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# Weather and Photoperiod Indices of Autumn and Winter Dabbling Duck Abundance in the Mississippi and Atlantic Flyways of North America

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Graduate Program in Biology A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science © Lena M. Van Den Elsen 2016

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## Abstract

Climate change may influence autumn and winter distributions of dabbling ducks throughout the Atlantic and Mississippi Flyways of North America. To determine how weather and photoperiod influenced autumn-winter abundances of dabbling ducks at staging areas in eastern North America, I modeled weather and photoperiod variables with rate of change in relative abundance of various dabbling duck species over space and time. Latitude was incorporated into models to determine if changes in duck abundance in relation to weather severity were influenced by locale. Changes in abundance were best described by weather models incorporating temperature and snowfall variables for all species except blue-winged teal (*Anas discors*), which was best explained by photoperiod. Latitude was present in all top models for all study species. My findings aid wildlife management efforts in predicting potential changes in the non-breeding distribution of ducks resulting from climate change.

## Keywords

Climate, duck, migration, snow, temperature, waterfowl, weather severity.

## **Co-Authorship Statement**

All work within this thesis has been authored by Lena M. M. Vanden Elsen and will be published with Michael L. Schummer and Scott A. Petrie.

Under the supervision of Dr. Scott Petrie and Dr. Michael Schummer, I was responsible for all intellectual and analytical aspects of the development and completion of this thesis. With the assistance of Dr. Samantha Richman I wrote a program to format all of my data and perform mathematical calculations prior to statistical analyses. I performed the statistical analyses for all aspects of this thesis under the guidance of Dr. Michael Schummer. All co-authors provided valuable editorial and intellectual guidance.

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# List of Abbreviations

- WSI Weather Severity Index
- GCM Global Circulation Models
- NWR National Wildlife Refuge
- WMA Wildlife Management Area
- USGS United States Geological Survey
- NARR North America Regional Reanalysis
- PCA Principal Component Analysis
- PC1 Principal Component 1
- AIC Akaike's Information Criterion

### Chapter 1 : Introduction

Photoperiod and weather severity are important proximate factors that trigger avian migration (Gwinner 1996, Newton 2008, Dalby et al. 2013). Decreasing day length is often the primary exogenous cue for initial movements from breeding towards wintering areas because it synchronizes the circadian (daily endogenous) and circannual (annual) rhythms in birds that are responsible for initiating migration (Gwinner 2003). Photoperiod likely becomes a less important migration cue as Nearctic birds move south through North America because photoperiod is decreasingly linked to probability of unfavorable weather conditions lasting for extended periods as birds move south (e.g., frozen lakes and wetlands; Terrill 1990). Long-distance migrants wintering in stable habitats use photoperiod as their primary migration cue, whereas shorter distance migrants wintering in less predictable habitats use weather cues to a greater degree (Temple and Cary 1987). Adjustment in timing of migratory movements with changes in weather can affect fitness, and may differ among species within the same family based on various life history traits (Visser et al. 1998, Newton 2008).

Seasonal mismatch between availability of resources and timing of arrival during spring has been observed in long distance migrants (Visser et al. 1998, Both et al. 2010). Annual variation in weather can also result in loss of synchrony between timing of reproduction and necessary food and habitat resources, which has been linked to population declines in some species (Both et al. 2010, Drever et al. 2012). Although generally lacking investigation, the potential for temporal mismatch between habitat and food resources and migration in birds also is possible during autumn and winter (e.g., timing of migration is timed with seasonal rain events and flooding that make foods functionally available to waterbirds; Cox and Afton 2000). Changes in climate can influence availability of habitat necessary to sustain wildlife populations, and can cause shifts in ranges as animals attempt to match resource needs with availability (Walther et al. 2002). Recent and continuing northward latitudinal shifts in distribution during winter for a variety of migratory bird species, suggests flexibility in timing of their migration based on weather cues (Walther et al. 2002, La Sorte and Thompson 2007, Brook et al. 2009).

Decoupling of correlations between photoperiod and seasonal weather events has resulted from climate change (Easterling 2000) and these changes can influence food availability for migratory birds (Drever et al. 2012). Changing weather patterns influence availability (e.g., timing of plant growth, seed production, senescence, agricultural planting and harvest) and accessibility (e.g., snow cover in fields and ice cover in wetlands) of food resources to wildlife (Myneni et al. 1997, Bradley et al. 1999). Although flexible migrants (those that adjust timing and distance of migration to annual variation in weather) may follow a latitudinal gradient of food availability throughout autumn and winter, foods available to fixed migrants (those that migrate based on photoperiod) may not match with the timing of their migration as climate changes (i.e., seasonal mismatch theory; Both and Visser 2001, Newton 2008).

Dabbling ducks (Anatidae) are a diverse group of birds that are abundant and have a variety of foraging strategies (Baldassarre 2014). Dabbling ducks feed on benthic plants and animals by tipping in water no deeper than the length between their feet and bills, by placing their heads under water, or dabbling on the surface. Some species of dabbling ducks also feed in terrestrial habitats on agricultural waste grains and native plant seeds (e.g., corn and acorns, respectively). The diversity of foraging habits of dabbling ducks results in interspecific differences in availability of foods during autumn and winter and thus, how weather influences the functional availability of food resources to these birds (Bellrose 1980, Dalby et al. 2013). In North America, dabbling ducks migrate south in autumn and winter during the non-breeding season to avoid extreme cold and to exploit abundant native and agricultural food resources produced throughout the summer growing season. Similar to other migratory birds, shifts in the timing and intensity of the southward migration of dabbling ducks has been documented in recent decades in Nearctic and Paleoarctic locales (Brook et al. 2009, Sauter et al. 2010, Schummer et al. 2014).

#### **DABBLING DUCKS**

Life history strategies vary among species of dabbling ducks and this includes differences in timing of autumn migration. Long-distance migrants, such as the Blue-winged Teal (Anas discors), are hypothesized to use photoperiod as a migratory cue while shorter distance migrants, such as the Mallard (A. platyrhynchos) are hypothesized to use weather cues (Bellrose 1980). Notably, timing of migration does not always scale to body size in dabbling ducks, largely because foraging strategies can cause differences in the functional availability of foods among species (Dalby et al. 2013, Baldassarre 2014). For instance, Green-winged Teal (A. crecca carolinensis) and Blue-winged Teal are both small-bodied dabbling duck species, but there is a substantial temporal difference in their autumn migration. Blue-winged Teal forage nearly exclusively in shallow wetlands, generally initiate migration from breeding grounds in August-September, and are typically on their Central and South American wintering grounds by late-October or early-November (Bellrose 1980, Botero and Rusch 1994, Baldassarre 2014). In contrast, Green-winged Teal, the smallest dabbling duck in North America and 40 - 75 g smaller than Blue-winged Teal, have a relatively protracted autumn migration (Baldassarre 2014) with some Green-winged Teal remaining at northern staging areas until ice and snow force them south in late autumn (Bellrose 1980, Baldassarre 2014). In contrast to Bluewinged Teal, Green-winged Teal are known to eat agricultural grains (e.g., corn and rice) and may remain at latitudes where there is open water for roosting and snow has not yet covered agricultural fields (Tamisier 1976, Baldassarre and Bolen 1984, Quinlan and Baldassarre 1984, Ringelman 1990, Lovvorn and Baldwin 1996).

Along with Blue-winged Teal, several species of dabbling ducks forage exclusively (e.g., Northern Shoveler, *A. clypeata*) or nearly exclusively (e.g., American Wigeon, *A. americana*) in wetlands, whereas other species vary in the amount of agricultural waste grains and other terrestrial foods in their diets (Baldassarre and Bolen 2006). Capacity to acquire nutrients likely influences migratory behaviour in ducks because waterfowl acquire and store lipids prior to migration. Lipid reserves in waterfowl are typically stored and are greatest in autumn and early winter when availability of food resources are at their annual maximum (Reinecke et al. 1982, Baldassarre et al. 1986, Schummer et al. 2012). Specific timing of maximum food availability differs among species because waterfowl have diverse foraging strategies (Baldassarre 2014). In dabbling ducks that feed primarily in wetland habitats, plant senescence, depletion of food from foraging, and ice cover make it necessary to migrate to more southern latitudes as weather becomes

more severe (Baldassarre and Bolen 2006, Schummer et al. 2010). Dabbling ducks that feed in terrestrial habitats in addition to wetlands may initiate migration later and winter at more northern latitudes because they can meet energy needs by feeding on agricultural grains, at least until open water freezes and snow makes feeding in terrestrial habitats too difficult (Schummer et al. 2010).

Understanding factors influencing seasonal distributions of dabbling ducks is necessary because they are ecologically, economically, and culturally important. Waterfowl are primary distributors of seeds and invertebrates among isolated wetlands because seed eaten in one wetland can pass through their gut and get deposited in other wetlands (Figuerola and Green 2002). Also, seeds and invertebrates are transported among wetlands on their feathers, feet, and bills (Figuerola and Green 2002, Brochet et al. 2010a, Brochet et al. 2010b, Figuerola et al. 2010). With climate change and the associated change in dabbling duck distributions (Schummer et al. 2014), it is possible that the movements of seeds and invertebrates among isolated wetlands may be altered. Waterfowl also have relatively high-energy needs and thus may cause trophic cascades at southern latitudes when latitudinal distributions of these abundant animals' shifts northward as a result of climate change, because available energy (e.g., seeds, tubers, submerged aquatic vegetation, agricultural grains) will not be depleted from their former wintering grounds. There is also the possibility that with a winter distribution shift northward, that northern locations, which have not historically supported year round waterfowl use, may not have enough available energy on the landscape to support this distribution change (Churchill 2015). Increased numbers of waterfowl wintering at northern latitudes could also reduce the carrying capacity of some wetlands for spring migrating waterfowl.

Another possible effect of shifting winter distribution for dabbling ducks is that their availability to waterfowl enthusiasts (e.g., birders, hunters, and birder-hunters; Cooper et al. 2015) may be reduced at southern locales. Waterfowl enthusiasts are more likely than non-recreationists to engage in pro-environmental behaviours such as conservation policy support, promotion of public land enhancement, and participation in environmental groups than non-recreationists (Cooper et al. 2015), and thus reductions in the abundance

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of waterfowl at historical southern wintering grounds could have substantial economic impacts and lead to a decrease in funding that supports wetland habitat conservation and research (Grado et al. 2001, Raftovich et al. 2011. Cooper et al. 2015).

In the face of a changing climate it is important for us to understand how weather influences distributions of waterfowl in North America during autumn-winter. Weather severity indices (WSI) can be useful tools in helping us understand and predict how animal distributions are influenced by long- and short-term weather patterns (Mitchell et al. 2014).

#### WEATHER SEVERITY INDICES

Weather severity indices were first created to obtain a composite index of climatic stress and winter mortality for white-tailed deer (*Odocoileus virginianus*) in the Great Lakes region of North America (Verme 1968). Despite that annual variation in weather is known to influence timing of migration in waterfowl, empirically based WSI remain few (Nichols et al. 1983, Ridgill and Fox 1990, Hepp and Hines 1991, Schummer et al. 2014). A WSI was developed for Mallards, which helped explain changes in abundances at staging areas during autumn and winter migration in Missouri, a mid-latitude staging area in the Mississippi Flyway (Schummer et al. 2010). Schummer et al. (2010) also investigated migration of other dabbling ducks, but combined these species because data from throughout Missouri lacked differentiation among species. The WSIs created for Mallards and other dabbling duck species were based upon weather variables known to influence availability of food (i.e., snow depth and consecutive days with snow cover) and energy expenditure by ducks (i.e., temperature and consecutive days <0°C; Schummer et al. 2010). However, because species-specific WSIs have only been created for Mallards (Appendix A), our capacity to estimate influences of changing climates on autumn-winter distributions of dabbling ducks and annual differences in the community structure of these birds on a latitudinal gradient remains limited. Developed WSI thresholds can be used to develop climate envelopes (i.e., the climate where a particular species currently lives) to estimate changes in distributions of waterfowl using global

circulation models (GCMs) for climate change (Notaro et al. 2014, Schummer et al. 2014, Watling et al. 2014).

Previously developed WSIs for Mallards using weather and waterfowl survey data from mid-continent North America provided scientists and wildlife managers with the opportunity to examine and predict how Mallards react to increasing severity of weather (Schummer et al. 2010). With an increasing availability of autumn and winter waterfowl survey data collected from a variety of federal and state agencies interested in quantifying waterfowl migration, along with readily accessible weather data for locations throughout North America, I was able to increase the spatial scope of the previous study to include additional areas in the Atlantic and Mississippi Flyways. As well, I was able to examine influences of weather severity on migration for most species of dabbling ducks in eastern North America. This expanded scope also enabled me to examine if previously developed Mallard WSIs were applicable at other latitudes throughout the Atlantic and Mississippi Flyways.

#### **THESIS OBJECTIVE**

The objective of this thesis was to develop models explaining variation in timing of autumn and winter migration in eastern North America for Gadwall; *A. strepera*, American Wigeon, American Black Duck; *A. rubripes*, Mallard, Blue-winged teal, Northern Shoveler, Northern Pintail; *A. acuta*, and Green-winged Teal. I used models adapted from Schummer et al. (2010) to determine the extent to which photoperiod and weather variables contributed to autumn and winter migration and distribution of dabbling ducks in eastern North America. I assumed that temperature and snow cover were predictors of waterfowl migration and distribution, because decreasing temperature and increase energetic expenditure in waterfowl. I also included latitude in my analysis to determine if dabbling ducks responded differently to weather severity dependent on their geographic location within the flyway. Species-specific WSI thresholds (i.e., the point on the index when rate of change in ducks is neither negative nor positive) were also determined as they can be used in a variety of applications allowing researchers and wildlife managers

to predict autumn-winter migratory movements using short-term and seasonal weather forecasts. Once developed, these WSI thresholds also may be applied to various climate change scenarios to predict changes to the probability of migration throughout autumnwinter, as well as the wintering distributions of each species.

I hypothesized that duck species would respond differently to migration cues based on different life history strategies (i.e., foraging strategies, habitat use, and ability to store lipids and thermoregulate; Table 1.1).

Species	<b>Migration Cues</b>	s Justification			Supporting Citations	
		Migration	Relative Body Size	Food Habits		
Gadwall	Mean Daily Temperature	Early	Medium	Feeds mostly on submerged aquatic vegetation; ice cover makes food functionally unavailable; also feeds in deep water areas with diving ducks	Knapton and Knudsen 1978, Bellrose 1980, Ryan 1981, McKnight and Hepp 1998, Baldassarre 2014	
American Wigeon	Mean Daily Temperature	Early	Medium	Feeds mostly on submerged aquatic vegetation; ice cover makes food functionally unavailable; also feeds in deep water areas with diving ducks	Knapton and Knudsen 1978, Bellrose 1980, Ryan 1981, Baldassarre 2014	
American Black Duck	Mean Daily Temperature	Late	Large	Opportunistic forager; feeds on submerged aquatic vegetation, invertebrates and agricultural grains	Mendall 1949, Jorde and Owen 1990, Baldassarre 2014	
Mallard	Mean Daily Temperature and Snow Cover	Late	Large	Opportunistic forager; feeds on submerged aquatic vegetation, seeds and tubers, invertebrates and agricultural grains	Bellrose 1980, Baldassarre 2014	
Blue-winged Teal	Photoperiod	Early; long distance migrant	Small	Feeds mostly in shallow wetlands; ice cover makes food functionally unavailable; feeds mostly on submerged aquatic vegetation	Rollo and Bolen 1969, Bellrose 1980, Temple and Cary 1987, Baldassarre 2014	
Northern Shoveler	Mean Daily Temperature	Early	Medium	Feeds mostly in shallow wetlands; ice cover makes food functionally unavailable; feeds mostly on invertebrates	Bellrose 1980, Tietje and Teer 1996, Baldassarre 2014	
Northern Pintail	Photoperiod	Early	Medium	Feeds mostly in shallow wetlands; ice cover makes food functionally unavailable; feeds on seeds, submerged aquatic vegetation, and agricultural grains	Bellrose 1980, Baldassarre 2014	
Green- winged Teal	Mean Daily Temperature and Snow Cover	Mid- to Late; protracted	Small	Feeds mostly in shallow wetlands; ice cover makes food functionally unavailable; mostly feeds on small seeds, invertebrates and sometimes on agricultural grains	Tamisier 1976, Baldassarre and Bolen 1984, Quinlan and Baldassarre 1984, Ringelman 1990, Lovvorn and Baldwin 1996, Baldassarre 2014	

 Table 1.1 Summary of species-specific dabbling duck migration predictions and justifications.

## Chapter 2 : Methods and Experimental Design

## 2.1 Study Area

I obtained aerial and ground-based survey data of autumn and winter waterfowl abundance from locations in the Atlantic and Mississippi Flyways of North America (Figure 2.1, Table 2.1). For a site to be included in my analysis it had to have a minimum of 10 years of species-specific dabbling duck count data to account for various weather conditions that could be experienced. As previously developed WSIs for Mallards were calculated using only data from Missouri (Schummer et al. 2010), I sought to broaden the geographic range by including areas throughout the Atlantic and Mississippi Flyways. The Central Flyway could not be included in this study because of the lack of waterfowl count data that was species-specific and conducted for a minimum of 10 years.



Figure 2.1 Autumn and winter duck abundance survey locations in the Atlantic and Mississippi Flyways used for this study. Each survey site (red dot) has a minimum of 10 years of data, with data collection ranging from 1979 – 2012.

## 2.2 Data Collection

### 2.2.1 Waterfowl Abundance Data

I acquired waterfowl abundance data from various US Fish and Wildlife Service National Wildlife Refuges (NWR), state agencies and non-profit conservation groups that responded to a request I posted on a web-based list service (Table 2.1). I also directly solicited data from agencies and locations known to conduct waterfowl surveys. Criteria for data to be included in this study were: 1) waterfowl surveys were species-specific (to calculate species-specific WSI thresholds), 2) conducted for ten years or more to include a range of variation in weather severity at sites throughout time, 3) surveys could be either aerial, ground or a combination of aerial and ground but methods within locations were standardized, and 4) surveys were conducted between 1 September and 28 February. Surveys were required to be standardized so that I could calculate rate of change in relative abundance per duck species between two consecutive surveys. I included all data acquired that met these requirements

#### 2.2.2 Weather Data

For each United States National Wildlife Refuge (NWR), wildlife management area (WMA), or survey area used as a survey site, I obtained shapefiles of the survey areas' boundaries courtesy of the agencies providing count data or online through the United States Geological Survey (USGS; Upper Midwest Environmental Science Center and Long Term Resource Monitoring Program 2001). I used polygons delineating the study area boundaries to calculate the centroid of the survey site. Using the coordinates of the centroid, I developed a 96 x 96 km square around the centroid (Release 11.0 EZ GeoWizard, ET Spatial Techniques 2013). I chose the dimensions of these polygons based on previous research indicating that the maximum home range size of dabbling ducks during the non-breeding season is 48 km (Jorde et al. 1983, Cox and Afton 1996), thereby the polygon extends 48 km out from the survey site centroid on any given side. The square polygons were all oriented north to south.

For each survey site polygon, I obtained weather data from the North American Regional Reanalysis (NARR) database supplied by the National Climatic Data Center (Mesinger et al. 2004). I queried and archived weather data from NARR database using software developed by David Douglas (USGS, Alaska Fish and Wildlife Research Center). Weather variables collected and used to develop candidate WSI models were mean daily temperature (°C) and snow depth (m).

### 2.3 Model Development

I used an information-theoretic approach for model selection (Burnham and Anderson 2002) to investigate how weather severity (i.e., decreasing temperature and increasing snow cover) and other variables (i.e., photoperiod and standard date) influenced rate of change in relative abundance of dabbling ducks during autumn-winter (Bellrose 1980, Ridgill and Fox 1990, Schummer et al. 2010; Table 2.2). I developed candidate WSI models because 1) declining air temperature increases energy expenditure in homeotherms and causes wetlands to freeze (Blem 2000), 2) depth of snow and an increasing number of days with snow cover will decrease the functional availability of food because terrestrial foods are covered with snow, and 3) the combined effects of declining temperature and snow and ice cover can increase energy expenditure while making energy intake increasingly difficult (Schummer et al. 2010). I reversed the algebraic sign (i.e., temperatures <0°C were given a positive algebraic sign and temperatures >0°C were given a negative algebraic sign) for all models containing temperature to ensure that increasing WSI values increased with weather severity. I also used a Principal Components analysis (PCA) to produce an index (the first principal component [PC1]) of weather variables for TEMP, TEMPDAY, SNOW and SNOWDAY (Table 2.2) that explained the maximum variance among these original variables. I used a Pearson product-moment correlation test to compare PC1 to my previously developed WSIs.

## 2.4 Statistical Analyses

Data analyses were performed using SAS software (Release 9.3, 2012, SAS Institute, Cary, NC). I applied PCA to the correlation matrix of TEMP, TEMPDAYS, SNOW and SNOWDAY because temperature and snow variables are seasonally correlated (Rebetez 1996, Schummer et al. 2010) and report eigenvectors to enable future application of PC1

in determining WSI (Rencher 1992). I determined correlation between predictor variables and did not include predictor variables together in models that were highly correlated ( $r \ge 0.70$ ; Dormann et al. 2013). I used an information theoretic approach for model selection (Burnham and Anderson 2002) and calculated an Akaike's Information Criterion (AIC) for each model. I used  $\Delta$ AIC and AIC weights ( $w_i$ ) to assess the relative support for the various WSIs, PC1, MINUTES, and PHOTO models (Table 2.2). I calculated rates of change (r) in relative abundance (i.e., the increases and decreases between two survey dates at a location) for each species to standardize waterfowl survey data between sites.

#### $r = \ln (duck \ abundance_t) - \ln (duck \ abundance_{t-1})$

I used rate of change in relative abundance as my response variable and incorporated weather and photoperiod metrics as my explanatory variables. I used a linear mixed effects model and tested candidate WSI, PC1, MINUTES and PHOTO models for linear and quadratic relationships. To distinguish between potential weather and photoperiod influences on rate of change in relative abundance of waterfowl, photoperiod based models (PHOTO and MINUTES) were tested as separate candidate models from all other weather-based models (Gwinner 1996, Schummer et al. 2010). I classified SITE and YEAR as random effects to enable inferences applicable at other areas used by dabbling ducks during migration and years beyond those used in my study. I also included SURVEY INTERVAL in models as a random effect to account for variation caused by differences in timing between consecutive surveys. I included SITE and YEAR as repeated measures among STND DATE to account for sampling the same site repeatedly during each given year across the potential range of standardized dates. I further included latitude and the interaction of WSI and latitude to investigate if the influence of WSI differed from north to south enough to improve model fit. I selected a Variance Component covariance structure for my analyses because it was suitable for my type of data and the candidate models used in this study (Kincaid 2005).

Candidate models within 2.0  $\Delta$ AIC units of the top-ranked models were considered to have biological significance, and I used model averaging to estimate parameters and 85%

confidence intervals for the top models to avoid variable-selection ambivalence (Arnold 2010). For all models I reported AIC and  $\Delta$ AIC units for PHOTO and NULL models for comparison with candidate WSI models. I used predicted values from top models and my model-averaged equation to identify the WSI threshold (i.e., the WSI value where duck abundance is neither increasing nor decreasing) for each study species. At values along trend lines below the x-axis, rate of change in relative abundance) and at values above the x-axis, rate of change in relative abundance) and at values above the x-axis, rate of change in relative abundance). I reported species-specific weather severity index threshold values (i.e., the x-intercept where rate of change in relative abundance is neither increasing) at the mean latitude of waterfowl survey sites included in this study for each species (39.884° N – 41.299° N).

Table 2.1 List of areas that were used for this study with standardized speciesspecific autumn-winter survey counts meeting the specified requirements for this study.

Area Name	<b>Province/State</b>	Latitude/Longitude	Survey Dates
Back Bay NWR	Virginia	36.614, -75.935	2000 - 2009
Chautauqua NWR	Illinois	40.382, -89.982	1990 – 2000; 2002 – 2011
Jack and Crane Lake	Illinois	40.146, -90.233	1990 – 2000; 2002 – 2011
Long Point	Ontario	42.750, -80.500	1979; 1984; 1986; 1988; 1991 - 2004
Mingo NWR	Missouri	36.995, -90.175	2002 - 2012
Montezuma NWR	New York	42.980, -76.756	1996 - 2011
Odessa WMA	Iowa	41.214, -91.119	1996 - 2011
Pocosin Lakes – Pungo Unit	North Carolina	35.708, -76.548	1999 – 2008; 2010 – 2012
Rice Lake WMA and Elk Creek Marsh WMA	Iowa	43.391 -93.468	1996 – 2011
Riverton WMA	Iowa	40.700, -95.582	1996 - 2011
Squaw Creek NWR	Missouri	40.095, -95.248	2002 - 2012
Swan Lake NWR	Missouri	39.613, -93.192	2002 - 2011
Tennessee NWR	Tennessee	36.107, -88.007	1993 - 2012
Upper Mississippi River NWR – Pool 4	Minnesota/ Wisconsin	44.474 -92.239	1995 – 2011
Upper Mississippi River NWR – Pool 5	Minnesota/ Wisconsin	44.257, -91.915	1995 – 2011
Upper Mississippi River NWR – Pool 5A	Minnesota/ Wisconsin	44.142, -91.759	1995 – 2011
Upper Mississippi River NWR – Pool 6	Minnesota/ Wisconsin	44.047, -91.588	1995 – 2011

Upper Mississippi River NWR – Pool 7	Minnesota/ Wisconsin	43.940, -91.321	1995 – 2011
Upper Mississippi River NWR – Pool 8	Iowa/Wisconsin	43.751, -91.249	1995 – 2011
Upper Mississippi River NWR – Pool 9	Iowa/Wisconsin	43.409, -91.190	1995 – 2011
Upper Mississippi River NWR – Pool 10	Iowa/Wisconsin	43.017, -91.136	1995 - 2011
Upper Mississippi River NWR – Pool 11	Iowa/Wisconsin	42.670, -90.862	1995 – 2011
Upper Mississippi River NWR – Pool 12	Iowa/Wisonsin/ Illinois	42.401, -90.523	1995 – 2011
Upper Mississippi River NWR – Pool 13	Iowa/Illinois	42.082, -90.200	1995 – 2011
Wheeler NWR	Alabama	34.597, -86.914	2001 - 2011

Models	Description	Calculation Examples
TEMP <sup>a</sup>	-(daily temp mean) <sup>b</sup>	Example 1: $-5^{\circ}C = 5$ ; Example 2: $5^{\circ}C = -5$
TEMPDAYS <sup>a</sup>	Consecutive days with mean temp $\leq 0^{\circ}$ C	Example 1: day 1, 2°C; day 2, -2°C; day 3, - 5°C = 2
		Example 2: day 1, 2°C; day 2, 1°C; day 3, - 5°C =1
SNOW <sup>a</sup>	(Snow depth in cm) x 0.394	Example 1: 3cm =1; Example 2: 26cm=10
SNOWDAYS <sup>a</sup>	Consecutive days $\geq$ 2.54cm of snow	Example 1: day 1, 0cm; day 2, 3cm; day 3, 26cm = 2
		Example 2: day 1, 0cm; day 2, 0cm; day 3, 26cm = 1
Cumulative WSI <sup>c</sup>	TEMP + TEMPDAYS + SNOW + SNOWDAYS	Example: temp (day 1, 2°C; day 2, -1°C; day 3, -5°C) snow (day 1, 0cm; day 2, 3cm; day 3, 26cm) Cumulative WSI (day 1=-2; day 2=4; day 3 = 19)
TEMPMean	Mean temp between 2 surveys	Example 1: day 1, 2°C; day 2, 0°C; day 3, - 2°C = 0 Example 2: day 1, 10°C; day 2, 0°C; day 3, -7°C =1
WSIMean <sup>d</sup>	TEMPMean + TEMPDAYS + SNOW + SNOWDAYS	
PC1	PCA <sup>e</sup> for TEMP, TEMPDAYS, SNOW, and SNOWDAYS	
STND DATE	Standardized date, with Day 1 starting 1 September	Example: 1 September = 1, 1 October =31, 1November = 62
РНОТО	Civil twilight day length on day of survey	
PHOTOMean	Mean civil twilight day length between surveys <sup>f</sup>	

Table 2.2 Variables adapted from Schummer et al. (2010)

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<sup>a</sup>Selected as the max. value between 2 surveys starting at time *t*-1 and ending 1 day before time *t*. <sup>b</sup> Temp < 0°C was given a positive algebraic sign (i.e., more severe), and temp > 0°C was given a negative sign. <sup>c</sup> Weather severity index (WSI) calculated daily and then selected as the max. value between 2 surveys stating at time *t*-1 and ending 1 day before time t.

<sup>d</sup>WSI calculated as the mean temp between 2 surveys plus values for TEMPDAYS, SNOW, and SNOWDAYS

ePCA, principal component analysis

<sup>&</sup>lt;sup>f</sup>PHOTOMean is calculated the same as the model MINUTES from Schummer et al. (2010)

## Chapter 3 : Results

The different sized wetland complexes in my study supported different maximum abundances of waterfowl among study sites (Appendix B). To account for these differences among study sites, I rescaled abundance data using a natural logarithm. Overall, I was able to obtain standardized survey data from 1979 through 2012, but most data were available between 1995 and 2012 (Table 2.1). The mean survey interval was 9.19  $\pm$  0.09 days. The median survey interval was 7.0 days, with a minimum and maximum survey interval of 1.0 and 79.0 days, respectively. For all species, principal component 1 (PC1) described positive correlations among 4 weather variables and accounted for 79.1% to 97.9% of variation (Table 3.1). The model PHOTO was highly correlated to STND DATE (r = -0.79, p < 0.01), so I used PHOTO as a proxy for STND DATE.

The Cumulative WSI (0.76 < r < 0.82, p < 0.001), TempMean WSI (0.75 < r < 0.83, p < 0.001), and WSIMean (0.77 < r < 0.85, p < 0.001) were all positively correlated to PC1 for all species. Also, Cumulative WSI was strongly correlated to WSIMean (0.92 < r < 0.94, p < 0.001) for all species.

#### WEATHER SEVERITY MODELS

Except for Blue-winged Teal, the combined effects of declining temperature, increased snow, and the latitude of these weather effects best explained variation in rate of change in relative abundance for all species investigated (Figures 3.1 - 3.7). Greatest weight of evidence in explaining variation in rate of change in relative abundance for American Black Ducks and Mallards was the quadratic PC1 model. Relative to other values, greatest loading for PC1 was on TEMP (Table 3.1). Model-averaged parameter estimates also included latitude as a quadratic function for American Black Ducks and an interaction between PC1 and latitude as a quadratic function for Mallards (Table 3.2). Specifically, I detected that greater severity in weather was needed at northern than southern latitudes to cause a decrease in relative abundance. The model-predicted WSI threshold (i.e., PC1) at the mean latitude for American Black Ducks and Mallards were 5.27 (LCL = 0.56, UCL = 9.07) and 5.08 (LCL = 0.77, UCL = 8.21), respectively

(Figures 3.1 and 3.2). These models predicted greatest increase in relative abundance at PC1 of -5.10 and -5.40 ( $\sim$ 5°C at time t) for American Black Ducks and Mallards, respectively. My models also predicted a decrease in relative abundance for American Black Ducks and Mallards when daily mean temperatures were > 16.4 °C and 17.1 °C, respectively. When a decrease in abundance of birds was observed during mild conditions, my data suggests it occurred early in the autumn migratory season, prior to peak migration and when numbers of ducks present were relatively less when compared to peak counts. For Gadwall, American Wigeon, Northern Shoveler and Green-winged Teal the greatest weight of evidence in explaining variation in rate of change in relative abundance was the quadratic WSIMean model. Model-averaged parameter estimates also included latitude as a quadratic interaction for Gadwall and American Wigeon, as a quadratic latitude function for Northern Shoveler, and a linear latitude interaction for Green-winged Teal (Table 3.2 and 3.3). I detected that greater severity in weather was needed at northern than southern latitudes to cause a decrease in relative abundance for Gadwall, and the reverse trend was observed for American Wigeon, Northern Shoveler and Green-winged Teal, where greater severity of weather was needed at southern latitudes than northern latitudes to elicit a decline in relative abundance. The modelpredicted WSI threshold (i.e., WSIMean) at the mean latitude for Gadwall, American Wigeon, Northern Shoveler and Green-winged Teal were -7.09 (LCL = -18.02, UCL = 4.42), -9.60 (LCL = -19.03, UCL = 23.99), -8.96 (LCL = -11.68, UCL = -6.47) and -10.12 (LCL = -17.21, UCL = 9.32), respectively (Figures 3.3 - 3.6).

For Northern Pintail the greatest weight of evidence in explaining variation in rate of change in relative abundance was a linear CumulativeWSI function with a linear latitude interaction (Table 3.3). Model-averaged parameter estimates also include a quadratic CumulativeWSI function. I detected that greater severity in weather was needed at southern than northern latitudes to cause a decrease in relative abundance of Northern Pintails. The model-predicted WSI threshold (i.e., CumulativeWSI) at the mean latitude for Northern Pintails was -4.29 (LCL = -15.72, UCL = 22.03; Figure 3.7).

#### PHOTOPERIOD MODELS

The greatest weight of evidence explaining variation in rate of change in relative abundance for Blue-winged Teal was the linear Photoperiod model with a linear latitude function. Model-averaged parameter estimates also included a latitude as a quadratic function (Table 3.3). The model predicted photoperiod threshold at the mean study latitude for Blue-winged Teal was 790.8 minutes with a LCL = 808.9 minutes, however, the UCL crosses the x-axis at a threshold of 860.9 minutes (Figure 3.8).

The presence of latitude in the model averaged equation indicated that the photoperiod threshold used by Blue-winged Teal varies depending on locale. The photoperiod threshold for Blue-winged Teal at the northern range of my study area (44.474° N) was 752.7 minutes which corresponds to15 September, whereas the photoperiod threshold at the southern range of my study area (34.597° N) was 686.2 minutes which corresponds to 12 October.



Figure 3.1 Relationship between rate of change in relative abundance of predicted model outputs for American Black Duck and Principal Component 1 (PC1) derived from North American Regional Reanalysis (NARR) weather dataset and waterfowl survey data from all study sites. The PC1 thresholds (x-intercepts) are -15.85 and 5.27, with dashed lines representing the upper and lower 85% confidence limits.



Figure 3.2 Relationship between rate of change in relative abundance of predicted model outputs for Mallard and Principal Component 1 (PC1) derived from North American Regional Reanalysis (NARR) weather dataset and waterfowl survey data from all study sites. The PC1 thresholds (x-intercepts) are -15.93 and 5.08, with dashed lines representing the upper and lower 85% confidence limits.



Figure 3.3 Relationship between rate of change in relative abundance of predicted model outputs for Gadwall and WSI Mean derived from North American Regional Reanalysis (NARR) weather dataset and waterfowl survey data from all study sites. The WSIMean threshold (x-intercept) is -7.09, with dashed lines representing the upper and lower 85% confidence limits.



Figure 3.4 Relationship between rate of change in relative abundance of predicted model outputs for American Wigeon and WSI Mean derived from North American Regional Reanalysis (NARR) weather dataset and waterfowl survey data from all study sites. The WSIMean threshold (x-intercept) is -9.60, with dashed lines representing the upper and lower 85% confidence limits.



Figure 3.5 Relationship between rate of change in relative abundance of predicted model outputs for Northern Shoveler and WSI Mean derived from North American Regional Reanalysis (NARR) weather dataset and waterfowl survey data from all study sites. The WSIMean threshold (x-intercept) is -8.96, with dashed lines representing the upper and lower 85% confidence limits.



Figure 3.6 Relationship between rate of change in relative abundance of predicted model outputs for Green-winged Teal and WSI Mean derived from North American Regional Reanalysis (NARR) weather dataset and waterfowl survey data from all study sites. The WSIMean threshold (x-intercept) is -10.13, with dashed lines representing the upper and lower 85% confidence limits.



Figure 3.7 Relationship between rate of change in relative abundance of predicted model outputs for Northern Pintail and cumulative weather severity index derived from North American Regional Reanalysis (NARR) weather dataset and waterfowl survey data from all study sites. The Cumulative WSI threshold (x-intercept) is - 4.29, with dashed lines representing the upper and lower 85% confidence limits.



Figure 3.8 Relationship between rate of change in relative abundance of predicted model outputs for Blue-winged Teal and photoperiod derived from North American Regional Reanalysis (NARR) weather dataset and waterfowl survey data from all study sites. The Photoperiod threshold (x-intercept) is 790.8 minutes, with dashed lines representing the upper and lower 85% confidence limits.

Species	Principal Component 1 Variables				Cumulative Variation
	TEMP	TEMPDAY	SNOW	SNOWDAY	(%)
Gadwall	0.98	0.15	0.03	0.15	87.74
American Wigeon	0.98	0.12	0.03	0.12	90.42
American Black Duck	0.96	0.17	0.03	0.20	83.33
Mallard	0.93	0.24	0.05	0.27	79.05
Blue-winged Teal	1.00	0.02	0.01	0.04	97.85
Northern Shoveler	0.99	0.11	0.03	0.10	91.84
Northern Pintail	0.99	0.11	0.03	0.11	91.73
Green-winged Teal	0.99	0.09	0.03	0.10	93.42

Table 3.1 Eigenvectors of the predictor variables that compose Principal Component 1 (PC1) and the cumulative variationthat the predictor variables represent for PC1 for all study species.

Table 3.2 Akaike's information criteria for relationships between rate of change in
relative abundance of Gadwall ( $n = 2717$ ), American Wigeon ( $n = 2360$ ), American
Black Duck ( $n = 1878$ ), Mallards ( $n = 3513$ ), Blue-winged Teal ( $n = 1390$ ), Northern
Shoveler ( $n = 1902$ ), Northern Pintail ( $n = 2501$ ), Green-winged Teal ( $n = 2529$ ) and
candidate weather severity indices from autumn and winter survey count data of
study sites located throughout the Atlantic and Mississippi Flyways.

Taxon	Models <sup>b</sup>	AIC	ΔAIC	Wi
Gadwall	WSIMean <sup>2</sup> x Latitude <sup>2</sup>	17036.8	0.0	0.41
	WSIMean <sup>2</sup> x Latitude	17037.7	0.9	0.26
	PHOTOMean <sup>2</sup> x Latitude <sup>2</sup>	17112.6	75.8	0.00
	Null	17434.7	397.9	0.00
American Wigeon	WSIMean <sup>2</sup> x Latitude <sup>2</sup>	15266.5	0.0	0.43
	WSIMean <sup>2</sup> Latitude <sup>2</sup>	15266.7	0.2	0.39
	PHOTOMean <sup>2</sup> Latitude	15327.3	60.8	0.00
	Null	15539.0	272.5	0.00
American Black	PC1 <sup>2</sup>	11904.4	0.0	0.45
Duck	PC1 <sup>2</sup> Latitude	11906.2	1.8	0.18
	PC1 <sup>2</sup> Latitude <sup>2</sup>	11906.4	2.0	0.17
	PHOTOMean <sup>2</sup> Latitude <sup>2</sup>	11978.1	73.7	0.00
	Null	12003.4	99.0	0.00
Mallard	PC1 <sup>2</sup> x Latitude	18120.3	0.0	0.54
	PC1 <sup>2</sup> x Latitude <sup>2</sup>	18121.8	1.5	0.25
	PHOTOMean <sup>2</sup> x Latitude <sup>2</sup>	18367.3	247.0	0.00
	Null	18538.2	417.9	0.00
Blue-winged Teal	Photoperiod Latitude	8960.2	0.0	0.34
	Photoperiod x Latitude	8961.8	1.6	0.16
	Photoperiod <sup>2</sup> Latitude	8962.0	1.8	0.14
	Null	9043.3	83.1	0.00
Northern Shoveler	WSIMean <sup>2</sup> Latitude <sup>2</sup>	12217.9	0.0	0.21
	WSIMean	12219.0	1.1	0.12
	WSIMean <sup>2</sup>	12219.0	1.1	0.12
	WSIMean <sup>2</sup> x Latitude <sup>2</sup>	12219.5	1.6	0.10
	PHOTOMean <sup>2</sup> Latitude	12281.0	63.1	0.00
	Null	12363.0	145.1	0.00

Northern Pintail	CumulativeWSI x Latitude	15897.6	0.0	0.36
	CumulativeWSI <sup>2</sup> x Latitude	15898.3	0.7	0.25
	CumulativeWSI <sup>2</sup> x Latitude <sup>2</sup>	15898.4	0.8	0.24
	PHOTOMean Latitude	15975.7	78.1	0.00
	Null	16167.9	270.3	0.00
Green-winged Teal	WSIMean <sup>2</sup> x Latitude	15999.9	0.0	0.50
-	WSIMean <sup>2</sup> x Latitude <sup>2</sup>	16000.7	0.8	0.33
	Photoperiod <sup>2</sup> x Latitude	16102.6	102.7	0.00
	Null	16327.4	327.5	0.00

<sup>a</sup> Abbreviations: AIC, Akaike's Information Criterion;  $\Delta$ AIC, change in Akaike's Information Criterion;  $w_i$ , Akaike's weight <sup>b</sup> Squared models (e.g., PC1<sup>2</sup>, WSIMean<sup>2</sup>) represent quadratic functions, all others are linear

Table 3.3 Parameter estimates ( $\theta$ ), standard errors, and 85% confidence intervals derived from candidate models ( $\Delta$ AIC $\leq$ 2) of rate in change of relative abundance for Gadwall (n = 2717), American Wigeon (n = 2360), American Black Duck (n = 1878), Mallards (n = 3513), Blue-winged Teal (n = 1390), Northern Shoveler (n = 1902), Northern Pintail (n = 2501), Green-winged Teal (n = 2529).

Taxon	Parameter	θ	SE	85% CI
Gadwall	Intercept	26.575	18.518	23.044 to 30.107
	WSIMean	0.175	0.221	0.133 to 0.217
	Latitude	-1.474	0.896	-1.645 to -1.304
	WSIMean x WSIMean	0.002	0.001	0.002 to 0.002
	Latitude x Latitude	0.019	0.011	0.017 to 0.021
	WSIMean x Latitude	-0.011	0.005	-0.012 to -0.010
American Wigeon	Intercept	72.218	28.071	66.909 to 77.528
	WSIMean	-0.049	0.153	-0.078 to -0.020
	Latitude	-3.599	1.412	-3.866 to -3.332
	WSIMean x WSIMean	0.002	0.001	0.002 to 0.003
	Latitude x Latitude	0.043	0.018	0.040 to 0.046
	WSIMean x Latitude	-0.005	0.003	-0.012 to -0.010
American Black Duck	Intercept	-7.900	6.936	-9.225 to -6.574
	PC1	-0.134	0.019	-0.138 to -0.131
	Latitude	0.442	0.333	0.378 to 0.505
	PC1 x PC1	-0.012	0.002	-0.012 to -0.012
	Latitude x Latitude	-0.005	0.004	-0.006 to -0.005
	PC1 x Latitude	0.000	0.000	0.000 to 0.000
Mallard	Intercept	-3.637	5.637	-4.713 to -2.561
	PC1	-0.410	0.128	-0.434 to -0.386
	Latitude	0.193	0.264	0.142 to 0.243
	PC1 x PC1	-0.008	0.001	-0.008 to -0.008
	Latitude x Latitude	-0.002	0.003	-0.003 to -0.002
	PC1 x Latitude	0.008	0.003	0.007 to 0.008
Blue-winged Teal	Intercept	-10.099	18.255	-13.55 to -6.643
	Photoperiod	0.029	0.031	0.024 to 0.035
	Latitude	-0.402	0.357	-0.469 to -0.334
	Photoperiod x Photoperiod	0.000	0.000	0.000 to 0.000
	Latitude x Latitude	0.000	0.000	0.000 to 0.000
	Photoperiod x Latitude	0.000	0.000	0.000 to 0.000
Northern Shoveler	Intercept	34.087	17.327	30.809 to 37.364
	WSIMean	-0.188	0.064	-0.200 to -0.176
	Latitude	-1.805	0.860	-1.967 to -1.642
	WSIMean x WSIMean	-0.001	0.001	-0.001 to -0.001
	Latitude x Latitude	0.022	0.011	0.020 to 0.024
	WSIMean x Latitude	-0.001	0.001	-0.001 to -0.001

CumulativeWSI Latitude CumulativeWSI x CumulativeWSI	0.693 -0.618 -0.001	0.204 0.391 0.000	0.654 to 0.731 -0.692 to -0.544
Latitude CumulativeWSI x CumulativeWSI	-0.618 -0.001	0.391	-0.692 to -0.544
CumulativeWSI x CumulativeWSI	-0.001	0.000	0.001 / 0.000
Latituda y Latituda		0.000	-0.001 to 0.000
Latitude x Latitude	0.006	0.004	0.005 to 0.007
CumuativeWSI x Latitude	-0.106	0.005	-0.023 to -0.021
Intercept	19.050	11.506	16.874 to 21.226
WSIMean	0.396	0.255	0.348 to 0.444
Latitude	-0.810	0.537	-0.912 to -0.709
WSIMean x WSIMean	-0.002	0.001	-0.002 to -0.002
Latitude x Latitude	0.007	0.006	0.006 to 0.008
WSIMean x Latitude	-0.017	0.006	-0.018 to -0.016
_	CumuativeWSI x Latitude CumuativeWSI x Latitude WSIMean Latitude WSIMean x WSIMean Latitude x Latitude WSIMean x Latitude	Latitude x Latitude0.000CumuativeWSI x Latitude-0.106Intercept19.050WSIMean0.396Latitude-0.810WSIMean x WSIMean-0.002Latitude x Latitude0.007WSIMean x Latitude-0.017	Latitude x Latitude         0.000         0.004           CumuativeWSI x Latitude         -0.106         0.005           Intercept         19.050         11.506           WSIMean         0.396         0.255           Latitude         -0.810         0.537           WSIMean x WSIMean         -0.002         0.001           Latitude x Latitude         0.007         0.006           WSIMean x Latitude         -0.017         0.006

## Chapter 4 : Discussion

Waterfowl migrate from north to south in North America during autumn-winter as declining temperatures and increased snow cover cause decreases in habitat suitability (Bellrose 1980, Schummer et al. 2010, Baldassarre 2014). In accordance, my results support that most species of dabbling ducks will migrate farther south during severe (i.e., decreased temperature and increased snow accumulation) than mild winters. The results of my study suggest that the weather variation summarized by WSIs appear to be generally good predictors of autumn-winter migratory movements for the majority of dabbling duck species included in my study (Ridgill and Fox 1990, Schummer et al. 2010, Schummer et al. 2014). Blue-winged Teal were an exception because I detected that photoperiod was their primary cue influencing migration chronology during autumnwinter. My results do not indicate that photoperiod is not a cue for migration, but rather that weather severity models explain additional variation in migration not explained by photoperiod alone because weather generally becomes increasingly severe with decreasing day length (Bridgman and Oliver 2006). Thus, other than Blue-winged Teal, dabbling duck autumn-winter migration was best explained by weather severity that likely also incorporated the influence of photoperiod. Additional variables potentially influencing migration not in my models include functional availability of food and disturbance (e.g., hunting; Evans and Day 2002, Béchet et al. 2003, Schummer et al. 2010). To control for these local effects, I blocked (random effect) by survey site and included survey site latitude in my models. Even after blocking by survey site, I still detected an influence of latitude which could be a biological difference in reaction of ducks to weather or result from latitudinal and landscape differences in food availability (habitat quality) and disturbance. Regardless of the reason for retention of latitude in my models, my methodology accounted for potential variation in migration from local and regional effects, thereby increasing the utility of models across a broad geographic scale.

Variation in migration by large-bodied, cold tolerant American Black Ducks and Mallards (Bellrose 1980, Baldassarre 2014) were best described by the combined influences of temperature and snow (i.e., PC1), where TEMP (i.e., daily mean temperature) had greater weight than TEMPDAY, SNOW and SNOWDAY (i.e., consecutive days with mean temp  $\leq 0^{\circ}$ C, snow depth, and consecutive days with snow on the ground, respectively; Table 3.2). My findings are similar to prior weather severity models developed for Mallards using data from waterfowl surveys and nearby weather stations in Missouri (Schummer et al. 2010). My models were developed using data from the Atlantic and Mississippi Flyways, and thus I suggest a comparison of these two models using historic weather data in a spatial modeling framework to determine if they predict similar winter distributions of Mallards (Mitchell et al. 2014). My paired, broad geographic investigation of American Black Duck and Mallard migration suggest they use similar cues to initiate autumn-winter migratory movement in response to declining weather conditions (e.g., extended freezing temperatures and snow cover) and they exhibited similar PC1 weather severity thresholds with overlapping confidence intervals in this study. Previous comparative studies between American Black Ducks and Mallards suggest that their migratory behaviours differ greatly as a response to the varying availability of habitat that each species occupies (i.e., American Black Ducks occupy coastal areas, Mallards occupy inland wetlands) and that American Black Ducks will delay migration to the point of affecting survival negatively to reduce energy costs associated with migration (Diefenbach et al. 1988, Mesinger et al. 2004, Ringelman et al. 2015). Although these differences in migratory behaviours may be observed at local scales, my large-scale study suggests that the response to weather exhibited by these two species were nearly identical. American Black Ducks wintering at the Atlantic Coast increased their home range size with extended period of freezing conditions, but did not make substantial migratory movements farther south (Ringelman et al. 2015). The majority of my data were from inland locations for American Black Ducks during winter migration, whereas those from Ringelman et al. (2015) were during winter in coastal, salt marshes where long-term freezing conditions are less common. In combination, these results suggest that American Black Ducks react similarly to Mallards at inland locales during autumn migration, but that American Black Ducks using coastal regions may react differently to severe weather (Ringelman et al. 2015).

My models predicted that dabbling ducks, other than Mallards and American Black Ducks, migrate prior to the onset of freezing conditions. Gadwall and American Wigeon are among the earliest autumn migrants (Bellrose 1980) when mean weekly temperatures were 7.1°C and 9.6°C (i.e., WSIMeans were -7.09 and -9.59, respectively). Gadwall and American Wigeon are known to migrate earlier than Mallards because they feed on submerged aquatic vegetation, whereas Mallards switch to waste agricultural grains enabling them to delay autumn migration (Bossenmaier and Marshall 1958, Anderson 1959, Havera 1999, Baldassarre 2014). However, despite the fact that many Gadwall and American Wigeon begin migrating for southern latitudes in milder weather than other ducks, my models indicate that their rate of decline in relative abundance slowed with increasing severity of weather. These results are consistent with the adaptation of Gadwall and American Wigeon to remain at northern locales even when food resources become unavailable in shallow wetlands (McKnight and Hepp 1998, Baldassarre and Bolen 2006). In northern and mid-latitudes some Gadwall and American Wigeon remain relatively late into winter because of their kleptoparasitic behaviour when foraging with mixed flocks of diving ducks (Aythya spp.) and American Coots (Fulica americana) that bring submerged aquatic vegetation to the surface, which they steal and eat (Knapton and Knudsen 1978, Ryan 1981, Baldassarre 2014). I think the general stabilization in rate of decline in relative abundance with the onset of freezing conditions is because these ducks can sustain energy through their kleptoparasitic foraging behavior, allowing some individuals to prolong their stay after shallow wetlands are ice covered.

Weather causing migration of Northern Shoveler and Green-winged Teal was similar to that of Gadwall and American Wigeon, but my models suggest that rate of decline in abundance continued decreasing linearly with declining temperatures and increased snow depth. Northern Shovelers feed exclusively in shallow wetlands and therefore they must migrate south prior to severe weather rendering their foraging habitat inaccessible (Baldassarre 2014). Green-winged Teal are the smallest dabbling duck in North American, and despite their habit or ability to incorporate feeding in terrestrial habitats on waste grain (Tamisier 1976, Quinlan and Baldassarre 1984, Baldassarre and Bolen 1986, Baldassarre et al. 1986, Ringelman 1990), they may not be able to maintain lipid stores with declining temperatures (Gwinner and Terrill 1990). Green-winged Teal migrate substantially later than Blue-winged teal, despite being slightly smaller in size (Bellrose 1980, Baldassarre 2014). I detected that the threshold for Green-winged Teal was 10.1°C, a point when snow and extending periods of freezing temperatures have not yet occurred. The decline of Green-winged Teal prior to freezing temperatures corresponds with the foraging behaviours of Green-winged Teal as they forage primarily in shallow wetlands on relatively small seeds. Although, Green-winged Teal are known to also feed on agricultural waste grains (Ringelman 1990), my models suggest that these small-bodied dabbling ducks do not remain at northern latitudes to feed on these resources similar to Mallard foraging behavior. Green-winged Teal make extensive use of waste corn during the winter in the High Plains of Texas (Baldassarre and Bolen 1984, Quinlan and Baldassarre 1984), but my results suggest that these ducks are leaving northern and midlatitude staging areas even when abundance of waste corn and other grains exist, and prior to ice and snow cover making their food sources unavailable.

The CumulativeWSI model differs from the WSIMean model in that it uses daily temperature rather than mean temperature from one survey date to the next. For Northern Pintails the model of best fit was a CumulativeWSI model and did not support my hypothesis that photoperiod would best explain their migration (best photoperiod model  $\Delta AIC = 78.1$ ). I predicted that Northern Pintails utilize photoperiod because of known arrival to coastal areas earlier than other dabbling ducks, even though they are foraging generalists and could potentially use waste grains after ice cover makes wetland food inaccessible (Tamisier 1976, Cox and Afton 2000, Baldassarre 2014). However, the CumulativeWSI threshold for Northern Pintails was -4.29 and equates to approximately 4.3°C, a temperature which snow and extended days of freezing temperatures would have not yet occurred. Although, Northern Pintails are only about 200 grams lighter than a Mallard and are known to feed terrestrially, my model suggests they initiate migration well-before the onset of severe weather tolerated by Mallards and American Black Ducks.

Blue-winged Teal winter in tropical climates in Central and South America, which experience stable mild weather and consistent habitat and food availability relative to the wintering grounds of other dabbling duck species (Bellrose 1980, Baldassarre 2014). My results for Blue-winged Teal are consistent with the theory that birds wintering in stable environments use photoperiod as their primary cue for migration (Newton 2008). When wintering habitat is readily available, the need for migration to be linked with weather

conditions is less likely and has resulted in many long-distance migrants using photoperiod as the primary cue for initiation of autumn and winter migration (Newton 2008). It has been demonstrated that many long distance passerine species wintering in the neotropics use photoperiod when initiating autumn migration and it had been proposed for Blue-winged Teal previously (Owen 1968, Bellrose 1980). As far as I am aware, my study is the first to empirically determine that Blue-winged Teal use photoperiod cues to migrate and to model estimated migration dates across latitudes in the Mississippi and Atlantic Flyways. My models suggest that Blue-winged Teal begin leaving northern staging areas in September and southern United States staging areas in mid-October.

For Gadwall, American Black Duck and Mallard, WSI threshold values were greater at northern latitudes than at southern latitudes indicating that weather needs to be more severe at northern latitudes to illicit southward migration than at southern latitudes. For example, in Mallards the WSI threshold using PC1 in the Great Lakes region was approximately 8.6, however, in northern Missouri the threshold was around 7.1 and further south in Tennessee the WSI threshold decreased to 5.5. The opposite trend was observed for American Wigeon, Northern Shoveler, Northern Pintail and Green-winged Teal, where the WSI threshold values were less at northern latitudes than at southern latitudes, indicating that more extreme weather was required for these species to migrate southward the further south they were located. For example, the threshold for Greenwinged Teal in the southern Great Lakes region was -10.42 and the threshold increases to -9.25 in mid-Missouri and -6.76 in Tennessee, which was approximately 10.4°C, 9.3°C and 6.8°C, respectively. I think that larger-bodied ducks like Gadwall, American Black Duck and Mallard are adapted to risking winter at more northern latitudes because of their large-body size and capacity to sustain themselves on wetland and agricultural foods. Gadwall have similar foraging behaviours to American Wigeon, but are the larger of the two species (Baldassarre 2014). One explanation for the decrease in WSI thresholds with decreasing latitude observed in Gadwall, American Black Duck and Mallards is that they follow a leapfrog migration pattern (i.e., populations breeding at the northern extent of the breeding range winter at the southern extent of the winter range; Boulet and Norris 2006). This seems unlikely, at least for Mallards, because previous

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analysis of band recoveries in Mallards has shown no evidence on leapfrog migration (Hestbeck et al. 1992). In contrast, American Wigeon, Northern Shoveler, Northern Pintail and Green-winged Teal are uncommon at northern latitudes during winter, and I think they move to southern wintering areas relatively early in the season where they establish winter home ranges and are less apt to leave because they learn the locations of local food resources before disturbance from hunting pressure is substantial. The different life history strategies among dabbling duck species have evolved to maximize survival and has resulted in different autumn-winter migratory behaviours among species.

For waterfowl using weather as a migratory cue, it is advantageous to migrate only as far south as necessary to survive, court and form pair bonds. Remaining farther north during winter reduces migration distances back to spring breeding grounds. Further, dabbling ducks arriving earlier on breeding grounds usually have greater nest success (Arzel et al. 2014). For cold tolerant species such as American Black Ducks and Mallards, if they can sustain extended periods of freezing temperatures it may be advantageous for them to do so rather than take on the risks, additional energy consumption costs, and movement to unknown areas with varying risk associated with migration (Bellrose 1980, Albright et al. 1983, Diefenbach et al. 1988). Dabbling duck species other than American Black Ducks and Mallards required less severe weather to illicit migratory movement southward, likely because these species are smaller-bodied than American Black Ducks or Mallards and thus, have greater thermoregulation costs during cold periods and do not feed in agricultural fields. My study was the first to use autumn waterfowl abundance data and corresponding weather data to make inferences pertaining to dabbling duck response to weather severity on a landscape scale, and highlights the importance of further investigation with regards to dabbling ducks in response to severe weather, particularly with climate change.

#### **Management Implications and Future Research**

Changes in timing and abundance of waterfowl autumn migration to southern latitudes throughout the 1990s and early 2000s prompted studies of migration chronology in these birds (Ridgill and Fox 1990, Schummer et al. 2010, Notaro et al. 2014, Schummer et al.

2014). In response to altered migration patterns and wintering distributions observed by waterfowl scientists and enthusiasts, and the need of wetland managers to ensure their actions are effective at providing food and habitat for migrating waterfowl, surveys to index waterfowl migration at local scales are needed and have recently become increasingly common (Soulliere et al. 2013). However, at most locales, lack of standardization reduces utility of location specific analyses and geographic comparisons (Schummer et al. 2010, Soulliere et al. 2013, Schummer et al. 2014, Andersson et al. 2015). Despite increased interest in surveying waterfowl during the non-breeding season (Andersson et al. 2015), I found a limited number of areas in the Mississippi (n=21) and Atlantic Flyways (n=4) with 10+ years of standardized ground or aerial survey data that quantified species-specific abundances and I received no responses that fit my criteria from areas in the Central Flyways after multiple inquiries. Although my study provides valuable insight about factors influencing autumn-winter migration in dabbling ducks, it also highlights the need for a database where long-term datasets can be archived, used and shared among individuals for the purpose of research. The Integrated Waterbird Management and Monitoring database is a potential solution to the lack of data stored in a centralized location; however, at the time of this study this database did not have >10 years of data (Soulliere et al. 2013). Continued refinement of our understanding of mechanisms influencing waterfowl migration will help predict their future distributions based on various climate change scenarios.

Species-specific WSI thresholds will be useful in modeling movements and distributions of dabbling ducks using historical and current weather data, as well as modeling potential autumn-winter distributions with future climate change scenarios (sensu Notaro et al. 2014). Waterfowl ecologists, conservationists, managers and hunters will be interested in how tolerances to weather severity differ between dabbling duck species and how this will influence migration chronology and waterfowl community composition under various climate change scenarios. Changing composition of winter waterfowl communities may lead to cascade effects thereby increasing foraging at northern latitudes that would be accompanied by decreased foraging at southern latitudes. Waterfowl managers may seek to adjust activities on lands aimed at sustaining healthy waterfowl populations during winter in these areas. If the likelihood for waterfowl to short-stop

migration intensifies in North America, then the carrying capacity of northern staging areas for spring migrating waterfowl could decline, thereby necessitating increased habitat management in these regions.

Future research should focus on application of the species-specific WSI thresholds on a landscape scale, accompanied with various climate change scenarios to develop climate envelope models that will help predict potential distribution changes associated with climate change. The ability to predict and map potential distribution changes will aid in forecasting ecological, environmental, economic and cultural implications associated with estimated changes to distributions of waterfowl on community, as well as a species-specific basis.

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## Appendices



Appendix A. Relationship between rate of change in relative abundance of Mallard and cumulative weather severity index derived from Historical Climatology Network weather stations 20.66 – 42.05 km from Missouri Conservation Areas, USA, 1995 – 2005 (Schummer et al. 2010). Data points above the x-axis represent an increase in abundance of Mallards, and below the x-axis represent a decrease in Mallard abundance. The Weather Severity Index increases with severe weather (i.e., snowfall and ice cover) and a general trend is observed that Mallard abundances decrease with increasingly severe weather.

Area Name	Gadwall	American Wigeon	American Black Duck	Mallard	Blue-winged Teal	Northern Shoveler	Northern Pintail	Green-winged Teal
Back Bay NWR	1157	450	488	988	1362	145	529	2206
Chautauqua NWR	18625	6000	6200	320300	9850	15000	24075	20100
Jack and Crane Lake	24600	4400	3000	86690	3300	4700	12800	17750
Long Point	1350	26068	16671	25200	5368	121	2913	6992
Mingo NWR	19469	6028	15	49146	964	9101	14190	6692
Montezuma NWR	697	2200	5344	24228	119	671	15371	3000
Odessa WMA and Port Louisa	4000	1000	350	80000	3500	795	6200	6000
Pocosin Lakes - Pungo Unit	750	3870	2122	21368	30	1280	840	37315
Rice Lake WMA and Elk Creek Marsh WMA	700	950	15	29000	2020	1200	1050	1775
Riverton WMA	5000	2000	10	110000	7000	2500	12000	15000
Squaw Creek NWR	25885	6015	2	193300	7774	19894	71815	27194
Swan Lake NWR	11479	2285	0	95641	1642	2328	30263	14073
Tennessee NWR	29711	12491	26036	241687	4922	1955	16455	12968
Upper Mississippi River NWR - Pool 4	4065	2900	80	11505	500	250	550	500
Upper Mississippi River NWR - Pool 5	5800	3070	145	6355	1040	170	295	565
Upper Mississippi River NWR - Pool 5a	1780	535	30	5310	100	100	70	150

Appendix B. Species-specific maximum duck abundances observed at each study site included in weather severity and photoperiod modeling analyses

Upper Mississippi River NWR - Pool 6	5300	2530	55	7825	795	705	490	775
Upper Mississippi River NWR - Pool 7	13880	7845	475	16515	775	2265	1320	1110
Upper Mississippi River NWR - Pool 8	21515	9030	180	63570	1055	165	4800	1215
Upper Mississippi River NWR - Pool 9	45685	7175	40	28240	1135	350	1690	1445
Upper Mississippi River NWR - Pool 10	2400	250	10	19035	150	0	200	515
Upper Mississippi River NWR - Pool 11	4695	2275	10	8335	295	10	450	860
Upper Mississippi River NWR - Pool 12	1000	190	20	670	285	100	700	650
Upper Mississippi River NWR - Pool 13	17810	5255	370	59925	1125	3830	12850	12665
Wheeler NWR	10475	3760	4255	31837	1650	3040	5170	4725

# Curriculum Vitae

Name:	Lena M. M. Vanden Elsen
Post-secondary Education and Degrees:	The University of Western Ontario London, Ontario, Canada 2006-2010 B.Sc.
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	Research Technician California Waterfowl August 2013
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	Teaching Assistant: Scientific Methods in Biology The University of Western Ontario September – December 2012
	Research Technician Ducks Unlimited Canada Studied brood survival of Northern Pintail June 2012

Research Technician Ducks Unlimited Canada Studied spatial and temporal variation in nest success of prairie ducks April – August 2011

### **Publications:**

Schummer, M. L. and L. M. M. Vanden Elsen. 2013. Estimated Effects of Climate Change on Autumn-Winter Distributions of Dabbling Ducks in Easter North America, USFWS LCC Technical Report, Port Rowan, Ontario.

#### **Presentations:**

- Vanden Elsen, L. M. 2015. Scientist-Stakeholder Engagement: Success and Failures While Conducting Research. (Oral Presentation). North East Climatic Science Center 3<sup>rd</sup> Annual Fellows Retreat. September 2015, Green Bay Wisconsin.
- Vanden Elsen, L. M., M. L. Schummer, M. Notaro, J. Coluccy, R. Kaminski, and M. Mitchell. 2014. Climate envelope models for forecasting and prioritizing conservation needs for migratory waterfowl throughout North America. (Oral Presentation). National Workshop on Large Landscape Conservation, October 2014, Washington D. C.
- Vanden Elsen, L. M., M. L. Schummer, and S. A. Petrie. 2013. Factors influencing autumn-winter distribution of dabbling ducks in the Atlantic, Mississippi, and Central Flyways of North America. (Poster Presentation). Sixth International North American Duck Symposium/Ecology and Conservation of North American Waterfowl Conference, January 2013, Memphis, Tennessee.
- Vanden Elsen, L. M., M. L. Schummer, S. A. Petrie, and C. G. Guglielmo. 2012. Factors influencing autumn-winter distribution of dabbling ducks in the Atlantic, Mississippi, and Central Flyways of North America. (Poster Presentation). Biology Graduate Research Forum, October 2012, London, Ontario.

#### **Co-authored Contributed Presentations:**

Schummer, M. L., J. C. Coluccy, R. Kaminski, M. Notaro, M. Brown, C. Wax, L. Vanden Elsen, and S. Petrie. 2014. An open-access web-based tool for quantifying daily Weather Severity Index values in eastern North America for application in waterfowl research and management. Mississippi Flyway Meeting, Nashville, Tennessee.

- Schummer, M.L., J.C. Coluccy, M. Notaro, R. Kaminski, M.Brown, C. Wax, J. Cohen, S. Petrie, and L. Vanden Elsen. 2013. Use of Weather Severity Indices for Estimating Influences of Climate Change on Waterfowl Populations, Waterfowl Habitat, & Hunter Opportunity & Demographics. Coping with Extreme Weather & Climate Change: Management Strategies for the Upper Midwest, Lacrosse, Wisconsin.
- Schummer, M.L. and L. Vanden Elsen. 2012. Timing of NY State duck seasons and weather severity indices for dabbling ducks. Annual Western NY Waterfowl Management Information Meeting, Iroquois National Wildlife Refuge, Basom, New York.