supported model is **bolded** (2) Full list of models explored, and all uninformative variables are displayed in *italics*. The null model includes the random effect of year.

1. Competitive models	<i>k</i>	Log. lik	AICc	ΔAICc	Weight
Age + Lag Mean Daily Min Temp_{3-10d} + (Lag Mean Daily Min Temp_{3-10d})²	4	-142.77	295.65	0.00	0.98
Age + Lag Mean Daily Min Temp _{7-14d} + (Lag Mean Daily Min Temp _{7-14d}) ²	4	-146.67	303.45	7.80	0.02
Age + Province	4	-150.16	310.43	15.39	0
Population density	2	-169.08	344.20	48.55	0
Null	1	-170.93	345.88	50.23	0

2. All models explored	<i>k</i>	Log. lik	AICc
Age + Lag Mean Daily Min Temp_{3-10d} + (Lag Mean Daily Min Temp_{3-10d})²	4	-142.77	295.65
Age + Lag Mean Daily Min Temp _{3-10d} + (Lag Mean Daily Min Temp _{3-10d}) ² + <i>BWTE density</i>	5	-142.28	296.72
Age + Lag Mean Daily Min Temp _{7-14d} + (Lag Mean Daily Min Temp _{7-14d}) ²	4	-146.67	303.45
Age + Lag Mean Daily Min Temp _{7-14d} + (Lag Mean Daily Min Temp _{7-14d}) ² + <i>BWTE density</i>	5	-146.30	304.73
Age + Lag Mean Daily Min Temp _{3-10d}	3	-150.69	309.45
Age + Province	4	-150.16	310.43
Age + Lag Mean Daily Min Temp _{7-14d}	3	-151.35	310.77
Age + Lag Mean Daily Min Temp _{3-10d} + <i>BWTE Density</i>	4	-150.47	311.04
Age + Lag Mean Daily Min Temp _{3-10d} + <i>Population density</i>	4	-150.64	311.39
Age + Lag Mean Daily Min Temp _{3-10d} + <i>BWTE density</i>	4	-151.14	312.39
Age + Lag Mean Daily Min Temp _{7-14d} + <i>Population density</i>	4	-151.32	312.74
Age	2	-155.31	316.66
Age + <i>Population density</i>	3	-154.70	317.46
Age + <i>Pond density</i>	3	-155.17	318.41
Age + <i>BWTE Density</i>	3	-155.27	318.60

Province	3	-161.34	330.75
Lag Mean Daily Min Temp _{3-10d}	2	-164.63	335.31
Lag Mean Daily Min Temp _{7-14d}	2	-164.78	335.40
Lag Mean Daily Min Temp _{0-7d}	2	-168.87	343.79
Population density	2	-169.08	344.20
Lag Mean Daily Temp _{7-14d}	2	-169.48	345.00
Lag Mean Daily Temp _{0-7d}	2	-169.86	345.77
Null	1	-170.93	345.88
<i>Lag Mean Daily Temp_{3-10d}</i>	2	-170.26	346.56
<i>Lag Mean Daily Max Temp_{3-10d}</i>	2	-170.57	347.19
<i>Pond density</i>	2	-170.66	347.49
<i>Sex</i>	2	-170.78	347.61
<i>Lag Mean Daily Max Temp_{0-7d}</i>	2	-170.83	347.71
<i>BWTE Density</i>	2	-170.91	347.86
<i>Lag Mean Daily Max Temp_{7-14d}</i>	2	-170.91	347.87
<i>CORTf</i>	2	-170.93	347.90

Abbreviations: k = number of parameters; Log lik = Log likelihood; AICc = Akaike's Information Criterion values adjusted for sample size; BWTE = Blue-winged teal; Lag Mean Daily Min Temp_{0-7d} = Mean daily minimum temperature 0-7 days prior to sampling day; Lag Mean Daily Max Temp_{0-7d} = Mean daily maximum temperature 0-7 days prior to sampling day; Lag Mean Daily Temp_{0-7d} = Mean daily temperature 0-7 days prior to sampling day; Lag Mean Daily Min Temp_{3-10d} = Mean daily minimum temperature 3-10 days prior to sampling day; Lag Mean Daily Max Temp_{3-10d} = Mean daily maximum temperature 3-10 days prior to sampling day; Lag Mean Daily Temp_{3-10d} = Mean daily temperature 3-10 days prior to sampling day; Lag Mean Daily Min Temp_{7-14d} = Mean daily minimum temperature 7-14 days prior to sampling day; Lag Mean Daily Max Temp_{7-14d} = Mean daily maximum temperature 7-14 days prior to sampling day; Lag Mean Daily Temp_{7-14d} = Mean daily temperature 7-14 days prior to sampling day; and CORTf = Feather corticosterone.

Appendix F: Mass (g) and estimated body condition index (BCI) of Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba), from 2007 to 2018, by age, sex, and province (n = 557).

Variable	Location	N	Mass (g) Mean (SE)	BCI Mean (SE)
Age	After Hatch Year	309	389.61 (2.75)	374.36 (4.79)
	Hatch Year	248	350.63 (2.57)	389.56 (6.48)
Sex	Females	203	348.02 (2.86)	422.79 (7.45)
	Males	354	386.16 (2.55)	357.23 (3.96)
Age-Sex	After Hatch Year - Female	84	356.52 (4.37)	425.09 (9.97)
	Hatch Year - Female	119	342.01 (3.69)	421.16 (10.62)
	After Hatch Year - Male	225	401.97 (3.02)	355.42 (4.87)
	Hatch Year - Male	129	358.58 (3.44)	360.40 (6.79)
Province	Alberta	231	365.49 (3.19)	384.92 (6.38)
	Manitoba	74	367.03 (4.75)	362.77 (10.62)
	Saskatchewan	252	379.99 (3.19)	383.03 (5.61)
Overall		557	365.5 (2.07)	381.13 (3.93)

Appendix G: Models explaining variation in body mass in Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba), from 2007 to 2018 (n = 557). Year was included as a random effect term. (1) List of competitive models used for calculating model weights. The table includes models containing only informative variables and excludes nested versions of the top models. Best-supported model is **bolded**. (2) Full list of models explored, and all uninformative variables are displayed in *italics*. The null model includes the random effect of year.

1. Competitive Models	<i>k</i>	Log. lik	AICc	ΔAICc	Weight
Province + Age + Sex + CORTf	6	-2850.63	5726.81	0.00	1.00
AIV	2	-2951.70	5912.85	186.04	0
Null	1	-2955.22	5916.49	189.68	0

2. All models explored	<i>k</i>	Log. lik	AICc
Province + Age + Sex + CORTf	6	-2850.63	5726.81
Province + Age + Sex	5	-2857.40	5729.00
Sex + Age	3	-2869.49	5749.10
Age	2	-2903.96	5816.00
Sex	2	-2909.69	5827.46
Province + AIV	4	-2939.14	5894.90
Province	3	-2944.23	5898.60
AIV + CORTf + AIV * CORTf	4	-2948.27	5910.14
AIV + <i>CORTf</i>	3	-2951.02	5912.60
AIV	2	-2951.70	5912.85
CORTf	2	-2954.08	5916.23
Null	1	-2955.22	5916.49

Abbreviations: *k* = number of parameters; Log lik = Log likelihood; AICc = Akaike's Information Criterion values adjusted for sample size; CORTf = Feather corticosterone; and AIV = Avian influenza virus infection.

Appendix H: Models explaining variation in Body Condition Index of Blue-winged Teal (*Spatula discors*) sampled in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba), from 2007 to 2018 (n = 557). Year was included as a random effect term. (1) List of competitive models used for calculating model weights. The table includes models containing only informative variables and excludes nested versions of the top models. Best-supported model is **bolded**. (2) Full list of models explored, and all uninformative variables are displayed in *italics*. The null model includes the random effect of year. Although the addition of AIV ($\beta = 11.39$, 95% CI = -12.10, 35.01), age ($\beta = -3.55$, 95% CI = -18.5, 11.6), and province (MB: $\beta = -10.41$, 95% CI = -34.66, 13.58; SK: $\beta = 1.70$, 95% CI = -13.38, 16.82) to top model further reduced AICc, these variables were deemed uninformative given that their 95% confidence intervals spanned zero, and hence were not included in the list of candidate models to calculate model weights.

(a) Competitive models	<i>k</i>	Log. lik	AICc	Δ AICc	Weight
Sex + CORTf + Sex * CORTf	4	-3254.51	6521.17	0.00	1.00
AIV + CORTf + AIV * CORTf	4	-3285.31	6582.82	61.60	0
Province	3	-3290.81	6591.72	70.56	0
Age	2	-3293.59	6595.25	74.08	0
Null	1	-3297.59	6601.22	80.06	0

(b) All models explored	<i>k</i>	Log. lik	AICc
Sex + CORTf + Sex * CORTf + <i>Province</i>	6	-3247.68	6511.60
Sex + CORTf + Sex * CORTf + <i>AIV</i>	5	-3250.81	6515.51
Sex + CORTf + Sex * CORTf + <i>Age</i>	5	-3251.44	6517.10
Sex + CORTf + Sex * CORTf	4	-3254.51	6521.17
Sex + CORTf + <i>AIV</i>	4	-3255.02	6522.30
Sex + CORTf	3	-3259.00	6528.12
Sex	2	-3261.98	6532.03
AIV + CORTf + AIV * CORTf	4	-3284.43	6582.76
Province	3	-3290.81	6591.72
AIV	2	-3293.51	6595.10
Age	2	-3293.59	6595.25
CORTf	2	-3295.03	6598.13
Null	1	-3297.59	6601.22

Abbreviations: *k* = number of parameters; Log lik = Log likelihood; AICc = Akaike's Information Criterion values adjusted for sample size; CORTf = Feather corticosterone; and AIV = Avian influenza virus infection.

Appendix I: Numbers of Blue-winged Teal (*Spatula discors*; BWTE) encountered and hunted following banding in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in August (2007-2018) and BWTE subset used in this study (n = 688).

Year	All BWTE banded				BWTE subset used in analysis		
	Total Banded	Total Encountered	Total Hunted	Hunted in first year	Total Banded	Total Hunted	Hunted in first year
2007	600	28	26	16	81	23	12
2008	442	23	22	16	75	18	11
2009	311	4	4	3	59	4	3
2010	620	27	25	19	84	21	16
2011	479	21	20	17	9	1	0
2012	492	28	27	17	90	26	15
2013	646	35	32	24	50	16	11
2014	899	41	33	27	47	9	7
2015	472	19	16	10	52	14	9
2016	1289	65	51	51	51	11	8
2017	1057	75	71	74	48	8	8
2018	242	4	3	3	42	3	3
Total	7549	370 (4.9%)	330 (4.4%)	277 (3.7%)	688	154	103

Appendix J: Age, sex and province numbers of Blue-winged Teal (*Spatula discors*; BWTE) encountered and hunted following banding in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in August (2007-2018) and BWTE subset used in this study (n = 688).

Variable		All BWTE banded				BWTE subset used in analysis		
		Total Banded	Total Encountered	Total Hunted	Hunted in first year	Total Banded	Total Hunted	Hunted in first year
Age	After hatch Years	3834	199 (5.2%)	176 (4.6%)	147 (3.8%)	382	89	58
	Hatch Years	3751	171 (4.6%)	154 (4.1%)	130 (3.5%)	306	65	45
Sex	Females	2798	133 (4.8%)	112 (4.0%)	109 (3.9%)	245	44	33
	Males	4751	237 (5.0%)	218 (4.6%)	168 (3.5%)	443	110	70
Province	Alberta	2261	99 (4.4%)	76 (3.4%)	68 (3.0%)	263	43	27
	Manitoba	840	39 (4.6%)	38 (4.5%)	27 (3.2%)	97	26	19
	Saskatchewan	4448	232 (5.2%)	216 (4.9%)	182 (4.1%)	328	85	57
Total		7549	370	330	277	688	154	103

Appendix K: Number of years following banding of Blue-winged Teal (*Spatula discors*) hunted in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in August (2007-2018).

Years following sampling/banding	Number of hunted birds	
	Full dataset	Subset
0-1	251	103
1-2	38	27
2-3	23	11
3-4	11	8
4-5	1	1
5-6	1	1
6-7	1	-
7-8	3	2
8-9	-	-
9-10	-	-
10-11	1	1
Total	330	154

Appendix L: Number of Blue-winged Teal (*Spatula discors*) hunted by months within the first year following banding in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in August (2007-2018), prior to fall migration of birds.

Years following sampling/banding	Number of bird hunted
September	56
October	9
November	12
December	11
January	11
February	3
March	1
Total	103

Appendix M: Location of where Blue-winged Teal (*Spatula discors*) were hunted within one year of banding in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in August (2007-2018; n = 103).

Country	State/Province	Number of hunted birds
Canada	Alberta	1
	Manitoba	2
	Ontario	3
United States	Arkansas	1
	Colorado	1
	Florida	3
	Illinois	1
	Indiana	2
	Iowa	2
	Kansas	5
	Louisiana	37
	Minnesota	3
	Missouri	1
	Nebraska	2
	New Mexico	1
	North Dakota	1
	Ohio	2
	Oklahoma	1
	South Dakota	1
Tennessee	1	
Texas	19	
Wisconsin	1	
Mexico	Hidalgo	4
	State of Mexico	1
	Veracruz	1
	Yucatan	3
Nicaragua	Chinandega	2
Columbia	Sucre	1
Total		103

Appendix N: Models explaining probability of Blue-winged Teal (*Spatula discors*) being hunted within the first year of banding. The birds were banded in in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in August (2007-2018) (n = 637). Year was included as a random effect term. (1) List of competitive models used for calculating model weights. The table includes models containing only informative variables and excludes nested versions of the top models. Best-supported model is **bolded** (2) Full list of models explored, and all uninformative variables displayed in *italics*. The null model includes the random effect of year.

1. Competitive models	<i>k</i>	Log lik	AICc	ΔAICc	Weight
Sex + CORTf + Sex * CORTf + Province	6	-274.33	562.85	0.00	0.92
Null	1	-281.85	567.72	4.88	0.08

2. All models explored	<i>k</i>	Log lik	AICc
Sex + CORTf + Sex * CORTf + Province	6	-274.33	562.85
Province	3	-277.49	563.04
Sex + Province	5	-276.96	564.01
Sex + CORTf + Sex * CORTf	4	-278.66	567.41
Null	1	-281.85	567.72
<i>Sex</i>	2	-281.26	568.56
<i>CORTf</i>	2	-281.29	568.61
<i>Body Mass</i>	2	-281.63	569.30
<i>AIV</i>	2	-281.66	569.37
<i>Sex + CORTf</i>	2	-280.74	569.55
<i>Age</i>	2	-281.81	569.66
<i>BCI</i>	2	-281.83	569.69

Abbreviations: *k* = number of parameters; AICc = Akaike's Information Criterion values adjusted for sample size; CORTf = Feather corticosterone; AIV = Avian influenza virus infection; and BCI = Body condition index.

Appendix O: Models explored using Brownie parameterization and logit link function in program MARK to estimate survival (S) and recovery (f). The Blue-winged Teal (*Spatula discors*) were banded in the Canadian prairie provinces (Alberta, Saskatchewan, and Manitoba) in August (2007-2018) prior to fall migration of birds (n = 688). The table includes models containing all variables explored with nested versions of top models. Best-supported model is **bolded**. All uninformative variables are displayed in *italics*. (.) Represents no variable or null.

Models explored for survival	k	Log lik	QAICc	Weight
S (Sex) f (.)	2	1173.92	847.01	0.16
S (Sex) f (<i>CORTf</i>)	3	1171.80	847.52	0.12
S (Sex + <i>Body mass</i>) f (.)	3	1173.48	848.72	0.07
S (Sex + <i>AIV</i>) f (.)	3	1173.57	848.79	0.07
S (Sex) f (<i>AIV</i>)	3	1173.65	848.84	0.06
S (Sex + <i>BCI</i>) f (.)	3	1173.83	848.97	0.06
S (Sex) f (<i>Body mass</i>)	3	1173.92	849.03	0.06
S (Sex) f (<i>AIV</i> + <i>CORTf</i>)	4	1171.57	849.38	0.05
S (Sex) f (<i>CORTf</i> + <i>Body mass</i>)	4	1171.80	849.55	0.04
S (Sex + <i>AIV</i>) f (<i>AIV</i>)	4	1172.11	849.77	0.04
S (.) f (.)	1	1181.04	850.10	0.03
<i>S (Sex + CORTf + Body mass) f (.)</i>	4	1172.65	850.16	0.03
<i>S (Sex + Age + AIV) f (.)</i>	4	1173.33	850.64	0.03
<i>S (Body mass) f (.)</i>	2	1179.82	851.24	0.02
<i>S (CORTf) f (.)</i>	2	1179.87	851.28	0.02
<i>S (BCI) f (.)</i>	2	1179.93	851.32	0.02
<i>S (Sex) f (CORTf + BCI + Body mass)</i>	5	1171.70	851.51	0.02
<i>S (Sex + Age + AIV) f (AIV)</i>	5	1171.96	851.70	0.02
<i>S (Sex + CORTf + BCI + Body mass) f (.)</i>	5	1172.24	851.90	0.01
<i>S (AIV) f (.)</i>	2	1180.79	851.94	0.01
<i>S (AIV + CORTf) f (.)</i>	3	1179.57	853.09	0.01
<i>S (AIV + Body mass) f (.)</i>	3	1179.64	853.14	0.01
<i>S (Sex + Age + AIV) f (Sex + AIV)</i>	6	1171.85	853.66	0.01
<i>S (Sex + Age) f (AIV)</i>	6	1171.96	853.74	0.01
<i>S (Sex + Age + AIV) f (Sex + Age + AIV)</i>	7	1171.85	855.71	0.00

Abbreviations: S = Survival; f = Recovery; k = number of parameters; QAICc = Quasi Akaike's Information Criterion values adjusted for sample size; CORTf = Feather corticosterone; AIV = Avian influenza virus infection; and BCI = Body condition index.

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