

The Role of Climate Variability in Duck Population Ecology

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By

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ABSTRACT

Climate change is having profound impacts on animal populations globally, and is expected to become a stronger stressor in future, influencing abundance and persistence of many species. In northern hemisphere bird populations, local weather and climate cycles play important roles via effects on components of individual fitness (i.e., survival and reproductive success), and thus annual fluctuations in population sizes. I used congruent long-term data for duck populations, individuals, and climatic variables to test hypotheses about the relative roles of climate and other factors in population dynamics, variation in vital rates, and timing of breeding. Where possible I used interspecific comparisons to evaluate whether responses were mediated by life-history traits.

First, I examined annual variation in the timing, length, and productivity of growing seasons on duck population growth rates in North American boreal forest, 1982-2013. I found limited evidence that spring phenology, growing season length or productivity influenced annual population growth rates, and effects were not always in the direction predicted based on species-specific timing of breeding. Second, I evaluated impacts and potential synchronizing forces of shared trends in temperature and precipitation on widely separated populations of ecologically equivalent duck species in North America and western Europe, 1976-2011. Several duck species-pairs shared increasing time trends but growth rates were not synchronized among years. This pattern of shared trends but no annual synchrony was mirrored in climate variables recorded over the major breeding areas on each continent. Third, at the individual-level, I found that ducklings of a late-breeding species, lesser scaup (*Aythya affinis*), had slower growth rates when hatched

late relative to their cohort but I detected no effect of spring phenology. Hatch date effects did not carryover to influence postfledging survival. In contrast, a negative effect of conspecific density on prefledging growth seemed to carryover to influence postfledging survival, and possibly first-year breeding probability. Fourth, examining breeding dates of individually marked females, I found that early-nesting species tracked spring phenology, while late-nesting species did not. Yet, annual variation in the timing of breeding in late-nesting species suggests that females respond to other unmeasured cues not related to spring phenology.

Collectively, results indicate that individual ducks are resilient to annual fluctuations in climatic drivers, so populations respond more strongly to sustained long-term trends in climate cycles. Species I studied have varying capacity to respond to annual phenological cues, but it may be that density dependence in vital rates mediates adverse environmental effects that occur in only one season. Therefore, climate trends that impact per capita resource availability (e.g., wetland area, food quality and quantity) may be the primary concern for conservationists assuming that annual climatic fluctuations remain within the range observed during my study periods. Experimental studies that manipulate environmental variables may be necessary to gain further insights into how ducks will respond to climate change predicted in this century.

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PREFACE

There will be some redundancy in the introduction and discussion sections of each data chapter because they were written in the format of independent manuscripts for publication in peer-reviewed journals. Although I use the pronoun “I” throughout the thesis and was primarily responsible for study conceptualization, methodology, data curation, analysis and writing, I would like to acknowledge the contributions of co-authors to each chapter: Chapter 2) Stuart Slattery, Mark Drever and Bob Clark aided with conceptualization, methodology, and review and editing; Chris Derksen contributed snow cover data and manuscript review; Chapter 3) Matthieu Guillemain, Mark Drever, and Bob Clark aided with conceptualization, methodology, and review and editing (BC also contributed to original draft preparation). Tom Langendon curated European duck population data and contributed to manuscript review; Chapter 4) Jeffrey Warren and Bob Clark aided with conceptualization, methodology, and review and editing. Cody Deane assisted with formal analysis; Chapter 5) Hannu Pöysä, Ray Alisauskas and Bob Clark aided with data curation, conceptualization, methodology, and review and editing.

CHAPTER 1 : GENERAL INTRODUCTION

1.1 Climate impacts on birds

Climate can be described as the statistical distribution of meteorological conditions prevailing over a particular region and period of time and the annual sequence of those conditions (Werndl 2016). Along with the abiotic characteristics of a landscape, past and present climates have shaped the diversity and productivity of all trophic levels in an ecosystem. For birds - a taxon with active metabolisms sensitive to weather conditions and a reliance on the production of primary and secondary trophic levels - diversity, distribution, and abundance are all shaped in part by climate (Møller et al. 2010). For birds that annually migrate among regions of widely varying climates, the annual sequence and timing of weather events have further impacts beyond that which may be expected for sedentary species (Møller et al. 2008).

While climates have undergone repeated changes over the course of millennia, the rate at which the earth is presently warming, and is expected to continue (IPCC 2007), raises profound concerns for the future of many avian species (Crick 2004, Møller et al. 2010). A wide variety of climate impacts have been documented in birds, including: i) changes in distribution (Brommer and Moller 2010), ii) changes in the timing of migration (Jenni and Kéry 2003, Visser et al. 2009), iii) changes in breeding dates and mismatches with the timing of peak resource availability (Dunn and Winkler 2010), iv) changes in habitats (Dale et al. 2001, Whitehead et al. 2009, Polley et al 2013), and v) metabolic impacts due to warming climates (Khaliq et al. 2014). Further, for many populations, these climate impacts are occurring simultaneously with other human-caused disturbances such as habitat loss and fragmentation, expansion of invasive

species, pollution, and human exploitation (Eglington and Pearce-Higgins 2012, Northrup et al. 2019). Further research is imperative to help us understand and attempt to mitigate the negative effects of these combined stressors.

1.2 Climate impacts on ducks

While the pace of research in climate-habitat-population interactions has accelerated in recent decades, much effort is still needed to quantify, understand, and predict impacts of climate change on birds (Jetz et al. 2007). Ducks are widely distributed aquatic birds representing several subfamilies of the Family Anatidae. In the northern hemisphere, most duck species are migratory and rely on a variety of seasonal aquatic and terrestrial habitats to complete their life cycles. While ducks are generally well-studied, comparatively few studies on the impacts of climate change are available and there remain many unknowns which hinder conservation planning (Guillemain et al. 2013).

Importantly for ducks, predicted large-scale changes in precipitation and temperature regimes will impact wetland ecosystems on continental scales (Bethke and Nudds 1995, Sorenson et al. 2005, Ballard et al. 2014). Additionally, increases in spring temperatures leading to earlier spring phenology (Solomon et al. 2007) could impact reproductive performance (Drever and Clark 2007, Drever et al. 2012, Clark et al. 2014). Next, I briefly review each of these topics and introduce how my thesis provides new information to understand potential impacts.

1.2.1 Large-scale variation and change in climate impacting duck populations

In North America, 50-75% of ducks breed in the prairie pothole region (U.S. Fish and Wildlife Service 2018), a semi-arid grass and cropland-dominated ecosystem dotted by millions

of small isolated wetlands. The shallow depths of these wetlands make them productive duck habitat, but also means their water balance and ecology are highly sensitive to climatic variability (Conly and van der Kamp 2001). Although conditions have generally become warmer and wetter in the prairie pothole region during recent decades (Millet et al. 2009, Shook and Pomeroy 2012), long-term predictions include further increases in temperature which will likely result in shorter wetland hydroperiods and a reduced area of the pothole region containing wetlands capable of supporting high densities of breeding ducks (Johnson et al. 2010).

A substantial, though smaller portion of North American ducks breed in the boreal forest, as do a large portion of European ducks (Slattery 2011, Birdlife International 2004). Here, wetlands are generally believed to be more stable. However, opposing recent trends and long-term predictions on each continent indicate increased drought stress in the North American boreal (Sulla-Menashe et al. 2018) but increased precipitation in the western Eurasian boreal (Solomon et al. 2007). How these changes will ultimately affect wetland habitats is presently unknown, but will likely have significant impacts on vast populations of breeding waterfowl (Holopainen et al. 2015).

1.2.2 Changes in spring phenology and reproductive performance

Advancing spring phenology is one of the most widely documented impacts of climate change in the northern hemisphere (Schwartz et al. 2006, Derksen and Brown 2012). Along with this change many bird species have begun migrating and breeding earlier (Crick 2004, Dunn and Winkler 2010) and, in many cases, species that have not adjusted have experienced population declines (Møller et al. 2008). A primary hypothesis for declines in birds that do not adjust to this change is the occurrence of a mismatch between breeding dates and peak resource availability,

typically for recently hatched young which are most vulnerable to food shortages (Visser et al. 1998, Both and Visser 2001, Both et al. 2006).

While negative impacts of trophic mismatches have primarily been documented in small-bodied passerines, ducklings rely almost exclusively on aquatic invertebrate food sources for growth (reviewed in Baldassarre 2014), and peaks in the abundance of many aquatic invertebrates appear tied to seasonal water temperature (Cooper 1965, Panov and McQueen 1998, Gerten and Adrian 2002). This creates the possibility for mismatches similar to those experienced by some passerines (but see Dessborn et al. 2009). Northern hemisphere duck populations have a wide range of mean nest initiation dates (Raquel et al. 2016), and early breeding ducks seem to have higher flexibility to spring conditions (Drever and Clark 2007), whereas late-nesting ducks seem less flexible (Gurney et al. 2011). Drever et al. (2012) hypothesized that this trait could lead to higher vulnerability of late-nesting ducks to advancing spring phenology, however this hypothesis has not been tested.

1.3 Thesis objectives

My thesis addresses these impacts of climate variability and change at population and individual levels in multiple duck species. In Chapter 2, I evaluate the response of annual population growth rates of eight duck species breeding in the North American western boreal forest to variation in spring phenology. Emphasis is placed on the comparison of responses from early versus late-nesting duck species breeding across a wide latitudinal gradient. In chapter 3, I evaluate the degree of synchrony between populations of ecologically similar duck species occurring in North America and western Europe. I evaluate whether shared large-scale climate patterns can account for similar trends occurring in duck populations on each continent. In chapters 4 and 5, I switch from population-level analyses to focus on data from individually

marked ducks. In chapter 4, I evaluate the roles of hatch date, spring phenology, and density on the pre fledging growth of lesser scaup ducklings and the possible carryover effects to post fledging survival. And finally, in chapter 5, I compare the plasticity for breeding dates in response to spring phenology among ducks with average breeding dates spanning from early- to late-season. Combined, I believe these studies will provide important insights on how climate change may affect individual ducks and their populations.

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CHAPTER 2 : INFLUENCE OF GROWING SEASON PHENOLOGY, DURATION AND PRODUCTIVITY ON THE POPULATION DYNAMICS OF BOREAL-BREEDING DUCKS

2.1 Abstract

Climatic variability is a major source of environmental stochasticity for breeding ducks in the western boreal forest (WBF). In particular, spring phenology (the timing of onset of spring) and other growing season parameters have been documented as important factors in the dynamics of some bird populations. Ducks breeding in the WBF occur over a long latitudinal gradient and have diverse life-history strategies that may affect their sensitivity to varying growing season parameters. I predicted population growth rates of early breeding species would be negatively associated with later spring phenology, while intermediate- to late-breeding species would have no association or a positive association. I also explored whether growing season length and an index of photosynthetic productivity could explain a portion of the variability in growth rates. I used breeding waterfowl population data for 8 species (or species groups) and normalized difference vegetation index (NDVI) data from 1982-2013 to test these hypotheses in a population modeling framework that allowed effects to vary with latitude.

I detected associations between spring phenology and the population dynamics of 4 species groups. The effects were uniformly positive (i.e., late phenology resulted in greater population growth) and only matched my predictions for 3 of 8 species and then only at high latitudes. The effects detected for growing season length and photosynthetic productivity were limited to a few species and generally did not match predictions that longer or more productive growing seasons would benefit population growth.

Overall the NDVI variables explained only a small amount of the observed variation in population dynamics of a few species. I conclude that the NDVI indices may have limited value in understanding the variability in boreal-breeding duck populations, despite having relatively high resolution and being clearly related to ground measurements of weather and phenology. Because climatic variability and its impacts on breeding habitat is an important factor in duck population dynamics in other regions (e.g., the prairie pothole region), I recommend further evaluation of other weather and wetland data in the boreal, particularly as the time series of promising new remote sensing products grow into the future.

2.2 Introduction

Climate variability causes substantial fluctuations in animal populations through impacts on reproduction, survival, and dispersal (Lande 2003). An important source of climate-driven stochasticity for birds in the northern hemisphere is the varying timing of annual environmental events (i.e., phenology), such as the melting of snow and ice, onset of the vegetative growing season, or timing of emergence for key prey species. Advancing average dates of these indicators of spring phenology have been broadly documented in the northern hemisphere (Barichivich et al. 2013, Ovaskainen et al. 2013), with implications for the demographic rates of several avian taxa (Crick 2004, Møller et al. 2008, Jones and Cresswell 2010).

The possible mechanisms for these phenology-related impacts are wide-ranging. They may be direct, such as the timing of favourable weather influencing survival during a particular life-stage, or indirect, such as with top-down or bottom-up impacts on trophic interactions (e.g., temporal trophic mismatch or climate-mediated changes in habitat [Foden et al. 2013]). In avian taxa exposed to changing environmental phenology, negative impacts have been documented in several species where a mismatch between the species' migration or breeding phenology and that

of important environmental events have occurred (Visser et al. 1998, Both et al. 2006, Saino et al. 2011). In other cases, earlier spring phenology resulting from climate change has seemed to benefit nesting efforts (Weiser et al. 2017). The degree of impact on population processes may be mediated by life-history traits such as average timing of nesting, nesting habitat selection, degree of prey specialization, and phenotypic plasticity of migration or nesting dates to varying environments (Verhulst and Nilsson 2008, Pearce-Higgins et al. 2015).

North American ducks (*Anatidae*) are a diverse taxon with widely differing life-history strategies which may lead to differential vulnerability to climate change. The boreal region of western Canada is a continentally important breeding area for ducks (Slattery 2011), with abundant wetlands in a relatively intact forest matrix. Despite relatively low intensity of direct human disturbance in this region to date (but see Foote and Krogman 2006), there is concern that recent, and forecasted, climate change could affect duck populations. In particular, populations of scaup (*Aythya affinis* and *A. marilus*) and scoters (*Melanitta spp.*) experienced largely unexplained declines in the western boreal forest (WBF) from the mid-1980s to the mid-2000s (Ross et al. 2012), driven by a decline in fecundity (Koons et al. 2017), possibly linked to breeding grounds conditions (Drever et al. 2012, Ross et al. 2015). And yet broadly, there is limited evidence of climate change impacts on ducks (but see Ross et al. [2017] and Guillemain et al. [2013] for evidence of impacts in arctic-breeding geese).

The northern latitudes of this breeding area (generally > 60° N) are characterized by short growing seasons. The phenology and seasonal abundance of food sources for ducklings, primarily aquatic macroinvertebrates, are believed to be driven by timing of ice-melt and increasing water temperatures (Panov and McQueen 1998, Gerten and Adrian 2002, Hansson 2014) and may have strong within-season patterns of abundance (Menon 1969, Gurney et al.

2017). These factors could lead to high sensitivity of reproductive success to the timing of breeding. Indeed, availability of high density aquatic macroinvertebrates has important consequences to duckling growth and survival (Cox et al. 1998, Nummi et al. 2000, Gunnarson et al. 2004). Duck species in the boreal have a range of average breeding dates from early May to late-June, with early-breeders such as mallards (*Anas platyrhynchos*) initiating nests shortly after ice-melt and late-breeders like scaup and scoter spending considerable time on the breeding area before nest initiation (Toft 1984, Gurney et al. 2011, Raquel et al. 2016). Females of early-breeding species may benefit from early onset of spring because i) they are more likely to re-nest if their initial attempt fails and will have more time to do so in years with early springs, and ii) they may also be more likely to adjust timing of breeding to match early cues of advanced environmental phenology (Clark et al. 2014) that could lead to a better match with food resources for their offspring at hatch. Species like scaup and scoters that generally breed late in the season might experience no benefit or be adversely affected by earlier springs if it results in a temporal mismatch with their prey.

In situ climatic monitoring in the boreal is spatially discontinuous due to the sparse distribution of weather recording stations. Fortunately, several climatic variables can be indexed from spatially continuous satellite remote sensing systems. Ross et al. (2015) examined the influence of remotely sensed spring snow cover duration on annual population growth rates of lesser scaup in the Northwest Territories, Canada, while simultaneously considering predator population indices and indices of drought severity. They found an influence of survey-year snow cover duration (i.e., a settling pattern or observation process effect), and a weak interactive effect between drought severity and mesopredators, possibly linked to climate effects on alternate prey (e.g., Brook et al. 2005). Drever et al. (2012) similarly found a survey-year impact of snow

cover duration on counts of scaup and scoter across the entire WBF, but neither study demonstrated direct impacts of phenology on population growth rates via the recruitment process.

Here, I build on previous analyses by evaluating annual population growth rates of 8 boreal-breeding species (or species groups) against an alternative index to breeding season phenology and productivity provided by remotely sensed normalized difference vegetation index (NDVI) from U.S. National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR) satellite (Pinzon and Tucker 2013). NDVI measures the “greenness” of the landscape, which in northern latitudes is sensitive to both snow-melt and the onset of photosynthetic activity (Shabanov et al. 2002, Dye and Tucker 2003). The seasonal progression of NDVI values are modeled and annual seasonality parameters are extracted. NDVI-derived seasonality and productivity variables have been successfully applied in the study of several aspects of animal ecology, including population dynamics (Pettorelli et al. 2011) and wetland habitats (Herfindal et al. 2012). From these data I inferred: i) spring phenology (dates of the onset of spring and peak photosynthetic activity), ii) growing season length, and iii) cumulative growing season photosynthetic intensity (i.e., productivity).

My primary question was whether annually varying environmental phenology, growing season length, and breeding season productivity – all measured on the breeding grounds via NDVI – had a measurable influence on the annual growth rates of several common duck species in the western boreal forest from 1982-2013. These species have a range of both mean nest initiation dates (i.e., early-May to late-June) and length of nesting period (including the propensity for re-nesting attempts; Table 2.1). Given this variation in life-history, environmental phenology may affect species differently. I hypothesized that; 1) population growth rates of

early-nesting species would be positively influenced by earlier spring phenology because they may be more flexible than late-nesting species to match environmental phenology (Gurney et al. 2011, Raquel et al. 2016), and may have more time to attempt re-nesting if the initial clutch fails, 2) population growth rates of all species would be positively related to total length of growing season (controlling for timing of the start of season), because longer growing seasons may increase time available for re-nesting and brood rearing, and 3) population growth rates of all species would be positively associated with overall growing season productivity (indexed as area under the NDVI-growing season curve) because of possible bottom-up trophic enrichment and absence of drought conditions (Beck and Goetz 2011). These latter 2 hypotheses are largely exploratory because links between terrestrial growing season length and productivity and the aquatic factors important to ducks have not been established.

2.3 Study Area

My study area comprised ~617,000 km² of the western boreal forest falling within the survey area of the Waterfowl Breeding Population and Habitat Survey (WBPHS described below; Figure 2.1). This study region covers mixed deciduous-coniferous forests on the southern boreal plain and Canadian shield regions of Saskatchewan, Manitoba, and Alberta, the predominately coniferous taiga forests of the Northwest Territories, the Yukon Flats wetland complex in the Yukon Territory, and three major river deltas (Saskatchewan, Peace-Athabasca, and Mackenzie).

2.4 Methods

2.4.1 Spring phenology datasets

Satellite-derived NDVI has seen broad use in ecology since the 2000s (e.g., Pettorelli et al. 2011). The index is derived from the near-infrared (NIR) and red wavelengths reflected from

earth surfaces, computed as $(\text{NIR}-\text{Red})/(\text{NIR}+\text{Red})$. NDVI provides an index of “greenness” which is sensitive to photosynthetic canopy and ground cover. In highly seasonal environments, such as the boreal forest, a pronounced seasonal signature is evident in intra-annual time series of NDVI values. The seasonal signature of NDVI in these northern high latitudes increases first due to snow-melt and lake ice break-up, and then with the onset of photosynthesis and new vegetative growth in spring and summer (Dye and Tucker 2003). It decreases with the senescence of vegetation and accumulation of snow and ice in the late summer, fall, and winter. While the phenology of aquatic systems is not likely to exert a strong direct influence on NDVI signals after ice melt, increasing air temperatures that drive snow and ice melt and the onset of plant growth in the spring also influence water temperature and hence the component of aquatic ecosystem phenology related to it. The coupling of water and air temperature is particularly strong in shallow water lakes and wetlands, like those common in the WBF, due to wind mixing. I interpret my findings with the caveat that NDVI-measured phenology is presently an unvalidated, yet promising, index to aquatic phenology in the boreal.

NASA Global Inventory Modeling and Mapping Studies (GIMMS) 3rd generation NDVI dataset

I used the 16-day composite, 8-km resolution GIMMS-3g NDVI dataset produced from the observation record of NOAA Advanced Very High Resolution Radiometer (AVHRR) satellite sensors by the NASA GIMMS group. This 3rd generation dataset updated the widely used 1981 to 2006 dataset (Tucker et al. 2005) by extending the time series and updating calibration and processing algorithms to provide better quality data for northern latitudes (Pinzon and Tucker 2014). I retrieved data from <http://ecocast.arc.nasa.gov/data/pub/gimms/>, on 1 September 2014.

I modeled the seasonal NDVI curve for each 64-km² pixel in the GIMMS-3g dataset overlaying my study area using a double logistic function in program TIMESAT 3.1.1 (Jönsson and Eklundh 2004). With these modeled data, phenology variables can be interpolated at 1-day resolution. I extracted several phenological variables; 1) date of start of season (SOS; calculated as the date when modeled NDVI reaches 25% of that year's maximum amplitude), 2) date of peak of season (date when modeled NDVI reaches 100% of amplitude for that year), 3) length of the growing season (number of days between the start and end of season dates), and 4) growing season productivity (the integral of the difference between the function describing the season and the base level from season start to season end, where season end is 25% of the right side of the curve). Because phenological and growing season length variables are derived from annual amplitudes they are not impacted by systematic changes in landscape that influence baseline or maximum NDVI values, such as forest fires or changes in wetland extent. However, growing season productivity could be confounded with landscape changes because it relies on absolute rather than relative NDVI values. I extracted the resulting spatial phenology data to the boundaries of the duck survey strata (described below), and averaged the values by year within each stratum. I standardized the resulting time series separately for each stratum by subtracting the mean and dividing by standard deviation. This ensures my regression analysis (described below) would not confound within and between stratum effects (between stratum effects being latitudinal gradients in mean of phenology variables; van de Pol and Wright 2009).

Comparison of NDVI indices to weather station data

Weather stations are sparsely distributed in the study area; however existing stations provide an opportunity to validate my assumptions that (i) air temperature strongly influences spring NDVI values and (ii) a combination of mean temperature and total precipitation

throughout the summer drive NDVI-derived productivity. I used weather data from 23 stations that operated during the study period and compared these to NDVI start of season and productivity estimated within a 50-km radius of the station. I used ordinary least squares regression to estimate the linear relationship to mean daily air temperatures from March to May. For productivity, I estimated the relationships with mean daily air temperatures and the sum of total precipitation from May to August. All variables were mean-centered by station to eliminate confounding of among-site and within-site relationships in the regression.

Snow cover extent dataset

Given previous research examining the influence of spring snow cover duration (SSCD) on duck counts and annual growth rates (Drever et al. 2012, Ross et al. 2015), I extracted SSCD for my study sites and time period to estimate effects for a point of comparison. The Rutgers University Global Snow Lab provides weekly estimates of snow cover extent over the globe at 190 km gridded resolution since 1966 from NOAA satellites (Robinson et al. 1993). The decrease in SSCD in the WBF during the past several decades (Drever et al. 2012) is consistent with other climate records indicating warming during the spring (Brown et al. 2007, Brown and Rote 2009). Annual variation in SSCD provides an index of boreal spring phenology (Drever et al. 2012, Clark et al. 2014, Ross et al. 2015), albeit at a lower spatial resolution than NDVI. Because NDVI is sensitive to snow and ice melt and one of the primary drivers of the length of SSCD is air temperature, I expected that NDVI would be correlated to SSCD. I calculated SSCD as in Drever et al. (2012) as the number of days with snow cover in the second half of the snow season (1 February – 31 July), interpolated to daily resolution. Duck survey stratum-specific SSCD values were calculated as the area-weighted average of SSCD values in pixels within the duck survey strata.

Duck Population Data

I used population estimates from the annual Waterfowl Breeding Population and Habitat Survey (WBPHS) aerial surveys of the WBF conducted by the U.S. Fish and Wildlife Service (Figure 2.1 and Figure 2.2; data were retrieved from <https://migbirdapps.fws.gov/mbdc/index.html>, on 1 September 2014) for duck species (or species-groups) with breeding ranges that encompassed the entire WBF. The survey is composed of 400-m wide transects where “indicated” breeding pairs are counted from fixed-wing aircraft (Smith 1995). Indicated breeding pairs refer to male-female pairs, as well as observations of lone-males or small groups of males from which the presence of females is inferred (Smith 1995). Counts are adjusted upward with a visual correction factor for each species and population estimates are derived for each survey stratum (strata are loosely delineated by changes in prevailing habitat composition and political boundaries; Smith et al. 1995). I divided annual stratum population estimates by stratum area to calculate population density which is the response variable in my regression analyses. I also acquired transect survey dates from the U.S. Fish and Wildlife Service Migratory Bird Program (Emily Silverman, U.S. FWS, unpublished data). Survey date may help account for observation error in population estimates when timing of the survey is not optimal for availability of species (i.e., early or late relative to migration or nesting phenology).

I retrieved annual population estimates for 8 species (or species groups); mallard (*Anas platyrhynchos*), American wigeon (*Mareca americana*), green-winged teal (*Anas carolinensis*), ring-necked duck (*Aythya collaris*), bufflehead (*Bucephala albeola*), generic goldeneye (common [*Bucephala clangula*] and Barrow’s [*B. islandica*]), generic scaup (lesser [*Aythya affinis*] and greater [*A. marila*] scaup), and generic scoter (surf [*Melanitta perspicillata*], white-

winged (*M. deglandi*), and black [*M. americana*] scoters). The title “generic” refers to closely related species which are not readily discernible during aerial surveys. Of generic scaup and generic goldeneye, lesser scaup and common goldeneye are believed to represent, respectively, the majority of birds observed in the boreal forest (greater scaup breeding range is primarily on the tundra, while Barrow’s is further west than the study area; Baldassarre 2014). If a species was absent from a survey stratum in >5 years out of the 32 year time series, this stratum was removed from that species’ analysis as it is likely on the fringe of its range, with dynamics being influenced relatively strongly by dispersal from other strata.

2.4.2 Statistical Analysis

Duck population growth models with phenology covariates

I used a formulation of the discrete Gompertz population growth model to describe annual population growth rate (Forchhammer et al 1998, Drever et al. 2012, Roy et al. 2016):

$$N_t = N_{t-1}^{\theta} \times e^{r + \varepsilon_t}$$

$$\varepsilon_t \sim \text{Normal}(0, \sigma_{\varepsilon}^2)$$

where θ is the parameter for the strength of density dependence, r is the population’s intrinsic growth rate (i.e., growth rate from small population size (mathematically, $N=1$) when density dependence has virtually no impact), and e_t is random variation in population growth rate caused by environmental stochasticity. The Gompertz model implies that expected annual population growth rate decreases exponentially as the population increases from low densities to its carrying capacity. Taking the natural logarithm (\ln) of population densities, the Gompertz model is equivalent to a lag-1 autoregressive model:

$$\ln(N_t) = x_t = \theta \times x_{t-1} + r + \varepsilon_t$$

Covariates to annual growth rate can be incorporated simply as additional additive terms in the linear predictor equation for x_t , e.g., $\beta \times \text{Covariate}_t$. In this way I could test hypotheses regarding phenological and growing season variables. I evaluated the strength of evidence for these hypotheses with the magnitude of the coefficient estimate and its precision (as summarised by t-values [estimate/ standard error] or 95% confidence intervals).

There are two major dependency structures in the duck population data: 1) observations within strata among years may be related due to stratum-specific intrinsic growth rates, and 2) observations within years among strata may be related due to dispersal of ducks between strata from the previous breeding season (i.e., breeding strata fidelity), or other large-scale synchronizing factors, not captured by my covariates. I accommodated these sources of non-independence by including random intercepts for year and stratum (i.e., a crossed random intercepts model). Further, I allowed variances to differ by stratum because 1) the number of transects surveyed in each stratum varies which leads to differing sampling variance, and 2) unique ecological factors in each survey strata could lead to differing variance in annual growth rates. I included a random effect to allow the density dependence coefficient to vary by stratum, because previous studies have indicated this is appropriate (Sæther et al. 2008, Drever et al. 2012). Finally, I included the mean date of aerial survey flights for each stratum to help account for the potential influence of survey date on counts. Hence, the general model used in my analyses is of the form:

$$x_{t,i} = \alpha + \text{stratum}_i + \text{year}_t + \theta_i \times x_{t-1,i} + \beta_1 \times \text{NDVI covariate}_{t-1,i} + \beta_2 \times \text{Survey Date}_{t,i} + \varepsilon_{t,i} \quad (\text{eq.1})$$

$$stratum_i \sim \text{Normal}(0, \sigma_{stratum}^2)$$

$$year_t \sim \text{Normal}(0, \sigma_{year}^2)$$

$$\theta_i \sim \text{Normal}(0, \sigma_{\theta}^2)$$

$$\varepsilon_{i,t} \sim \text{MVN} \left(0, \begin{bmatrix} \sigma_1^2 & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & \sigma_m^2 \end{bmatrix} \right)$$

Where $x_{t,i}$ is the population density in year_{*t*} and stratum_{*i*}, Phenology index_{*t-1,i*} is the NDVI-derived index (i.e., SOS, date of peak, length of season, or seasonal productivity), and β s are estimated coefficients. I estimated model parameters using restricted maximum likelihood methods available in nlme package (version 3.1-131.1; Pinheiro et al 2018) for program R (version 3.4.3; R Core Team 2018). I evaluated model assumptions regarding homoscedasticity of residuals following Zuur et al. (2009) for each species. I only report and interpret parameter estimates relative to my hypotheses because estimates of random effects and density dependence are not reliable due to observation error (Dennis and Taper 1994) and confounding of growth rate and density dependence (Roy et al. 2016). However, estimates for non-autocorrelated covariates are believed to be unbiased (Linden and Knape 2008).

Modeling strategy

I first evaluated collinearity amongst the NDVI, SSCD and survey date variables. Correlation amongst predictor variables complicates the estimation and interpretation of parameters in regression analysis, particularly when the partial effect of a given variable is of interest (Dormann 2013, Cade 2015). For example, I expect *a priori* that NDVI start of season would be related to spring snow cover duration (snow and ice have very low NDVI values) and

to length of growing season. Understanding these correlations is necessary to interpret and discuss the individual effects on population growth rates estimated in the proceeding steps.

For each species group, I first fit survey date-only Gompertz models (i.e., eq. 1 without the NDVI covariates). I also fit a model with a ‘survey date \times latitude’ interaction. This interaction model allows for the effect of survey date to increase or decrease with latitude if, for example, survey timing mismatch was more acute at higher latitudes. I standardized the latitude variable as $\text{latitude}_i - \min(\text{latitude}_i)$, such that the main effect’s coefficient is the estimated effect at the lowest latitude stratum and a positive sign for the interaction coefficient indicates that the effect increases with latitude. If the interaction effect was supported by a p-value ≤ 0.05 , this was chosen as the “null” model for comparisons with the NDVI covariate models to follow (survey date was not correlated to climatic variables;

Table 2.2). Otherwise the main effect-only model was used.

I then fit models with a lag-1 ‘NDVI start of season date (SOS)’ and lag-1 ‘SOS \times latitude’ effects added to the null model selected above. Interactions with latitude are possible if, for example, SOS effects are stronger at higher latitudes with shorter overall growing seasons. I present these estimates and their 95% confidence intervals as tests of the spring phenology hypothesis for each species group.

I then tested for effects of the other three lag-1 NDVI variables, date of peak, length of season, photosynthetic productivity, and their interactions with latitude. I tested each of these additional variables, separately, in models with and without lag-1 SOS. This limited the fixed effects component of the models to ≤ 2 NDVI variables. I report the estimated effects for each variable with and without SOS in the model, because collinearity with SOS may affect their

estimates, and because it is not possible to disentangle which variable is actually responsible for influence on population growth or if they operate mutually exclusively. Because Drever et al. (2012) and Ross (2015) found effects of snow cover duration in the same spring as the survey, I fit models from the step above with lag-0 SOS and lag-0 SSCD and their interactions with latitude. Of the 4 NDVI variables, lag-0 SOS is the only one that occurs before the duck survey.

Estimating false discovery rate

False discovery results continue to be a concern in ecological research (Anderson 2001, Forstemeier et al. 2017). The modeling strategy outlined above entails 22 null hypothesis tests per species (176 tests total). While an alpha level of 0.05 entails a 5% false positive rate this assumes each test is statistically independent. The collinearity of climate variables, tests for interactions, tests of effects with and without SOS, and shared trajectories of some duck populations (e.g., scaup and scoter) makes the expected false positive rate in my study unclear. Procedures to reduce the risk of false discovery increase the risk of false negatives, so rather than make this trade-off I compared the rate of false discoveries in simulated data to the number of significant results in my study.

I simulated 30 datasets of random normally distributed covariates that mimicked the real data in 1) the number of covariates, 2) their multi-collinearity, 3) their spatial correlation among strata. Replacing real with simulated covariate data, I replicated the analysis described above for all species and recorded the number of false positive findings for each replicate. The distribution of the resulting counts was approximated by a negative binomial distribution, so I used regression with this error distribution to test the hypothesis that the number of significant results in the real data were different than in the simulated data. I used this estimated false

positive rate to temper my conclusions and avoid over-interpretation of statistical effects which may actually be spurious.

2.5 Results

2.5.1 Trends and relationships among phenology variables and to weather station data

SSCD declined about 4 days on average between 1982 and 2012 (Figure 2.S1), whereas there was not a discernable linear trend in NDVI SOS (Figure 2.S2). Despite this lack of shared trend, SOS date was correlated with spring snow cover duration, although the strength of this relationship decreased substantially in northern survey strata. Among other NDVI variables, SOS was strongly related to season length and, to a lesser extent, the timing of peak NDVI (Table 2.2). Correlation of mean survey dates to other variables were minimal ($r \leq 0.11$), suggesting that confounding of survey date and NDVI variable effects is not a concern in interpreting the analyses.

Mean daily spring temperatures (March to May) in the 50-km radius around weather stations was negatively related to SOS. Linear model results indicated a 1 degree increase in mean spring temperature was expected to advance NDVI SOS by -1.6 days (95% CI: -1.8, -1.4). A quadratic regression model fit the data better (change in Akaike's information criterion [ΔAIC_c] from linear effect model = 4.5) indicating that relationship may be slightly non-linear and NDVI SOS is somewhat insensitive to air temperatures at lower values (< 1 standard deviation [SD] below mean). Total precipitation was weakly related to SOS with an expected 0.3 day delay (95% CI: 0.1, 0.4) in NDVI SOS for each 1 cm of total precipitation. The best model with a quadratic effect of temperature and linear effect of precipitation had an adjusted- R^2

= 0.36. NDVI productivity had similar relationships to air temperature. A 1 degree increase in summer (May to August) temperatures was associated with an expected 0.29 SD change in NDVI productivity (95% CI: 0.22, 0.37), while a 1 cm change in total precipitation was associated with a 0.02 SD change (95% CI: 0.01, 0.03). The best model for NDVI productivity had an adjusted- $R^2 = 0.11$.

2.5.2 Survey Date

Stratum-level mean survey dates occurred over an average annual window of 24 days (SD = 6) across approximately 15 degrees of latitude (~2,000 km). Within strata, the SD of survey dates across years averaged 5.3 days, so 95% of annual survey dates were roughly ± 10 days from the mean. This variation in stratum survey date was independent of stratum latitude. There was evidence of an increasing linear trend in mean survey date during the study period, but this only amounted to an estimated 2 day increase in expected mean survey date from the beginning to end of the time series (Figure 2.S3). Confidence intervals (95%) indicated that mean survey date influenced counts for all species except goldeneye and ring-necked duck (Figure 2.3). Regardless of latitude, fewer scaup, mallard, and bufflehead were counted when survey dates were later resulting in lower stratum population estimates. For wigeon, green-winged teal, and scoter, a ‘survey date \times latitude’ interaction was supported and for each species the effect was near 0 at low latitudes but became increasingly negative at higher latitudes.

2.5.3 Influence of Environmental Variables on Annual Population Growth Rates

Start of Season and Spring Snow Cover Duration

I detected effects of NDVI start of season (SOS) on annual population growth rates for four of eight species, primarily at northern latitudes. Significant negative interactions indicated that the effect was near 0 at lower latitude strata, but that later SOS dates at higher latitudes

resulted in higher expected annual growth rates for mallard, wigeon, scaup, and scoter (Figure 2.3). These four species with significant SOS effects spanned the range of mean nest initiation dates for ducks in the boreal and the results were opposite of my prediction that early- and intermediate nesting species would have greater growth rates following early springs (Table 2.3). Instead early- to intermediate-season breeders had higher growth rates in late springs at higher latitudes (mallard and green-winged teal) or were unrelated to this index of spring phenology (goldeneye, bufflehead, wigeon, and ring-necked duck). For the two late-breeding species, scaup and scoter, the pattern matched my predictions, but only at high latitudes.

Despite the correlation of SSCD with SOS ($r = 0.62$) there was only evidence that two species, wigeon and bufflehead, were influenced by SSCD (without SOS in the model). With SOS in the model, the 95% CI on the effect for wigeon overlapped 0, and for bufflehead, the interaction term remained very close to, but > 0 . With or without SOS in the model, bufflehead followed the same pattern as the species above that were influenced by SOS - higher growth rates at northern latitudes when longer SSCD indicated later onset of spring.

Date of peak NDVI, length of growing season, and photosynthetic productivity

Controlling for SOS, there was evidence that date of peak NDVI influenced annual growth rates for mallard and wigeon, regardless of latitude, and for goldeneye, primarily at low latitudes with the effect decreasing further north (Figure 2.4). For mallard, SOS had a significant ($p < 0.05$) positive effect and date of peak had a negative effect, suggesting that mallards had highest growth rates when spring green-up occurred early and rapidly (i.e., the time between onset and peak was short). Although there was no evidence that wigeon were directly influenced by SOS, the SSCD and date of peak terms were significant only when SOS was in the model.

These effects implied the same pattern as was favourable for mallard (i.e., greatest growth rates following early, rapid onset of spring).

Controlling for SOS, length of growing season had associations with mallard and wigeon growth rates, although in the opposite direction of my predictions - for both species, expected annual growth rates decreased with increasing length of season. Length of growing season was highly correlated with SOS ($r = -0.85$; i.e., years with early springs, typically had longer growing seasons), so it is also worth considering that length of season could be the true reason that SOS is an important variable for several species (although possible mechanisms are unclear). Without SOS in the model there was evidence that mallard, wigeon, teal, and scoter were each negatively impacted by longer growing seasons (teal and bufflehead, only at high latitudes). Additionally, the sign of the estimated (but non-significant) effects for scaup, ring-necked duck, and bufflehead were in the same direction (i.e., negative). Overall the results are inconsistent with my hypothesis for higher annual growth rates following years with longer growing seasons (Table 2.3).

Evidence for an association of population growth rates with photosynthetic productivity (i.e., the integral of the seasonal NDVI curve), while controlling for SOS, was present at high latitudes for mallard (estimated effect moved from near 0 to positive with increasing latitude) and at low latitudes for bufflehead (moved from near 0 to positive with decreasing latitude). Goldeneyes were positively impacted with no evidence for a latitude interaction. Without SOS in the model, the productivity effect was no longer significant for mallard, but shifted very slightly to become significantly negative for scoter. Estimates for bufflehead and goldeneye remained relatively unchanged. My hypothesis for higher annual growth rates in years with

higher photosynthetic productivity had limited support for only a few species (and only at specific latitudes for some; Table 2.3). For scoter, the pattern was opposite of my prediction.

Influence of Environmental Variables on the Current Year's counts.

There was evidence that SOS and SSCD in the survey-year influenced apparent annual growth rates for several species (Figure 2.5). The qualifier “apparent” is important here, as it is likely these effects indicate error in the observation process or possibly breeding pairs settling outside the survey area. For SOS, apparent growth rates of four of eight species groups were positively influenced by later counts and the sign was in the same direction for all species groups; however for green-winged teal, scaup, and bufflehead, the strength of the effect decreased and became negative with increasing latitude. The results for SSCD showed a similar pattern to SOS, but with only 1 interaction with latitude supported (for scaup). Otherwise, scoter was the only species group with a significant estimated effect in the SSCD analysis, but not in the SOS analysis.

2.5.4 False positive rate

In 30 replicated datasets of randomly generated covariates, I found an average of 2.2 false positive results per species, a roughly 10% false positive rate. This contrasted with an observed mean of 6 significant results per species in the real covariate data which was significantly greater ($p < 0.01$) than expected under the null hypothesis of no difference in positive finding rates between the simulated and real data.

2.6 Discussion

2.6.1 Trends and relationships among phenology variables

I found no evidence of a linear trend toward earlier NDVI SOS or season length during 1982-2013, despite documented climate warming over much of North America (IPCC 2007) and a slight trend for decreasing spring snow cover duration. Nevertheless, these findings corroborate those of Barichivich et al. (2013) who found no significant change in start of thermal potential growing season nor photosynthetic growing seasons nor in the length of the growing season, over a larger area of northern North America during a similar time period (1982-2011). Similarly, my analysis of data from 23 weather stations across the study area did not reveal linear increases in spring or summer temperatures. Despite not sharing a time trend, there remained a correlation between SOS and SSCD, particularly in southern strata. Breeding ducks could plausibly be affected by each variable differently (e.g., if snow cover duration was more closely related to aquatic ecosystem phenology, while SOS was more closely related to terrestrial vegetation for nesting cover); however, as discussed below, there was little evidence of additive effects from both variables. Further study of the relationships of these indices to *in situ* habitat conditions is needed.

2.6.2 Effects on annual population growth rates

Spring Phenology

I found mixed evidence regarding my hypotheses for the effects of spring phenology on population growth rates. I predicted that annual population growth rates of early- and intermediate- nesting species would be positively influenced by earlier spring phenology (indexed by NDVI). Early nesting species may be more likely to adjust their timing of breeding

to early cues of environmental phenology (Oja and Poysa 2007, Dessimond et al. 2009, Gurney et al. 2011), leading to possibly better synchrony of their hatching ducklings with peak prey abundance and also benefiting from the longer growing season. Further, there is some evidence that early-nesting (in terms of absolute date) is associated with higher reproductive success, although this can be difficult to distinguish from the effects of parental quality (i.e., high-quality individuals tend to nest earliest; Blums et al. 2002, Elmberg et al. 2005, Verhulst and Nilsson 2008, Weiser et al. 2017). Conversely, I predicted late-breeding species would either be unaffected or negatively affected by early springs because they may be less likely to match the (possibly) earlier phenology of aquatic macroinvertebrate abundance.

In contrast to these predictions, early- and intermediate-breeding species either had no detected effects (bufflehead and goldeneye), or the effects were in the opposite direction predicted (positive for mallard and green-winged teal) and occurred in the northern strata of the study area. Predictions were matched only for the intermediate-breeding ring-necked duck (no effect detected) and the relatively late-breeding scaup and scoter species groups (positive effect) at high latitudes. Because scaup and scoter have their highest breeding abundances at these high latitudes, these effects could be relatively more important to continental population dynamics, however they were relatively weak (t -values [estimate / standard error] < 2.7) indicating they explained only a small portion of observed variance in abundance. Neither relative nesting phenology nor foraging behaviour and prey specialization could explain the significant positive results shared by mallard, green-winged teal, scaup and scoter which differ markedly in these life-history traits. For instance, mallard and green-winged teal forage in relatively shallow water and are believed to forage more opportunistically than scaup and scoter (Fast et al., 2004, Haszard and Clark 2007, Lewis et al. 2015).

When I considered SSCD as an alternative indicator of spring phenology (i.e., without NDVI SOS in the model), only bufflehead growth rates had significant relationships with SSCD. Drever et al. (2012) had previously reported slower growth rates of late-breeding species following early springs in the WBF, however it appears that the SSCD time series in their analysis was indexed to the current year and not the previous breeding season, hence the results reflect a survey-year effect of SSCD on duck counts rather than an effect on growth rates. Survey-year effects in this analysis are discussed below. Date of peak NDVI is yet another indicator of spring phenology, and an effect while controlling for SOS would suggest the rate of green-up influences population growth rates. I found higher population growth rates for mallard and wigeon when spring green-up proceeded rapidly, but the opposite for goldeneye (goldeneye effect detected in southern strata only). Overall most species did not appear affected by the rate of green-up and given differing life-history traits among mallard, wigeon and goldeneye a simple life-history explanation is not apparent.

Overall, these results (including the absence of detected relationships at low latitudes and entirely in wigeon, goldeneye, and ring-necked duck) seem to corroborate previous evidence that duck species which have been studied to date are either: a) flexible enough in their life-history traits to accommodate the variation of spring phenology which has been observed in the last several decades (Drever and Clark 2007, Sjöberg et al. 2011, Arzel et al. 2014, Clark et al. 2014), or b) compensate through density dependent mechanisms later in the life-cycle. At northern latitudes where most effects were detected, further study is necessary to understand why late environmental phenology is associated with positive growth rates in several dissimilar species. Perhaps because northern latitudes require the furthest migration, years with later aquatic phenology are more in line with constraints on arrival and timing of nesting for ducks. Indeed,

other studies of ducks at high latitudes have shown that the interval between clutch initiation and spring phenology is less in late springs (Oja and Poysa 2007, Arzel et al. 2014). Another possibility is that advanced environmental phenology caused by warmer weather in early spring is not necessarily followed by warmer weather during the post-hatching period. In this situation, newly hatched ducklings could face harsher conditions than if egg-laying had been delayed (Blums et al. 2002, also see Ludwig et al. [2006] for an example in Finnish black grouse [*Tetrao tetrix*]).

Growing season length

I predicted that longer growing seasons would have positive effects across species by allowing more time for re-nesting after failed nesting attempts and providing a longer brood-rearing period. Growing season lengths varied substantially over the study period, and the observed range of lengths also varied with latitude (29-48 days difference between shortest and longest growing season among strata $<60^\circ$ latitude vs. 10-30 days among strata $>60^\circ$ latitude). However, after controlling for SOS only mallard and wigeon had significant effects and these were in the opposite direction of what I predicted. For at least one species, scaup, the lack of effect could be related to an apparent inflexibility of nest initiation to growing season length across latitudes (Gurney et al. 2011), but this explanation does not work for other species believed to be more flexible in nest initiation dates. It is possible that the amount of additional time provided by longer growing seasons in the WBF may not be adequate to trigger re-nesting or is otherwise insufficient for ducklings resulting from second attempts to fledge at a high rate. Without SOS in the model, I detected more negative effects (again, opposite of prediction), however the very high correlation between SOS and length of growing season makes interpretation difficult. Most of the variation in growing season length was driven by SOS,

however both SOS and growing season length could plausibly affect growth rates and possible mechanisms may not be mutually exclusive.

Photosynthetic Productivity

While many of the previous variables had relatively high intercorrelations, photosynthetic productivity was fairly independent and therefore its specific effect could be estimated unambiguously. I found only limited evidence of an association with growth rates as predicted for two species (mallard and goldeneye), and an unpredicted negative effect for bufflehead. While primary productivity has been used to explain spatial patterns in species richness of birds (Ding et al. 2006) and other animals (Rosenzweig and Abramsky 1993, Mittelbach et al 2001), studies on the effects of *annual* fluctuations in photosynthetic productivity on the dynamics of secondary consumers like breeding ducks and their predators are rare (although they are well-documented in primary consumers; Andreo et al. 2009, Pettorelli et al. 2009). Further research on this linkage as well as research on this variable as an index to drought, or terrestrial vegetation successional stage (Kasischke et al. 1995, Peters et al. 2002, Maselli et al. 2003) which could affect interactions with the terrestrial and semi-aquatic predator community (e.g., through availability of alternate prey), would be informative. For instance, Lewis et al. (2016) found that waterfowl are insensitive to disturbances to terrestrial vegetation caused by immediate and lagged effects of fire which strongly impacts the terrestrial environment and NDVI productivity measurements.

2.6.3 Effects of Survey Date and Current Year Conditions on Counts

Although survey dates trended later during the study period, the average 2-day increase seems insufficient to create a systematic temporal bias in population estimates during the study. The general pattern for all six species-groups with significant effects was for decreasing counts

when survey dates were later than average, although for scoter, teal, and wigeon this was only evident at northern latitudes. Counts of scaup were the most strongly affected by survey date, with an expected -7% (95% CI: -4 to -12%) change in apparent growth rate for a 1 SD increase in mean survey date, regardless of latitude. However, the effect for species with latitude interactions could be similarly strong at high latitudes, e.g., in green-winged teal at the highest latitude stratum, the expected decrease in apparent growth rate was -9% (95% CI: - 5 to -14%) for a 1 SD increase in survey date. These survey date effects are somewhat concerning because they are not currently considered in calculating population estimates used by waterfowl managers (U.S. Fish and Wildlife Service 2017).

For scaup, it has long been acknowledged that surveys occur earlier than optimal in most (if not all) years in the more southern portions of the survey area (Afton and Anderson 2001, Austin et al 2002, Schummer et al. 2018); however, there is no agreement on how this affects population estimates. For instance, double-counting is possible if scaup are still migrating during surveys (i.e., individuals could be counted multiple times as they migrate north along with survey crews moving northward). However it is also likely that under-counting at high latitudes could occur under these same conditions (i.e., crews get ahead of migrating scaup). My results indicating lower counts from late surveys do not provide clear support for either mechanism. Further, the tendency for larger survey date effect at higher latitudes in species other than scaup seems to suggest that surveys could be later than optimal. More detailed analysis of transect-level survey dates and counts are necessary, and I suggest proposed mechanisms for survey date effects will need to accommodate similar results across several species with differing migration chronology, rather than focusing on single species.

Beyond survey date, indicators of spring phenology in the year of the survey were also associated with duck counts. More scaup, scoter, green-winged teal, and mallard were counted when spring phenology was relatively late (although for scaup this effect decreased with latitude). This indicates survey error, possibly related to duck “availability”, which could be affected by the relation of survey timing to migration or nesting phenology (e.g., whether ducks have finished settling in the strata when surveys are flown or whether pairs and lone males are more or less visible as females begin to lay eggs or incubate). Associations with spring snow cover duration are particularly concerning because, unlike SOS, this variable has been trending negative by about -0.25 days/year (Figure 2.S3). As with survey date effects, scaup counts were also the most strongly influenced by spring phenology. This suggests their migration or nesting phenology makes their counts particularly vulnerable to observation error, although somewhat reassuringly, post-hoc evaluations of an interaction between survey date and spring phenology indicators did not reveal a multiplicative effect on counts ($p > 0.05$).

2.6.4 Overall Explanatory Power of NDVI Variables

Many of the relationships detected with NDVI-covariates were relatively low magnitude and estimated with low precision, i.e., they had absolute t -value < 4 (t -value = slope coefficient/SE; p -value = 0.05 corresponds to absolute t -value ~ 1.96). Low t -values indicate 95% confidence intervals that are close to 0 (or equivalently p -values ≥ 0.05) and low portion of observed variance explained by the covariates. While I did not calculate variable specific (“semi-partial”) R^2 statistics (sensu Jaeger et al. [2017]) due to the class of models I used, I did compute these for a simpler version of the model (which assumed constant residual variance across strata). Semi-partial R^2 was $< 3\%$ for all NDVI-variable effects on annual growth rates and $\leq 4\%$ for survey-year effects. Finally, the estimated magnitude of NDVI effects rarely

exceeded an expected 5% change for a 1 SD change in the covariate (Figure 2.6 illustrates an example of the typically large variance in growth rates around a fitted model for mallard growth rates vs. length of growing season).

I estimated the false positive rate in my analyses to be ~10%, however it is not possible to know which results are most likely to reflect a true underlying biological process and which belong in the false positive category. The exploratory analysis of the date of peak, length of growing season, and photosynthetic productivity variables did not produce a large number of positive results, and of those statistically significant effects, few were in the direction I predicted or otherwise consistent across species or species groups sharing similar life-history traits (e.g., early vs. late nesters, diving vs. dabbling foragers). This contrasted somewhat with the SOS effect which had a larger number of positive results and a similar pattern among species (though not necessarily as I predicted). Based on these *a priori* considerations I suggest SOS results may be the most robust to replication with separate data or at different scales. New data and further development of mechanistic hypotheses are important to continue exploring the role of climatic fluctuations in the population dynamics of boreal-breeding ducks.

2.6.5 Conclusion

The importance of climatic variability to duck populations has long been recognized in the North American prairie pothole region where a majority of the continent's ducks breed. The WBF has generally been believed to have more stable climate and habitat conditions. Despite this perceived stability, duck numbers still fluctuate widely in this region. Because weather stations and other in situ habitat measurements are sparse or lacking for the WBF I attempted to evaluate the effect of climatic variability on the environment with NDVI-derived indices. The NDVI indices I calculated (start of season, date of peak, length of growing season,

photosynthetic productivity) had little explanatory power, and the direction of effects were often not as predicted from my limited basis for *a priori* reasoning based on life-history traits. Perhaps this was somewhat foreseeable given that NDVI is primarily a terrestrial measurement and a large part of duck habitat requirements are aquatic or along wetland edges. Further investigation of the linkage between terrestrial and aquatic phenology is necessary to determine if NDVI is simply a poor indicator of aquatic phenology or if aquatic phenology is a poor predictor of duck population growth. A logical place to start would be in examining whether SOS is correlated with the phenology of aquatic invertebrate life cycles and intra-seasonal abundance and how this relates to synchrony with female ducks and their broods. Secondly, the mechanism of seasonal change in predator activity should be considered.

Despite the low explanatory power found in the AVHRR NDVI metrics, I encourage the continued exploration of other remote sensing products which provide a variety of indices to habitat and climatic conditions. Given the vast scale of the WBF, remote sensing is likely to remain the most practical source of large-scale environmental monitoring data for the WBF for the foreseeable future. A times series of wetland availability across the WBF would be invaluable as these data are available in the PPR and are predictive of duck population growth rates and trajectories. There are several recently developed satellite products that can index surface (or near-surface) water availability (Mahdavi et al 2017) and a variety other habitat and climatic parameters (reviewed in Pettorelli et al 2018). These relatively new products will become increasingly practical for the study of population dynamics as their time series grow into the future.

An unexpected outcome of this investigation was finding importance of both survey date and the current year's spring phenology on counts, indicating the possibility of systematic bias in

surveys. This further corroborates the findings of Drever et al. (2012) and Ross et al. (2015) for an effect of survey-year SSCD on scaup counts. I recommend a finer scale investigation of this phenomena which could be largely conducted with existing sub-survey strata level raw data (i.e., transect counts and dates).

Still unanswered is what environmental factors could have contributed to scaup and scoter declines during the study period (Afton and Anderson 2001, Austin 1999). Koons et al. (2017) identified a decrease in fecundity as the primary driver behind the decrease in scaup between 1983 and 2006. Clearly, a major environmental change would have occurred to impact vital rates to this extent, however there is no pattern in the NDVI variables that could account for this. More broadly, it appears that duck populations in the WBF are resilient to the wide-ranging fluctuations in environmental phenology and productivity that I indexed from the longest continuous time series of NDVI data currently available.

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2.8 Tables and Figures

Table 2.1 Breeding characteristics of duck species (or species groups) breeding in the western boreal forest study area. Summarised from sources within Baldassarre (2014).

Taxon	Timing of Clutch Initiation	Re-nesting propensity	Diet during breeding season	Primary Wintering Area
American Wigeon	June	Can re-nest if first clutch lost	Aquatic invertebrates; seeds and fruits	US Pacific Northwest, California, Atlantic and Gulf Coast US States south of Massachusetts
Mallard	Late April, May, June	Commonly re-nests if first clutch is lost	Aquatic invertebrates	East Central US States
Green-winged teal	May, June	Can re-nest if first clutch lost	Aquatic invertebrates; seeds	Pacific, Atlantic and Gulf coasts, Interior US and Mexico
Bufflehead	Late April, May	Unlikely to re-nest after clutch loss	Aquatic invertebrates	Atlantic, Pacific and Gulf coasts, lower Great Lakes
Goldeneye	Late April, May	Unlikely to re-nest after clutch loss	Aquatic invertebrates, molluscs	Atlantic and Pacific coasts, large interior waterbodies of US and Canada
Ring-necked duck	May, June	Can re-nest if first clutch lost	Aquatic invertebrates; seeds	Atlantic coast south of Massachusetts, East Central US states
Scaup	June	Unlikely to re-nest after clutch loss	Aquatic invertebrates (esp. amphipods), molluscs, seeds	US Atlantic and Gulf Coasts south of Maine, including Mexico
Scoter	June	Unlikely to re-nest after clutch loss	Aquatic invertebrates (esp. amphipods), molluscs	Pacific coast from Alaska to California

Table 2.2 Correlations among 4 NDVI-derived predictor variables, spring snow cover duration, and mean survey date in the 14 duck survey strata, 1982 to 2013.

	Start of Season ^a	Length of Season	Date of Peak	Productivity	Spring Snow Cover	Survey Date
Start of Season	1	-0.85	0.62	-0.3	0.62	0.01
Length of Season	-0.85	1	-0.47	0.32	-0.47	0.08
Date of Peak	0.62	-0.47	1	-0.23	0.51	0.11
Productivity	-0.3	0.32	-0.23	1	-0.2	0.05
Spring Snow						
Cover	0.62	-0.47	0.51	-0.2	1	0
Survey Date	0.01	0.08	0.11	0.05	0	1

^aAll variables are mean-centered by stratum meaning that correlation coefficients reflect strata-level synchrony and not shared latitudinal gradients in means.

Table 2.3. Results relative to predictions for NDVI variables. For growing season length and photosynthetic productivity results from models with and without the collinear variable NDVI ‘start of season’ were considered. ‘Opposite’ in parenthesis indicates result was opposite the prediction. Mallard, goldeneye, and bufflehead were considered early nesters; wigeon, green-winged teal, and ring-necked duck were considered intermediate; and scaup and scoter were considered late.

Species or Species Group	Matched prediction for start of season? (Predicted negative for early nesters, neutral/negative for intermediate, neutral/positive for late)	Matched prediction for growing season length (Predicted positive for all)	Matched prediction for photosynthetic productivity (Predicted positive for all)
American wigeon	No*	No (opposite)	No*
Mallard	No (opposite at high latitudes only)	No (opposite)	Yes (high latitudes only)
Green-winged teal	No (opposite; at high latitudes only)	No (opposite at high latitudes)	No*
Bufflehead	No*	No*	No (opposite at high latitudes)
Goldeneye	No*	No*	Yes
Ring-necked duck	Yes*	No*	No*
Scaup	Yes (high latitudes only)	No*	No*
Scoter	Yes (high latitudes only)	No (opposite at high latitudes)	No*

* No effect detected

Figure 2.1. North American Breeding Waterfowl Survey strata (numbered polygons) and transects (dashed lines). The irregular underlying polygon represents the extent of Canadian western boreal forest.

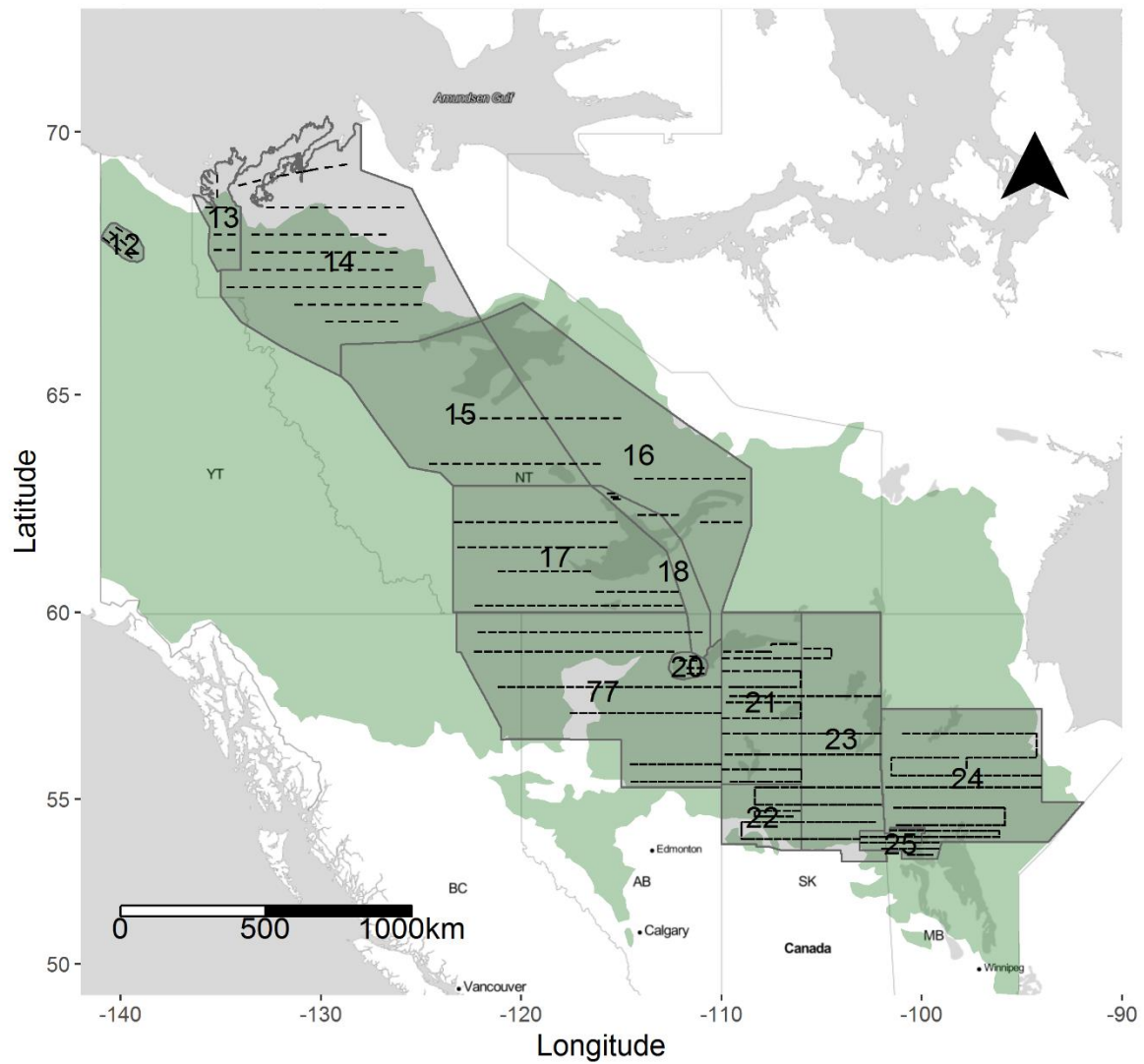


Figure 2.2. Population estimates and 95% CI for all survey strata in the western boreal forest (Figure 2.1), 1982-2013 obtained from U.S. Fish and Wildlife Service Migratory Bird Data Center. Goldeneye, scaup, and scoter estimates include similar species that are not distinguished during aerial surveys (discussed in text).

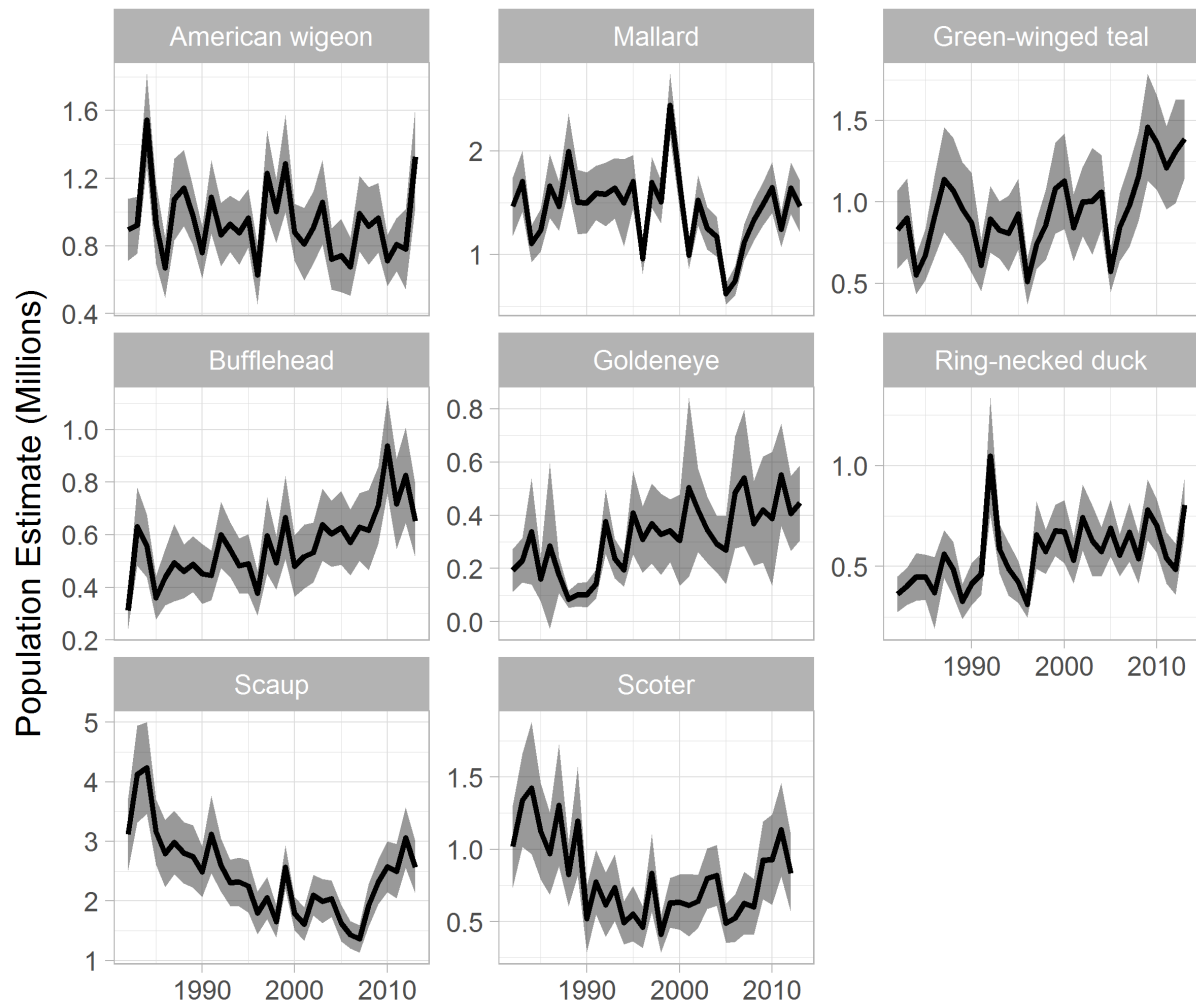


Figure 2.3. Regression coefficient estimates and 95% CI for NDVI start of season date and survey date covariates. Covariates are standardized to mean=0, SD=1, and hence can be interpreted as the percent change in annual population growth expected for a 1 SD change from the mean of the covariate. Interactions with latitude were considered for all variables, but are only presented when confidence intervals did not overlap 0. Latitude was standardized as 'latitude- min(latitude)', hence the main effect in the presence of an interaction term is the expected effect at the minimum latitude of the study area and the interaction estimate is the expected additional change for each 1° increase in latitude.

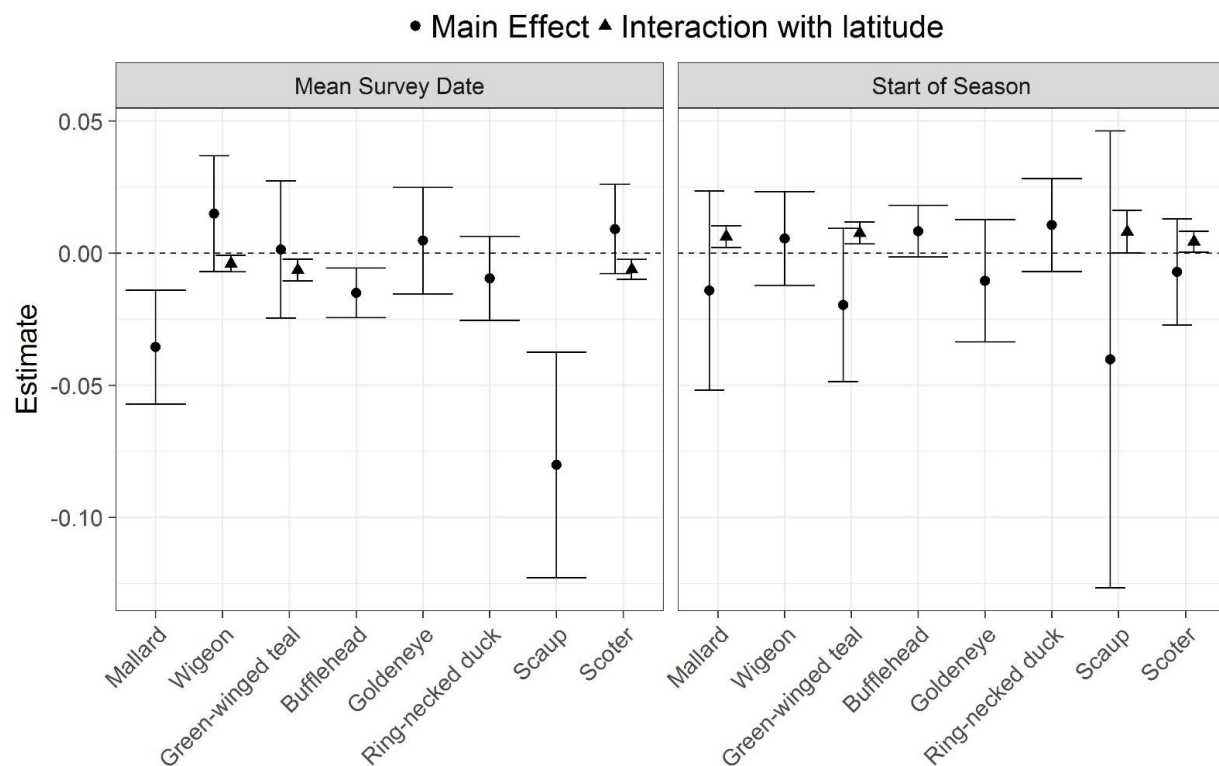


Figure 2.4. Regression coefficient estimates and 95% CI for spring snow cover duration, date of peak NDVI, length of growing season, and photosynthetic productivity. Estimates are presented from models both with (orange) and without (blue) start of season date. Covariates are standardized to mean=0, SD=1, and hence can be interpreted as the percent change in annual population growth expected for a 1 SD change from the mean of the covariate. Interactions with latitude were considered for all variables, but are only presented when confidence intervals did not overlap 0. Latitude was standardized as ‘latitude- min(latitude)’, hence the main effect in presence of an interaction term is the expected effect at the minimum latitude of the study area and the interaction estimate is the expected additional change for each 1° increase in latitude.

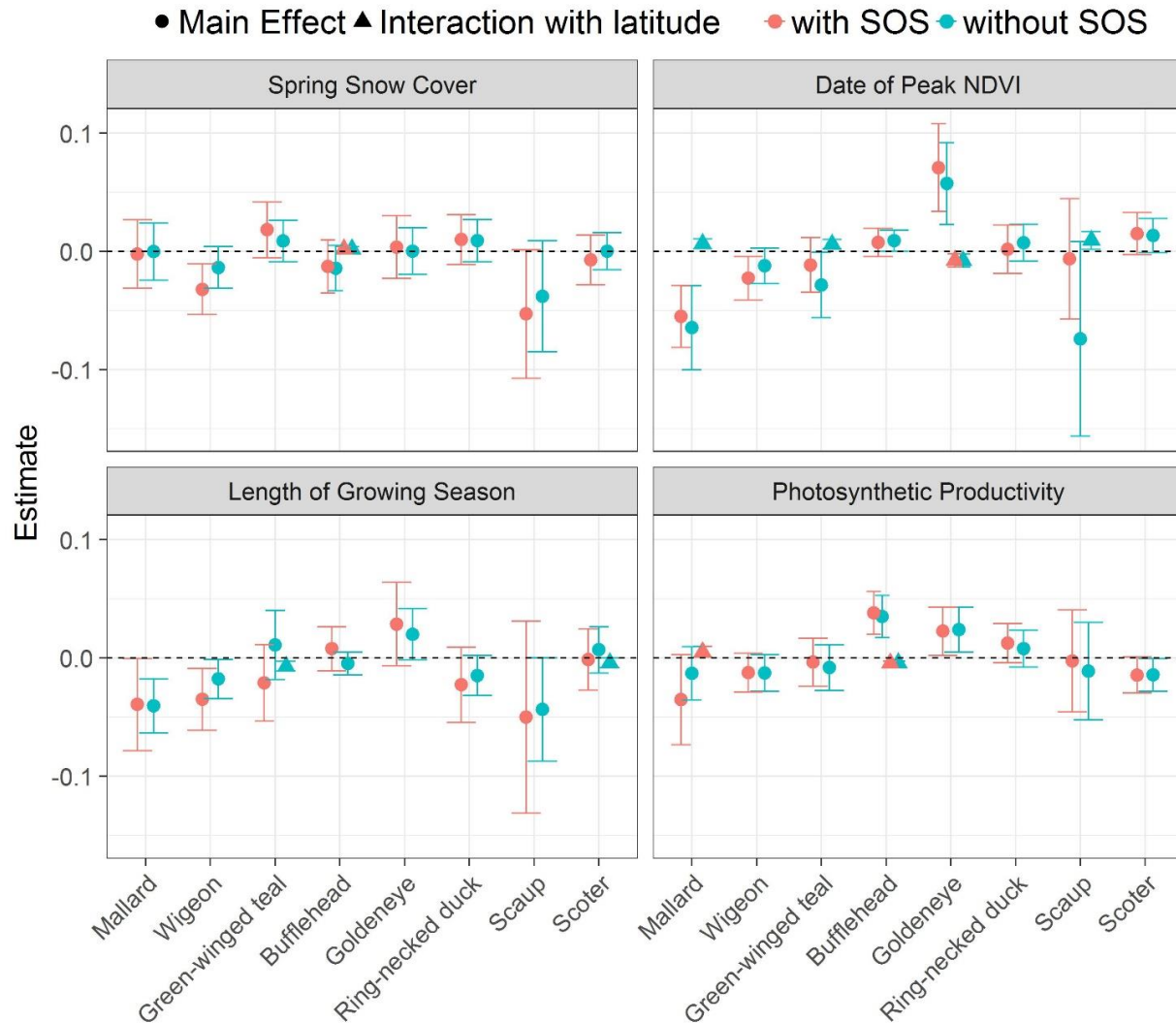


Figure 2.5. Regression coefficient estimates and 95% CI for spring snow cover duration, NDVI start of season, and mean survey date all measured in the same year as the survey. These effects indicate influences on counts (i.e., observation error), rather than influences on annual growth rates. Covariates are standardized to mean=0, SD=1, and hence can be interpreted as the percent change in observed population density for a 1 SD change from the mean of the covariate. Interactions with latitude were considered for each variable, but are only presented when confidence intervals did not overlap 0. Latitude was standardized as ‘latitude- min(latitude)’, hence the main effect in presence of an interaction term is the expected effect at the minimum latitude of the study area and the interaction estimate is the expected additional change for each 1° increase in latitude.

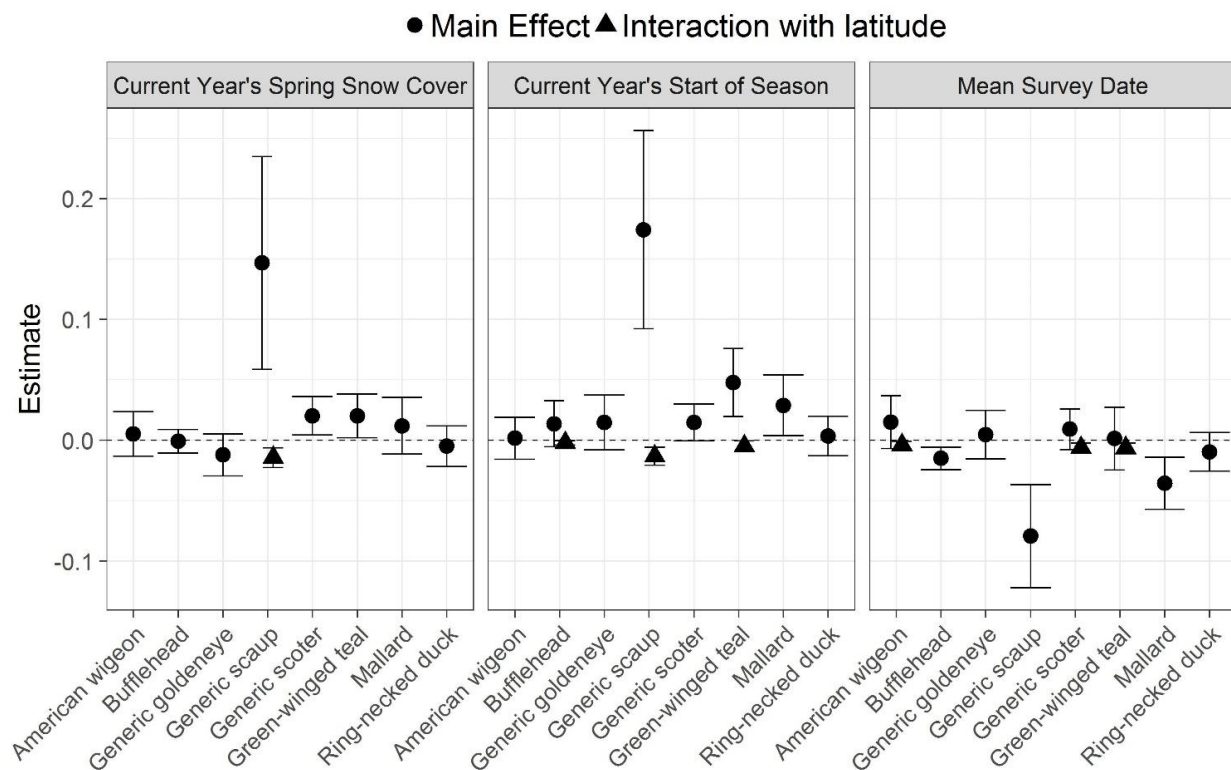


Figure 2.6. Partial regression plot of population growth for mallard against the length of growing season in each survey stratum. Plot is residuals of the null model including survey date, against the residualized covariate (standardized to mean=0, SD=1).

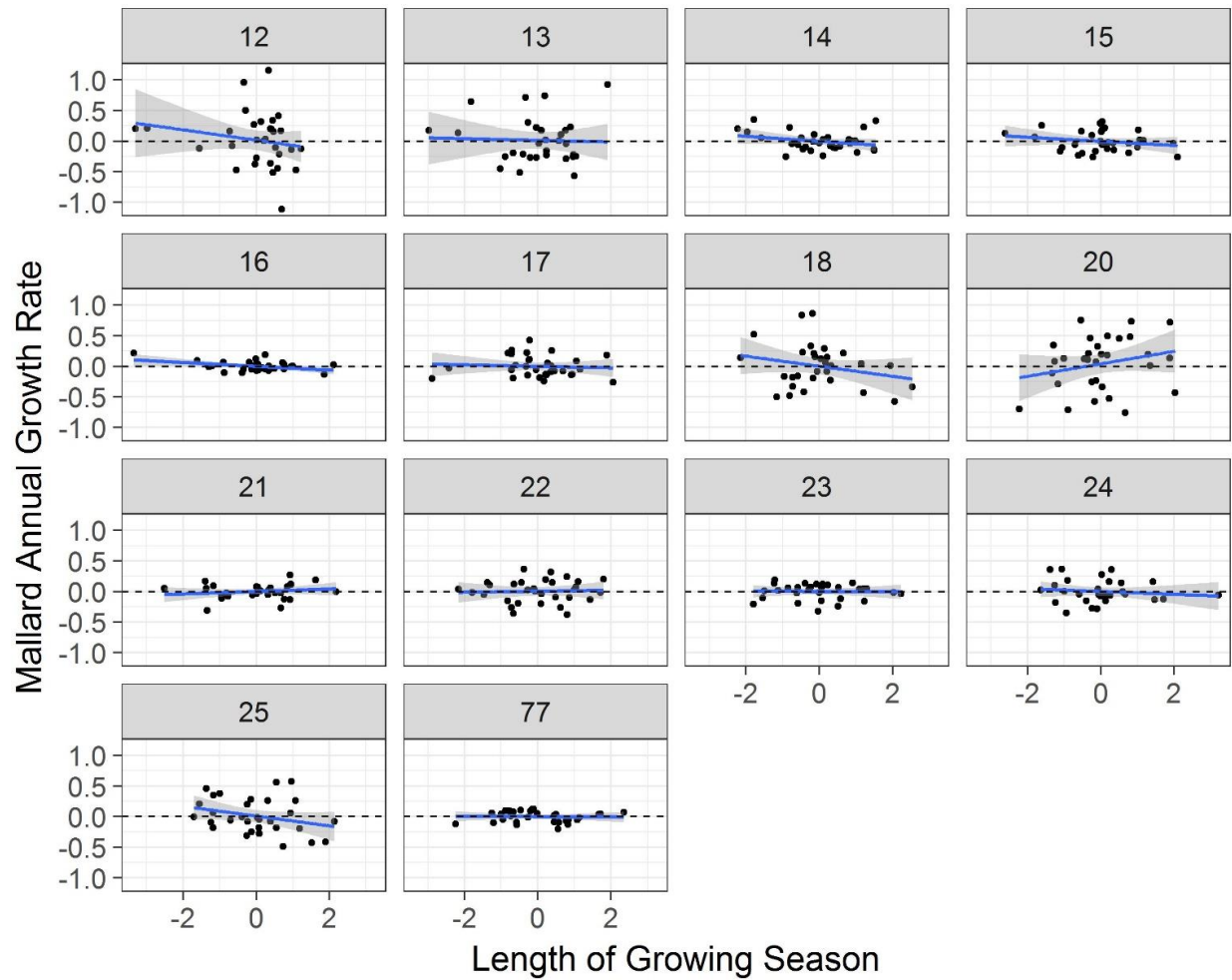


Figure 2.S1. Spring snow cover duration by stratum in the Waterfowl Breeding Pair Survey 1982 to 2013. Thin coloured lines are linear regression by stratum, and the thick black line is overall linear regression with shaded 95% confidence interval ribbon.

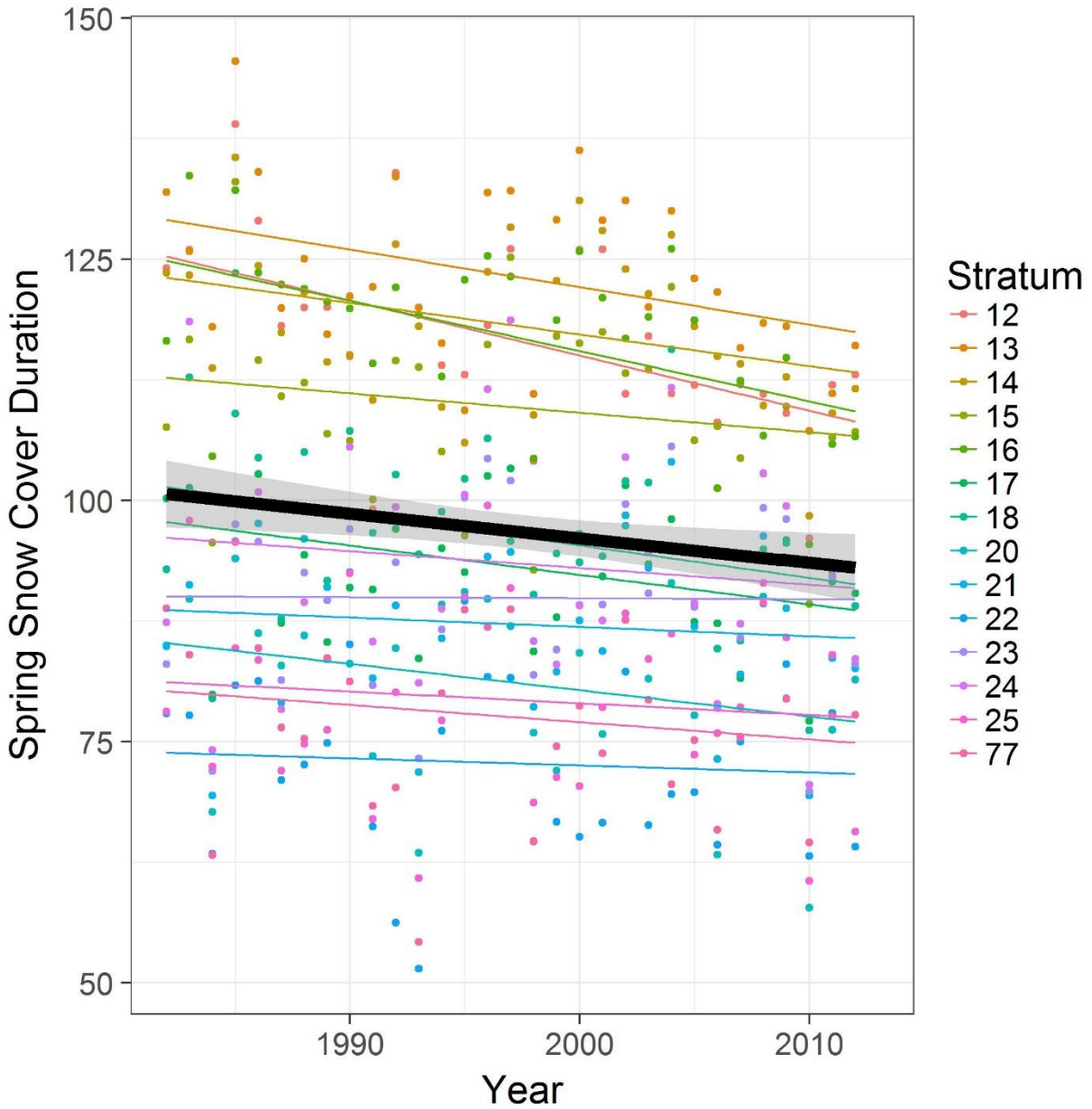


Figure 2.S2. Normalized difference vegetation index (NDVI) start of season dates by stratum in the Waterfowl Breeding Pair Survey 1982 to 2013. Start of season is defined as the date at which 25% of the seasonal amplitude of the interpolated NDVI curve is reached. Thin coloured lines are linear regressions by stratum, and the thick black line is the overall linear regression with shaded 95% confidence interval.

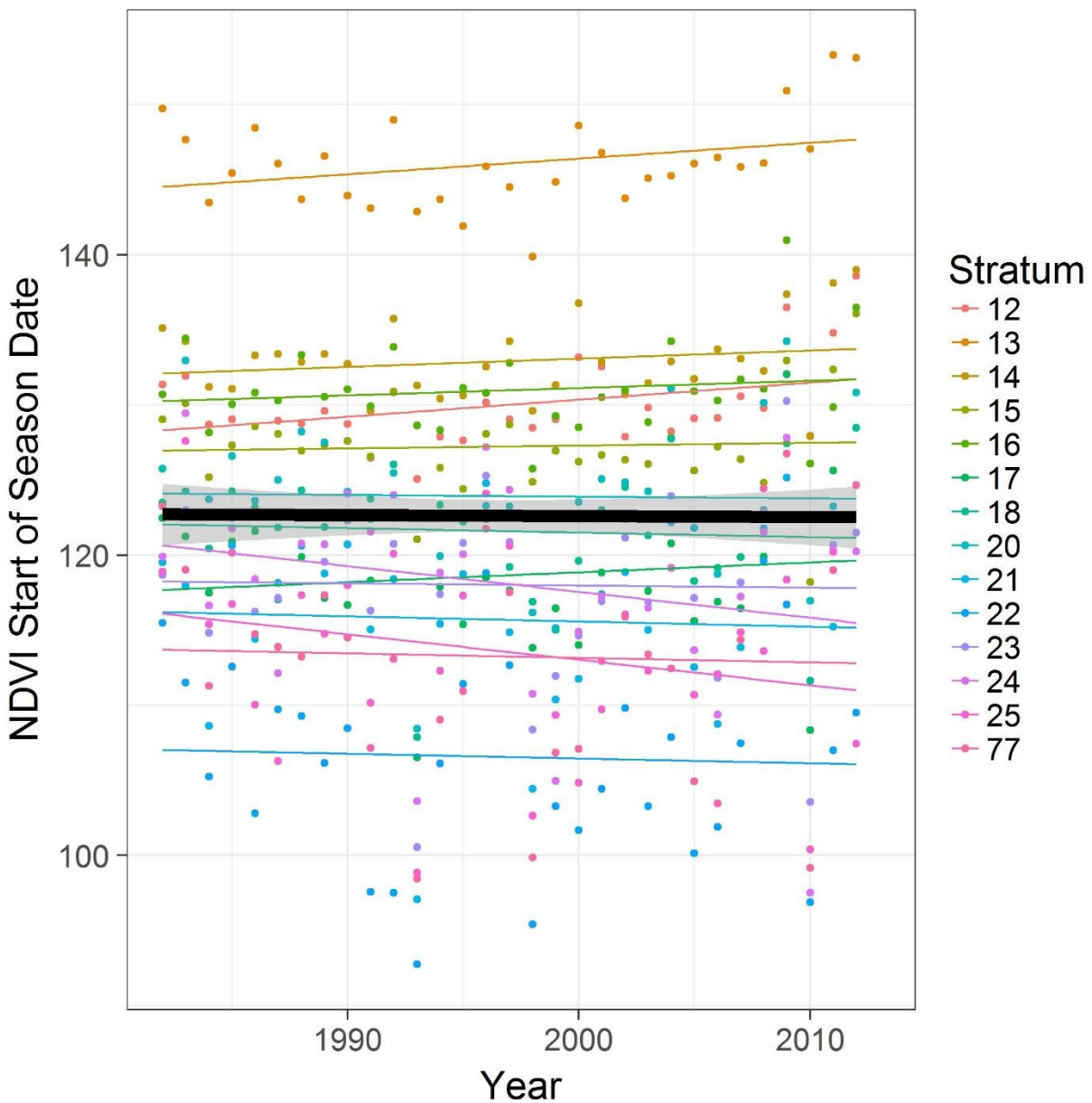
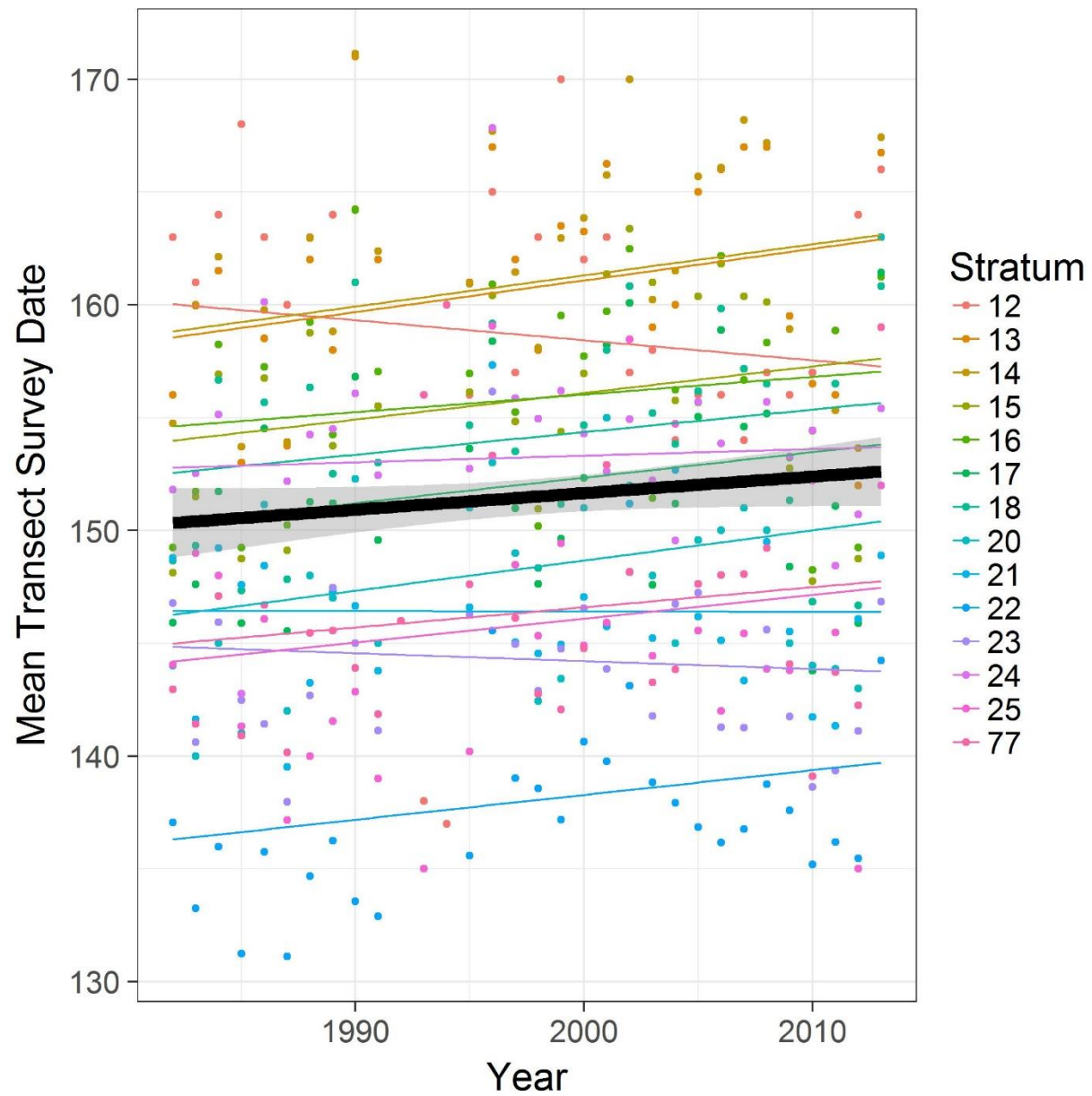


Figure 2.S3. Mean transect survey dates by stratum in the Waterfowl Breeding Pair Survey 1982 to 2013. Thin coloured lines are linear regression by stratum, and the thick black line is the overall linear regression with shaded 95% confidence interval.



CHAPTER 3 : CROSS-CONTINENTAL SYNCHRONY OF AVIAN POPULATIONS: A POSSIBLE ROLE FOR LARGE-SCALE CLIMATE CYCLES?

3.1 Abstract

Few studies have explored dynamics of species sharing life-history and life-cycle traits that may be affected by common environmental drivers such as climate cycles in widely-separated regions or continents. I tested for synchrony in population dynamics of ecologically equivalent duck species in Western Europe (WEU) and central North America (NA), 1976-2011, and where I found evidence of shared dynamics, asked whether common climatic conditions on each-continent related to the Atlantic Multi-Decadal Oscillation (AMO) index or winter North Atlantic Oscillation (NAO) index could explain it. Annual population growth rates and population sizes of eight ecologically or taxonomically equivalent species-pairs of dabbling and diving ducks on each continent were estimated with Gompertz population models fit in a state-space modeling (SSM) framework to reduce impacts of observation errors. Annual synchrony was assessed as the evidence for correlation in annual growth rates, while a weaker form of synchrony, shared time-trends, were assessed as the linear correlations between SSM estimates of population sizes. Shared (increasing) time-trends in WEU and NA were found in four of eight species-pairs, but in no species-pair were changes in population growth synchronous on an annual basis. All species-pairs sharing trends were positively correlated with the AMO index which generally increased during my study period. Positive cycling of the AMO seems to be associated with increased temperature and precipitation in breeding areas of both continents which may have produced favourable conditions (earlier springs, more ponds) for some duck

populations. Differences in the local effects of weather on environmental conditions, in addition to other continent-specific extrinsic factors or forms of density regulation, may mask annual synchrony in the response of different continental populations to AMO. Spurious correlation or confounding of AMO effects with other extrinsic factors such as shared changes in anthropogenic drivers (e.g., climate and land use interactions) should be addressed in future studies.

3.2 Introduction

Environmental variation and changes can affect population processes of widely-separated organisms sharing life-history traits and demographic drivers. For instance, temporally-varying components of population dynamics such as survival, dispersal and reproductive rates have been directly linked to fluctuations in climatic and oceanographic conditions, and land use modifications (Stenseth et al. 2002, Sæther et al. 2003, Scharlemann et al 2004). These investigations have typically focused on single or few species at spatial scales ranging from local to sub-continental (e.g., Stenseth et al. 1999, Sæther et al. 2007, Cheal et al. 2007). Furthermore, population synchrony has been well-documented from long time-series data sets at biome-specific spatial scales in birds (Liebhold et al. 2004). Hypothesized synchronizing factors have been evaluated in some cases whereas in others, shared population patterns have been described for avian guilds at regional or continental scales (Michel et al. 2016). Studies of population dynamics of species affected by common environmental drivers operating on the same time scale on different continents are rare. Yet, such studies could provide deeper insights into global forces affecting animal populations (Ranta et al. 1997, Koenig 2002, Stephens et al. 2016).

Synchrony can arise in widely-separated populations of ecologically equivalent species via two major mechanisms. First, environmental changes across widely separated regions of the

globe can synchronize populations if demographic rates (i.e., survival, reproduction) are affected by similar environmental drivers and stochasticity, termed the Moran effect (reviewed by Liebhold et al. 2004), or via shared trophic mechanisms such as bottom-up timing of resource pulses or top-down predation rates (Nudds 1992, Koons et al. 2014). Second, dispersal of individuals among sub-populations can produce synchrony if animals move from higher to lower density areas, a pattern that attenuates with distance between subpopulations (Ranta et al. 1995). However, in the second case, if focal areas are continents and separated by major barriers like oceans, dispersal would be impeded and prevent this mechanism from producing synchronization between populations.

Population synchrony may be evident as a shared time-trend or population cycle, or related, as covariation of annual growth rates. Synchrony of annual growth rates is not a pre-condition for shared time-trends, which nonetheless may be driven by a common underlying factor. For instance, two continents could have similar environmental changes over decades (e.g., warming climate) but fluctuations may not be temporally coincident each year, or their effects on animals may be differently buffered by natural or human-mediated continent-specific factors such as local weather, lags in habitat or predator community responses to changing environments, and agricultural or water protection policies. Ecologically equivalent species are expected to react similarly on each continent to the extent climate has similar effects on their habitats, predators, or energy requirements.

The winter North Atlantic Oscillation (NAO) and annual Atlantic Multi-decadal Oscillation (AMO) are examples of climate cycles known to affect marine and terrestrial ecosystems in Europe and North America (Stenseth et al. 2003, Nye et al. 2014). Strong negative phases of the winter NAO are associated with cold dry conditions, especially across

Europe and the east coast of North America. These conditions can have adverse effects on survival and reproductive rates of some duck species (e.g., Blums et al. 2002b, Lehikoinen et al. 2006); consequently duck population growth rates may decrease *after* severe winters, i.e., a synchronizing effect would be evident in annual growth rates. Compared with the NAO, few studies have assessed AMO effects on terrestrial vertebrate populations (Boyd and Fox 2008, Nye et al. 2014, Fox et al. 2015). However, over the past decade our understanding of large-scale climate effects linked to AMO has improved, and AMO is now recognized as a leading indicator of climate variability in many regions (Nye et al. 2014). Increases in North Atlantic sea surface temperature across the northern hemisphere produce positive phases of the AMO, with concomitant warming of terrestrial temperatures, earlier onset of spring-like conditions and, at least in Europe, higher summer precipitation (Sutton and Hodson 2005, Knight et al. 2006, Nigam et al. 2011). Thus, I anticipated that the increasing phase of AMO could have positive impacts on ducks either directly via annual growth rates, or through more gradual mechanisms where an effect may be evident only in a shared time-trend. For example, increases in wetland area or abundance, beneficial to ducks, may lag behind increases in precipitation as water storage in wetland basins or near-surface water tables gradually builds up over several years.

Here, I test for evidence of synchrony in both annual population growth rates and long-term population trends of ecologically or taxonomically equivalent species-pairs of dabbling and diving ducks from Western Europe (WEU) and central North America (NA) (Table 3.1). Ranges of duck species span large areas of each continent, many species even having a Holarctic distribution over both WEU and NA, although ringing and genetic data suggest very limited exchange of individuals between WEU and NA (e.g., Guillemain and Elmberg 2014, for common teal *Anas crecca*). Global climate cycles, and similar land use practices could induce

common environmental changes that affect availability and quality of breeding, migration and wintering. If synchrony in growth rates or time-trends are found, I evaluate the evidence that the broad-scale climate fluctuations associated with the AMO or NAO indices could be the synchronizing environmental factors.

3.3 Methods

3.3.1 Duck population surveys

I used 36 years of duck population counts from WEU and NA, 1976-2011. International monitoring of wintering ducks began in WEU in 1964. However, the number of WEU countries and sites counted per country gradually increased over years, while monitoring protocols were gradually improved. By the mid-1970s, mid-winter counts were well-established, standardized and coordinated in most WEU countries including France, the Netherlands, United Kingdom, Germany and Switzerland, which are the strongholds of ducks in the region. The duck population data used for WEU are mid-winter counts carried out in countries which together represent a consistent region within the core wintering range, often termed the North-West Europe flyway. Survey methods are provided in Delany (2005). Briefly, counts of duck species were generally carried out from the ground by volunteer ornithologists (including professionals and amateurs) in a coordinated manner during the week of 15 January each year, and data were compiled by Wetlands International (see synthesis at iwc.wetlands.org).

The survey covered much of the winter range of focal duck species in the Western European and Mediterranean Flyways, and data were recorded in a relatively short period of the winter to reduce potential for double-counting. During very severe winters, it is possible that some species could migrate to areas within and possibly outside of the survey region in search of suitable foods (e.g. Spain; Ogilvie 1983, Ridgill and Fox 1990, Dalby et al. 2013). Some ducks

have been wintering progressively farther north in WEU as a result of warming winter conditions, but such shifts have occurred over time largely within the survey region (Lehikoinen et al. 2013, Dalby et al. 2013). The number of protected areas, especially along the French Atlantic, English Channel and North Sea coasts, has also increased over time, which likely explained a part of the positive trends in European duck counts (Guillemain et al. 2002). Such sites were however mostly covered by the International Waterbird Censuses since the mid-1960s, so the protection status likely improved habitat quality for the ducks, but probably did not increase the spatial coverage of the duck surveys.

Counts of breeding ducks in mid-continent NA were obtained from surveys conducted by the United States Fish and Wildlife Service and the Canadian Wildlife Service (<https://www.fws.gov/birds/surveys-and-data/migratory-bird-data-center.php>), following standard operating procedures which are extensively documented by Smith (1995). The survey area covers the primary duck breeding habitats in central North America and any changes in distributions of breeding ducks during the study period have occurred primarily within the survey area. Briefly, aerial surveys were flown annually over the same transects starting in the U.S. prairies, then traversing the Canadian prairies and parklands and extending northward across the western boreal forest in Canada and Alaska. All ducks were assigned to species and social grouping (pairs, singles, groups, flocks) which are used to estimate the number of breeding pairs present. Greater scaup are not differentiated from lesser scaup on the survey; however field studies indicate that lesser scaup are rare on the tundra where most greater scaup breed, therefore I used only survey strata that cover tundra regions to estimate greater scaup populations. In the prairie-parkland region of the U.S. and Canada, visibility corrections rates were derived from ground counts of ducks made by revisiting sub-sets of wetlands along aerial survey transects. A

constant visibility correction factor was applied to counts of ducks in the boreal forest and farther north. Duck population estimates are based on survey methods developed after 1955, with occasional improvements to data collection and analysis.

These two large-scale data sets represent standardized counts of ducks on each continent and are considered the most reliable sources of information on duck population sizes and trends. Although the surveys rely on different field procedures, data were comparable in being recorded in the same sampling regions during a relatively short time interval each year (mid-January in WEU, May in NA) after most hunting has occurred (hunting season being closed in most WEU countries by the end of January) and prior to the main influx of juvenile birds that occurs during the breeding season.

Eight species-pairs were analyzed (Table 3.1). In some cases, populations of the same species were compared between the two continents (e.g., northern pintail, gadwall [scientific names in Table 3.1]). For species present in only one continent I matched these with congeners sharing general ecologies and life-histories on the opposite side of the Atlantic (e.g. common teal with American green-winged teal). I excluded mallard (*Anas platyrhynchos*) populations because massive releases of pen-raised mallards in WEU could confound the winter counts of wild birds (Champagnon et al. 2013), and because genetic analyses question the existence of genuinely distinct populations in NA and WEU (Kraus et al. 2013).

3.3.2 Climate data

I obtained monthly indices of the Atlantic Multi-decadal Oscillation (AMO) and North Atlantic Oscillation (NAO) from the NOAA web site (<https://www.esrl.noaa.gov/psd/data/timeseries/AMO/>) for the period 1975-2011. If I detected

synchrony in a species-pair's annual growth rates, I summarized the AMO index as the mean of the twelve monthly values, and as the mean of the six month summer period (April to September; AMO_{A-S}), immediately prior to counts on each continent. Absent annual synchrony, but in presence of shared time-trends, I summarized AMO over the same 12-month period for both continents (June to May preceding the NA survey). This allowed for the effect on long-term trends of the species-pairs to be evaluated in the same model and is commensurate with mechanisms producing a gradual change in habitat conditions. I only hypothesized direct effects of winter NAO index on duck populations (i.e., as would be apparent in annual growth rates) therefore I summarized the index as the mean of December-March values during the winter overlapping (in WEU) or just preceding (in NA) the surveys.

While the effects of AMO on weather patterns in Europe are reasonably characterized, there is little direct information on the relationship within the NA breeding area. To help assess the degree to which AMO leads to similar climatic conditions on both continents, I extracted temperature and precipitation data over both continental breeding areas from the Climate Research Unit v4.02 time series (CRU TS v4.02; Harris et al. 2014). These data are gridded ($0.5 \times 0.5^\circ$) monthly summaries based on interpolation between global land-based meteorological stations. Because I was not incorporating these continent-specific data into my duck population modeling, I buffered my study period by 5 years on both ends (1971-2016) to improve the sample size and context to evaluate the relationships. I delineated areas of core breeding habitat for which to summarize climate on each continent (Figure 3.1). For NA this was simply the area covered by the May breeding duck survey (described above). For WEU I used the cumulative area identified as core breeding range for ducks in my analysis from Scott and Rose (1996) and truncated this breeding area to the East following Guillemain et al (2014) to more accurately

reflect the likely geographic origin of ducks wintering in WEU. I summarized the monthly values in these study areas into 3 annual periods; i) pre-breeding season (January-May for precipitation and April-May for temperature), ii) breeding (June-August) and iii) annual (January-December). The longer pre-breeding period for precipitation reflects the effect of snowpack and spring precipitation on spring wetland conditions, while the shorter period for temperature is meant to reflect the relative timing of spring. I looked for evidence of correlations and shared long-term linear trends between the study areas in these periods. To help separate my assessment of time trend and annual correlation, I detrended the weather variables in the correlation analysis by taking the residuals of a linear response-by-year regression.

3.3.3 Statistical analyses

Population Models

Population estimates for ducks on both continents are subject to observation errors. The magnitude of these errors is a function of sampling variability, imperfect detection, and an inability to optimally time surveys for each species in each year (Kéry and Schaub 2012); for example, timing of migration or nesting phenology vary by species and these could influence “availability” along survey routes. To accommodate this observation error, I used a state-space modeling (SSM) framework that, by incorporating an explicit model for observation error, can reduce observation error impacts on parameter estimation and inference made in the population model (Clark and Bjørnstad 2004, Dennis et al. 2006).

Observation model

WEU and NA surveys follow a standardized protocol from year-to-year and are conducted by trained personnel (details above), so I assumed that observation errors (i.e., over- or under-counting, sampling variance) are random from year-to-year, and can be approximated

by a log-normal probability distribution (Lebreton 2009). Hence, I modeled the observation process as:

$$y_t = x_t + \partial_t , \quad (\text{eq. 1})$$

where y_t is the log of the observed data (i.e., population estimates) in year t , x_t is the log of the true but unobserved population sizes, and the error term ∂_t is log-normally distributed as:

$$\partial_t \sim \text{Normal}(0, \sigma_{\text{observation}}^2) ,$$

where the variance is estimated in the model. Log-normal observation errors imply that observation errors (∂_t) are proportional to population size (N) on the real scale.

Biological model

I used a discrete Gompertz population model to represent the dynamics of duck populations on each continent. This model has been applied to ducks (Sæther et al. 2008, Ross et al. 2015, Roy et al. 2016) and more generally to vertebrate populations with synchronous annual birth pulses and growth rates subject to environmental stochasticity and density dependence (Royama 1992, Lande et al. 2003). The Gompertz model implies a concave density dependence between the previous year's population size and the current year's population growth. Using the natural log (ln) of population size in year t (N_t), the model takes the linear form:

$$\ln(N_t) = x_t = \theta \times x_{t-1} + r + \varepsilon_t \quad (\text{eq. 2})$$

where θ is the density dependence coefficient ($\theta < 1$ indicates density dependent dynamics), r is the population growth rate from low populations (i.e., mathematically, from $N = 1$), and ε_t is the unexplained variation in growth rate caused by environmental stochasticity. I assume ε_t to be log-normally distributed as:

$$\varepsilon_t \sim \text{Normal}(0, \sigma_{process}^2)$$

This model can easily be extended to estimate effects (β) of environmental covariates on population growth rates as additive terms (on the log scale).

$$\ln(N_t) = x_t = \theta \times x_{t-1} + r + \beta \times \text{covariate}_{t-1} + \varepsilon_t$$

Synchrony of Western European and North American duck populations

To estimate synchrony of annual growth rates in the eight WEU-NA populations of ecological counterparts, I modified equation (2) to be a multivariate model where subscript i is an indicator for the WEU or NA population, and terms defined above:

$$x_{t,i} = \theta_i \times x_{t-1,i} + r_i + \varepsilon_{t,i}$$

The error term is multivariate log-normally distributed (MVN), where ρ is the correlation of fluctuations in the population growth rate between the WEU and NA populations:

$$\varepsilon_t \sim \text{MVN} \left(0, \begin{bmatrix} \sigma_{EU}^2 & \rho \\ \rho & \sigma_{NA}^2 \end{bmatrix} \right)$$

The estimate of ρ for each transcontinental species-pair is therefore a measure of the linear correlation between their population fluctuations (i.e., synchrony). I evaluated the evidence for annual synchrony using the estimate of ρ and its 95% credible intervals. To evaluate synchrony of long-term trends in population size I tested for correlation between population sizes of species-pairs using the SSM-estimated population sizes from the eq. 2, and testing the null-hypothesis of 0 correlation.

Influence of climate indices on synchrony

If synchronous annual growth rates were detected in analyses above, then I evaluated whether the large-scale climate indices could explain them. Furthermore, it is possible that climate indices do not detectably influence the year-to-year population fluctuations of ducks, but that populations nevertheless are influenced by habitat conditions produced by climate trends associated with AMO over longer time periods (sensu Hefley et al. 2016). Thus, if synchrony in annual growth rates was detected I extended equation (2) to include terms for the climate index covariates, and evaluated support for the index variable as a synchronizing factor by the direction and magnitude of the relationships and their 95% credible intervals (estimation discussed below). If instead only correlated long-term trends were present in a species-pair, I evaluated evidence for AMO as the synchronizing factor. I used the SSM population size estimates (extracted from the models above with no climate covariates) rescaled to mean=0 and SD=1 and pooled these data for each species-pair. I used the scaled SSM population estimates as the response variable in ordinary least-squares regressions against the AMO index with an interaction term to test for a difference in the effect of AMO on each continent. I evaluated support for an association based on shared direction of the continent-specific effects and their 95% confidence intervals.

3.3.4 Model Fitting

Because fitting SSMs in a frequentist framework is currently unreliable, I estimated parameters of the above SSMs in a Bayesian framework (using uninformative priors) with Markov chain Monte Carlo (MCMC) simulations in JAGS (Plummer 2003) using the jagsUI package in R (Kellner 2016, R Core Team 2017). Parameter estimates for environmental covariates and environmental stochasticity are believed to be robust using these methods despite potential difficulties in estimating intrinsic growth rate and density dependence (coefficients α

and θ from eq. 2; Roy et al. 2016). I report only the estimates for parameters regarding my main hypotheses.

All model parameters were given uninformative priors relative to the plausible biological values of the parameters: θ and r were specified as $Normal(0, \sigma = 4)$, variances for process and observation error were specified as uniformly distributed between 0 and 3, ρ uniformly between -1 and 1, and initial population sizes were $x_{1,i} \sim Normal(y_{1,i}, \sigma = 1)$. I ran 3 chains for 100,000 iterations with a burn-in of 10,000 and thinning interval of 5. Convergence was monitored with criterion that parameters of interest would have Brooks-Gelman-Rubin statistic, $\hat{r} < 1.05$, and via visual confirmation of well-mixed chains (Kéry 2010). Model adequacy was evaluated by calculating a Bayesian p -value for the sum of residuals of the actual and simulated “ideal” datasets with values near 0.5 considered adequate (Gelman et al. 1996). Finally, when testing for shared time trends and the association of AMO with these trends, I fit the linear regression models using the base statistics package in R.

3.4 Data deposition

North American survey data can be freely downloaded from the U.S. Fish & Wildlife Service web site: <https://www.fws.gov/birds/surveys-and-data/migratory-bird-data-center.php>. European data may be obtained by contacting Wetlands International (iwc.wetlands.org). Climate data are freely available from the University of East Anglia website: <https://crudata.uea.ac.uk/cru/data/hrg/>.

3.5 Results

3.5.1 Evaluation of shared weather patterns associated with AMO

As with AMO, there was a clear upward trend in temperatures in both study areas during most periods, although this was not apparent in the NA study area during the spring pre-breeding months (April to May;

Figure 3.2) indicating no trend in spring phenology. In the WEU study area trends for precipitation were positive during all periods and over nearly all regions of the study area (Figure 3.3a). In NA there was little evidence of linear trend except a slight increase during summer ($\beta_{\text{summer}}=0.32$, 95% CI: -0.12, 0.60). However, unlike WEU, there appeared to be contrasting regional trends with much of the prairie region having notable positive increases in precipitation (Figure 3.3b). This is corroborated by wetland counts recorded in the prairie region of the NA duck survey which have documented increased wetness during the study period (U.S. Fish and Wildlife Service 2018).

Annual fluctuations in detrended temperature were positively correlated between continents only during the breeding season months (Figure 3.4). Detrended precipitation was negatively correlated across continents during the pre-breeding months (January to May) and over the full calendar year, but there was no correlation during the breeding season. Annual fluctuations in the detrended precipitation were positively correlated with detrended AMO in WEU only ($r = 0.39$, $p = 0.01$), whereas detrended temperature was positively correlated with AMO during the breeding season on both continents ($r_{\text{NA}} = 0.30$, $p = 0.05$; $r_{\text{WEU}} = 0.31$, $p = 0.03$) and annually in NA ($r_{\text{NA}} = 0.40$, $p < 0.01$).

3.5.2 Duck population synchrony and climate indices

Duck population estimates derived from the SSM framework resulted in a “mechanistic smoothing” of the time series (Bolker 2008) when compared with naïve counts of ducks (Figure 3.5 and Figure 3.6). There was considerable annual variability, and a general trend for higher estimates towards the end of the time series in several species of ducks in both WEU and NA.

I found no correlations in annual population growth rates, indicating a lack of annual synchrony for species-pairs from WEU and NA (

Figure 3.7). Correlations ranged from -0.24 (95% CRI: -0.88, 0.40) in scaup-greater scaup to 0.14 (95% CRI: -0.78, 1.0) in the gadwall-gadwall comparison.

Looking next to shared long-term trends, I found correlations among state-space model estimated population sizes for teal, gadwall, shoveler and ring-necked duck-tufted duck species-pairs. I detected no correlation between transcontinental estimates for wigeon, northern pintail, pochard-redhead and scaup. Both AMO and NAO indices fluctuated annually, but they were not correlated ($r = -0.07$, $p = 0.69$) and only the AMO index increased from the beginning to the end of the study period, indicating a gradual increase in North Atlantic sea surface temperatures during the study period (Figure 3.8). Because my hypothesis for NAO as a synchronizing factor pertained only to annual growth rates, only AMO is considered as a candidate explanation for the shared time-trends outlined above. Results obtained below with AMO_{A-S} were qualitatively similar to AMO, and were not considered further.

Of the 4 species-pairs with correlated population sizes, each became progressively larger during the extended positive (warmer) phase of the AMO and the slope of the relationships were statistically indistinguishable between continents for gadwall, shoveler, and teal species-pairs. There was weak evidence that population response of the WEU tufted duck was less strongly related to AMO than ring-necked duck ($p=0.09$); although slopes for each species were positive (Table 3.2, Figure 3.9).

3.6 Discussion

Populations of ecologically similar duck species in Western Europe and North America fluctuated independently from year to year, with no indication that annual population growth

rates were correlated for any species-pair. I speculate that annual environmental conditions and other factors affecting annual changes in duck population sizes must be sufficiently different to prevent synchronization between continents. For instance, while both continents appear to have become warmer, and possibly wetter (see below), during the study period these changes were not necessarily synchronized on an annual basis and there was some tendency for opposite conditions to prevail, despite shared long-term trajectories.

Although annual cross-continental synchrony was absent, several species-pairs shared increasing trends in population size during the study period. The increasing AMO phase observed over the same period was correlated with the increasing trends of species-pairs and with increasing temperatures on both continents and increasing precipitation across most of the WEU study area and the prairie region of NA. These results corroborate other research associating AMO with warmer and wetter conditions, albeit occurring over different time frames and geographies (Sutton and Hodson 2005, Knight et al. 2006, Nigam et al. 2011). While spurious correlations in time series sharing trends are clearly possible, there are mechanisms whereby AMO-induced climatic trends could gradually influence duck habitats and populations on both continents.

Because annual growth rates did not directly follow anomalies of AMO, the hypothesized effects would have to occur gradually on habitats rather than immediately on duck survival and reproduction. Hafley et al. (2016) demonstrated that gradual changes in key resources can cause major changes in population size, but can go undetected in density-dependent growth models such as the Gompertz or Ricker models. I therefore posit that gradual cumulative changes to landscapes (anthropogenic or natural) may have resulted from AMO's sustained influence on climate, such as warmer temperatures, and more ponds and associated food resources that

improve duck reproductive success (Dzus and Clark 1998, Krapu et al. 2000) and, possibly, survival.

The mechanism of increased precipitation associated with AMO positively influencing duck populations is particularly plausible. Variation in wetland area and abundance are important factors driving duck populations (Drever et al. 2006, Walker et al 2013), and they are strongly influenced by patterns in precipitation over multi-year periods which affect net water storage (Ballard et al. 2014, LaBaugh et al 2018). While I did not detect clear increases in precipitation across the full NA study area, the prairie region, which has the highest density of breeding waterfowl (50-75% of those counted during the NA survey; U.S. Fish and Wildlife Service 2018), did show increased precipitation during the study period. This regional pattern is further corroborated by wetland counts recorded during the survey (U.S. Fish and Wildlife Service 2018) and other research finding increased precipitation over a similar area and time period (Shook and Pomeroy 2012). Unfortunately, because time series of wetland abundance are not available for the breeding areas of WEU ducks I am not able to make similar conclusions about the impacts of increased precipitation on wetland habitat there.

Regarding the increased mean temperatures observed on both continents, there is evidence that population trends of many avian communities in Europe and NA are positively affected by temperature trends (Stephens et al. 2016). Counts of some duck species I investigated were included in Stephens et al.'s (2016) temperature-avian trend analyses, but surveys they used were not explicitly designed to monitor duck populations and there was no overlap with my data sources. Importantly, the similar climate-duck count patterns produced here and by Stephens et al. are based on independent data sets, providing some corroboration of each.

I have focused on changing climate as a likely cause of shared temporal trends on each continent. Although harvest management has improved during the past several decades, I feel that this alone cannot account for the strong positive trends in several duck populations on both continents. Rather, in NA, harvest has been liberalized as populations have increased and duck harvest seems to track population sizes rather than depress them (Cooch et al. 2014).

Conservation efforts have intensified on both continents, but their extent is not commensurate with the increases in populations observed and wetlands continue to be drained and degraded. Indeed, in North America, agricultural intensification appears to depress many other avian populations which overlap geographically with the core breeding range of my study species (reviewed by Stanton et al. 2018).

Fluctuations in AMO could be leading to shared climate patterns on both continents discussed above and these changes might gradually improve the breeding habitat and productivity of ducks. However, it is also possible that the patterns in climate observed are caused by anthropogenic climate change or cycles in climate which are not fully characterized by AMO. Furthermore, despite these possible links between climate indices and population trends, the possibility exists of confounding climate effects with long-term land use change (Eglington and Pearce-Higgins 2012). During the past 30 years, changes in agricultural equipment and crops in WEU and NA have generally increased the availability and abundance of high-quality foods in winter, reducing food constraints amongst granivorous birds, especially several dabbling duck species. Conversely, differences in land use may help explain why some species-pairs did not share trends. Changes in fish farming in Europe may be responsible for the recent decline of several WEU diving ducks, in particular the common pochard (Fox et al. 2016), whereas their congener in NA, the redhead, is not dependent on these habitats. Similarly, the decline of

northern pintail in NA and not WEU seems to be due to the proclivity of NA populations to nest in cropland areas (rather than primarily boreal for WEU populations) where the nests are subsequently destroyed by seeding activity (Devries et al. 2018).

In conclusion, I have shown that populations of ecologically equivalent duck species on each continent fluctuate independently of each other on an annual basis, but that several shared increasing trends during my study period. I posited gradual changes in climate, possibly induced by AMO, as a plausible explanation. The link between AMO and the shared climate patterns on each continent need further investigation as do mechanisms by which changes in land use could also explain some portion of the trends in duck populations observed. To test hypothesized mechanisms (Ranta et al. 1995), it would be instructive to look for correlations in demographic rates for species-pairs on each continent; for example, using vulnerability-corrected age ratios obtained from wing samples donated by hunters and band-recovery analyses could give insights into respective changes in reproductive and survival rates (Arnold et al. 2017).

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3.8 Tables and Figures

Table 3.1. Characteristics of duck species representing eight pairs of ecological analogues in Western Europe and North America. Species are characterized by relative life-history pace (slow, intermediate, fast). Also shown are dominant foraging mode and diet, and migration distance between breeding and wintering areas. All life-history information were summarized from Baldassarre (2014).

Species-analogue	Species	Continent	Life-History	Foraging	Diet	Migration
1	Northern pintail (<i>Anas acuta</i>)	Europe	Intermediate	Dabbler	Granivore	Long
1	Northern pintail	North America	Intermediate	Dabbler	Granivore	Long
2	Common teal (<i>Anas crecca</i>)	Europe	Fast	Dabbler	Granivore	Long
2	American green-winged teal	North America	Fast	Dabbler	Granivore	Long
3	Northern shoveler (<i>Spatula clypeata</i>)	Europe	Fast	Dabbler	Invertivore	Short
3	Northern shoveler	North America	Fast	Dabbler	Invertivore	Short
4	Gadwall (<i>Mareca strepera</i>)	Europe	Inter	Dabbler	Herbivore	Short
4	Gadwall	North America	Inter	Dabbler	Herbivore	Short
5	Eurasian wigeon (<i>Mareca penelope</i>)	Europe	Intermediate	Dabbler	Herbivore	Long
5	American wigeon (<i>Mareca americana</i>)	North America	Intermediate	Dabbler	Herbivore	Short
6	Tufted duck (<i>Aythya fuligula</i>)	Europe	Intermediate	Diver	Mixed	Short

6	Ring-necked duck (<i>Aythya collaris</i>)	North America	Intermediate	Diver	Mixed	Short
7	Common pochard (<i>Aythya ferina</i>)	Europe	Intermediate	Diver	Herbivore	Short
7	Redhead (<i>Aythya americana</i>)	North America	Intermediate	Diver	Herbivore	Short
8	Greater Scaup (<i>Aythya marila</i>)	Europe	Slow	Diver	Invertivore	Long
8	Greater scaup	North America	Slow	Diver	Invertivore	Long

Table 3.2. Parameter estimates from linear models testing the association of species-pair population sizes with the AMO index (summarized as mean June [t-1] to May[t]). The reference continent is western Europe (WEU) and the interaction term AMO×Continent tests whether the effect of AMO in North America differed from WEU.

Species-pair	Term	Estimate	Standard Error	<i>p</i> value
Gadwall	AMO	4.14	0.61	<0.01
	AMO×Continent	-0.49	0.86	0.57
RNDU-TUDU	AMO	1.44	0.79	0.07
	AMO×Continent	1.94	1.12	0.09
Shoveler	AMO	3.22	0.68	<0.01
	AMO×Continent	0.57	0.96	0.55
Teal	AMO	3.95	0.62	<0.01
	AMO×Continent	-0.24	0.88	0.7

Figure 3.1. General breeding areas of the ducks included in the analysis.



Figure 3.2. Slope estimates and 95% CI for the linear regression model evaluating annual trend in temperature and precipitation from the CRU TS v4.02 dataset on each continental study area, 1971-2016. Slope for precipitation is estimated change in the sum of precipitation (mm) per year and temperature is °C per year.

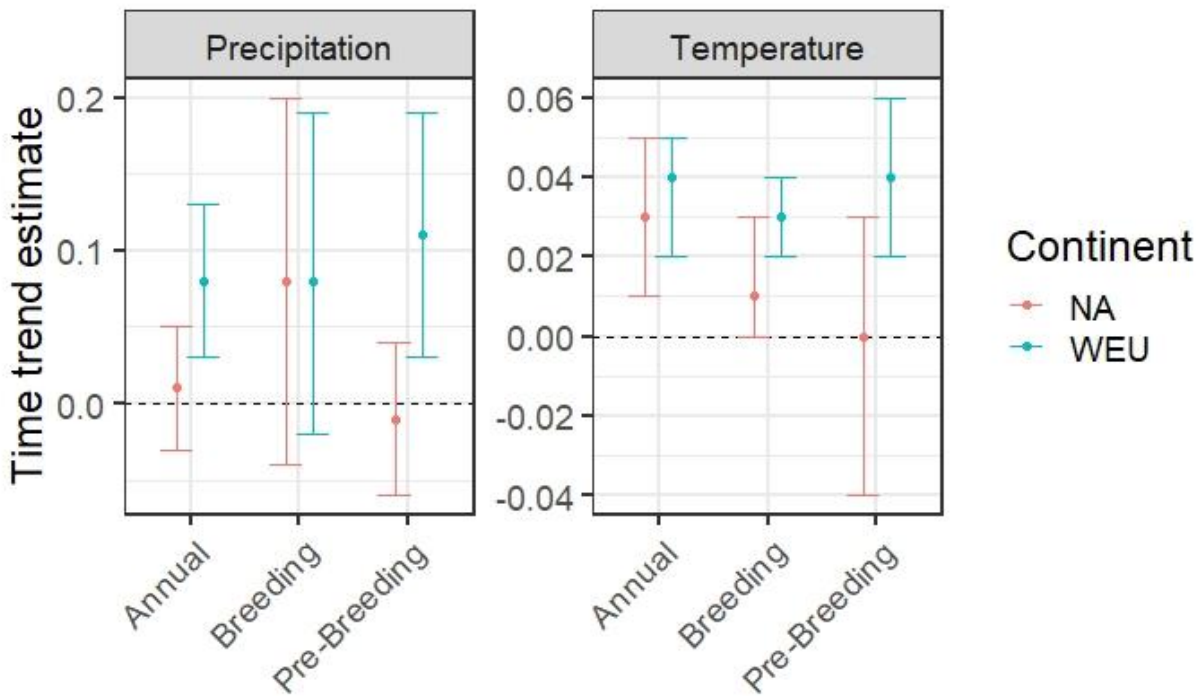


Figure 3.3. Spatial heterogeneity in the trend of total annual precipitation from the CRU TS v4.02 in the North American (a) and Western European (b) breeding areas, 1971-2016. Slope for precipitation is the estimated change in the sum of precipitation (mm) per year.

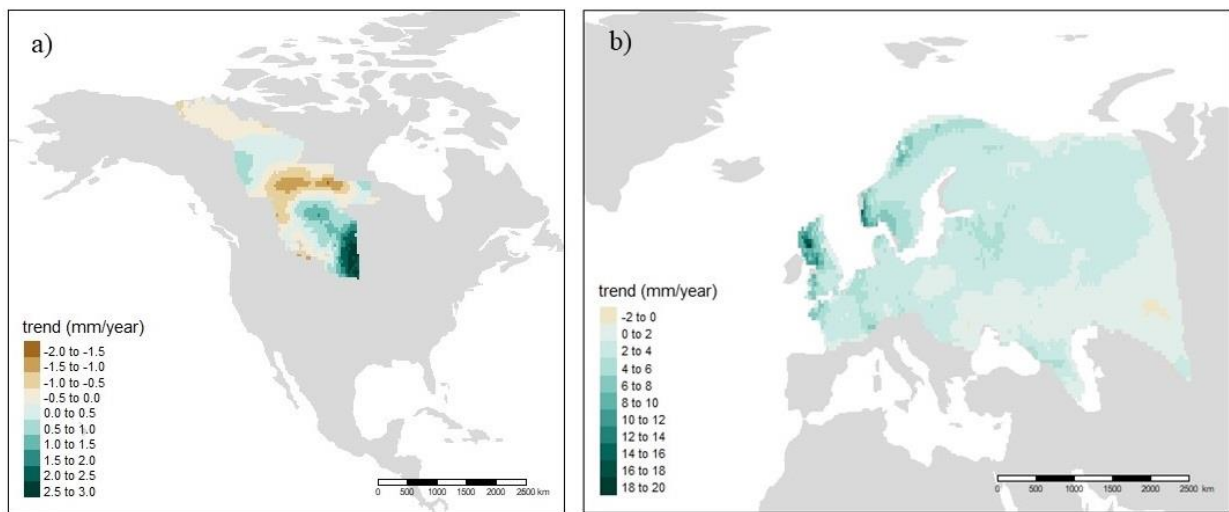


Figure 3.4. Correlation and 95% CI between continental study areas for detrended temperature and precipitation data from CRU TS v4.02 dataset, 1971-2016.

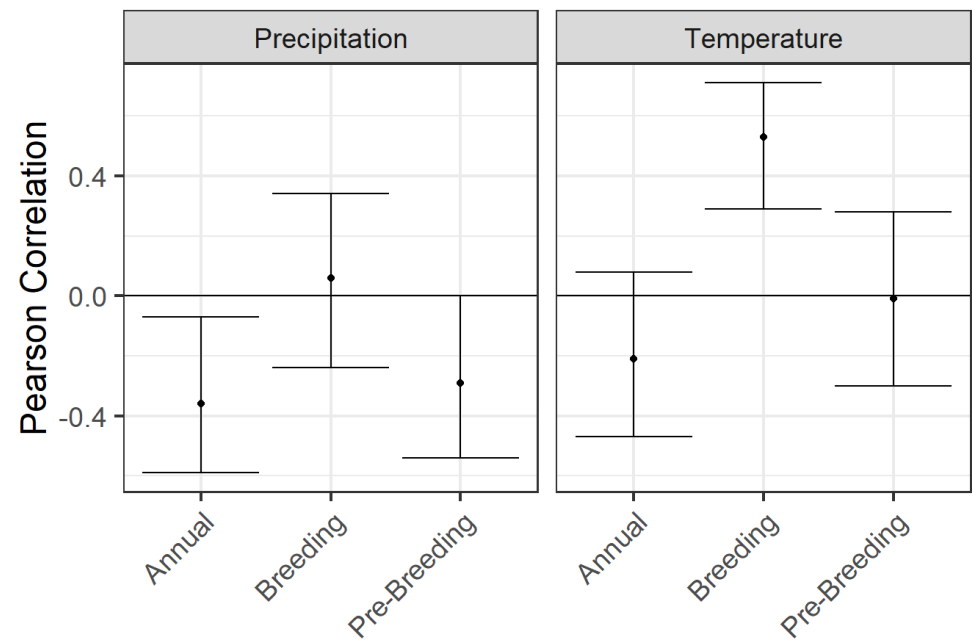


Figure 3.5. Annual counts (closed black circles; in thousands) of dabbling duck populations in Western Europe (WEU) and mid-continent North America (NA), 1976-2011, and state-space model population estimates (solid blue line) with 95% credible intervals (shaded). Species-pairs are composed of ecologically similar or equivalent species (Table 3.1). Note that the y-axis scales differ between species-pairs, and WEU and NA.

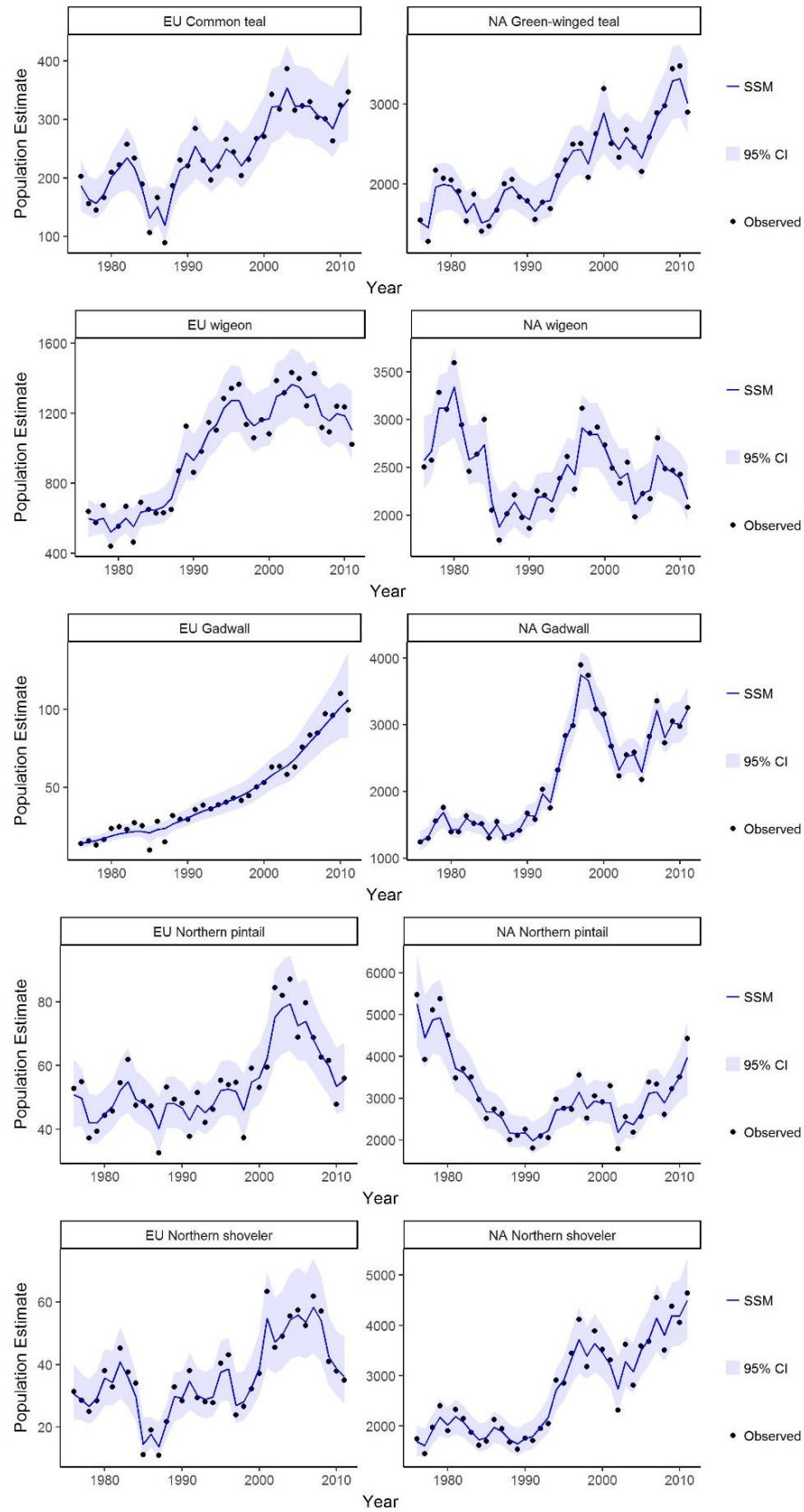


Figure 3.6. Annual counts (closed black circles; in thousands) of diving duck populations in Western Europe (WEU) and mid-continent North America (NA), 1976-2011, and state-space model population estimates (solid blue line) with 95% credible intervals (shaded). Species-pairs are composed of ecologically similar or equivalent species (Table 3.1). Note that the y-axis scales differ between species-pairs, and WEU and NA.

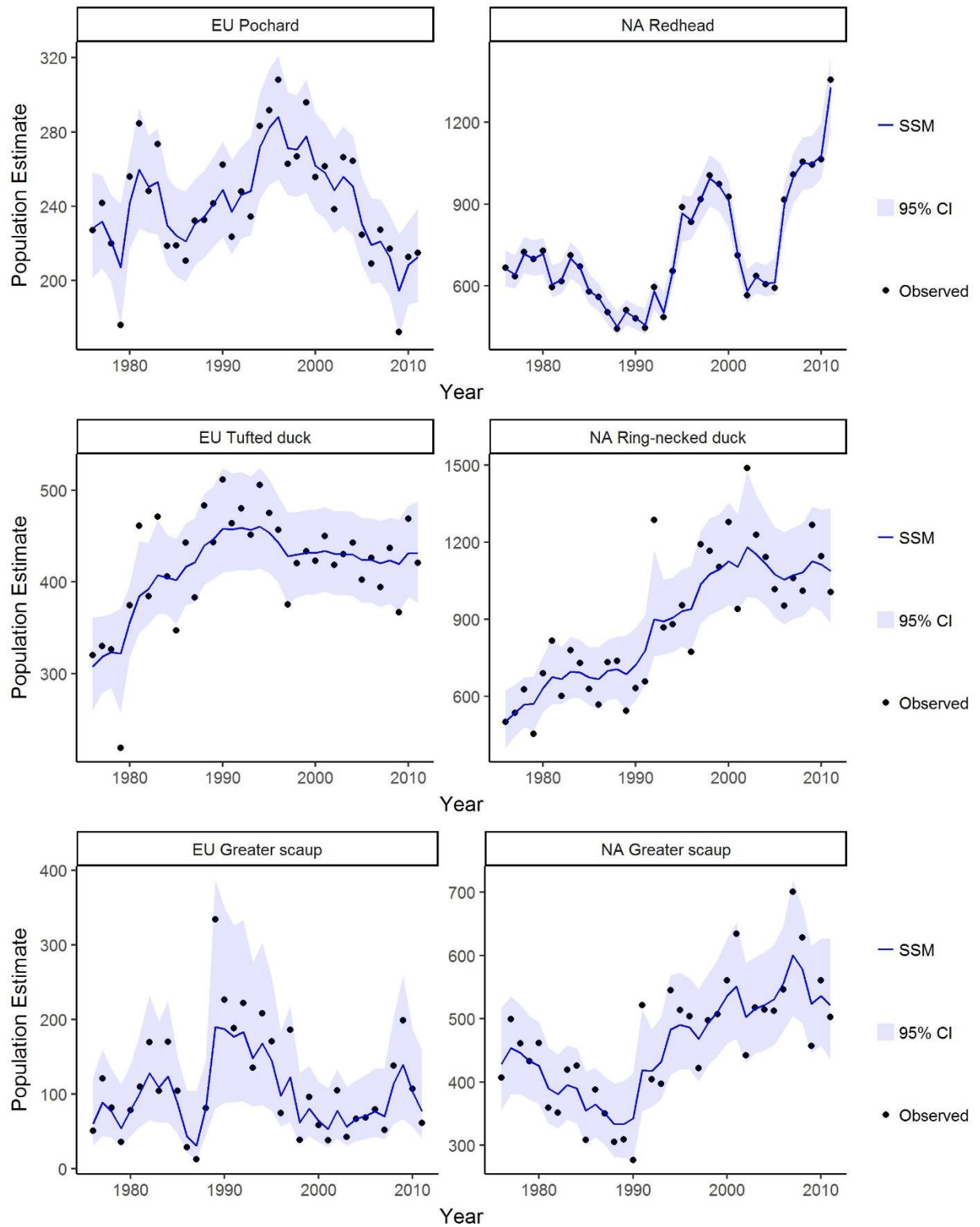


Figure 3.7. Estimates of annual duck population synchrony for eight species-analogues from Western Europe and North America. Shown are correlation estimates (\pm 95% credible intervals) for residuals of species-pairs Gompertz population models. REDH-POCH refers to Redhead/Pochard, and RNDU-TUDU refers to Ring-necked Duck/Tufted Duck species pairs.

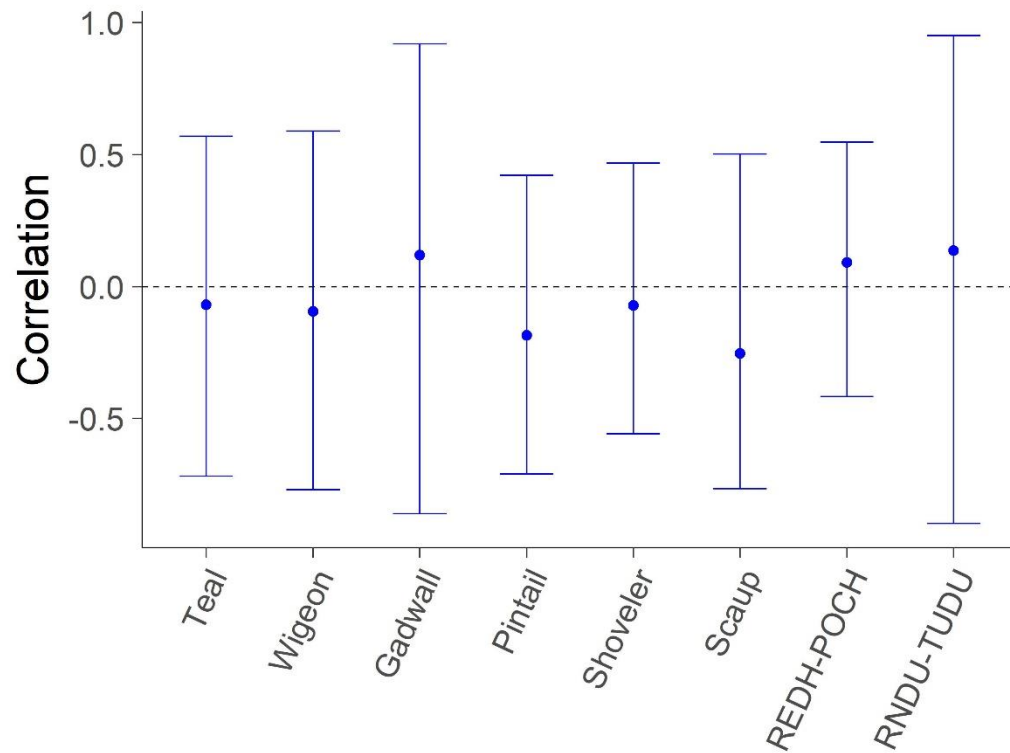


Figure 3.8. Time series of annual mean Atlantic Multidecadal Oscillation and North Atlantic Oscillation during my study period (bold lines 1976-2011) and a longer period 1950-2017 for context.

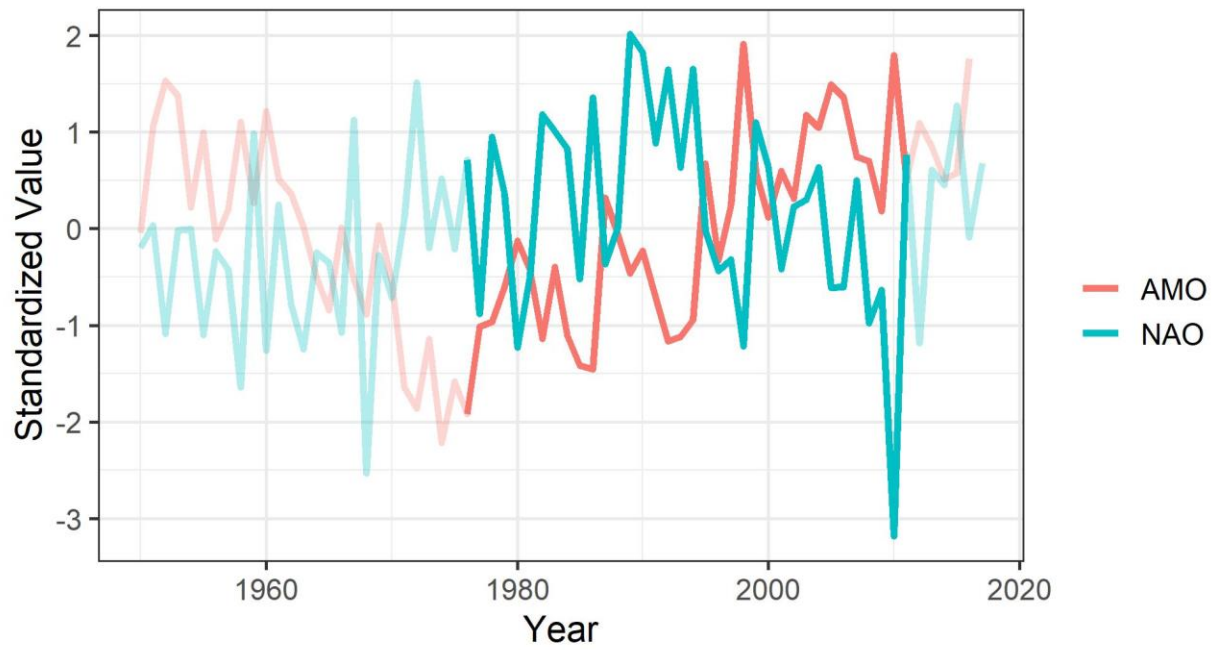
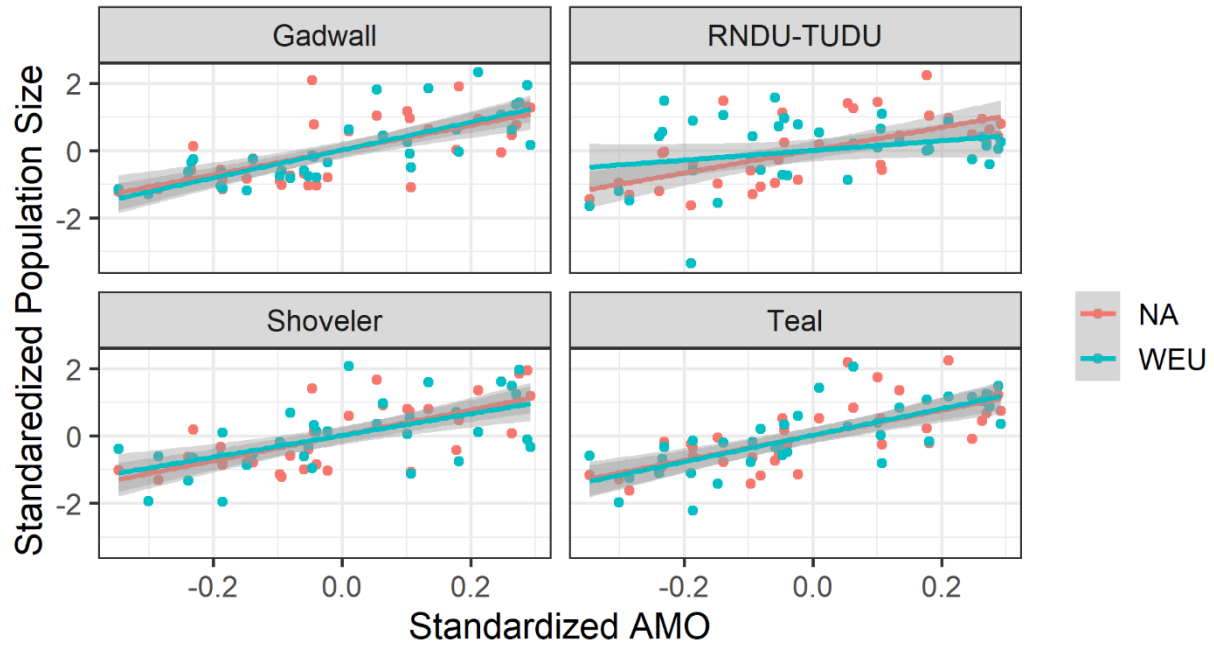


Figure 3.9. Patterns of association between standardized state-space model estimates of duck population sizes (y-axis, z-scores) in Western Europe and North America, 1976-2011, and Atlantic Multi-decadal Oscillation (AMO). RNDU-TUDU refers to Ring-necked Duck/Tufted Duck species pairs. Only RNDU-TUDU had possibly distinguishable differences in slopes as indicated by a continent \times AMO interaction ($p=0.09$). The shaded regions are the 95% confidence interval for the coefficients.



CHAPTER 4 : POSTFLEDGING SURVIVAL OF FEMALE LESSER SCAUP: EVALUATION OF CARRY-OVER EFFECTS FROM THE PREFLEDGING PERIOD

4.1 Abstract

Annual variability in the recruitment rate of juvenile females into breeding populations is an important component of duck population dynamics, yet little is known about the factors affecting the survival of ducks during the postfledging period (i.e., from fledging until they return to their breeding grounds the subsequent year). Two hypothesized mechanisms to explain annual variability are indirect ‘carry-over’ effects (COEs) from conditions experienced during the prefledging period and direct effects from prevailing weather conditions during the postfledging period. I used Cormack-Jolly-Seber apparent survival models to evaluate COEs from hatch date, hatch date \times spring phenology, and duckling density as well as direct effects of prevailing weather during migration and winter periods (indexed by the El Nino Southern Oscillation [ENSO]) on postfledging survival and detection rates of 643 female lesser scaup (*Aythya affinis*) captured and marked just prior to fledging at Red Rock Lakes National Wildlife Refuge in southwestern Montana, 2010-2018. In addition, I used growth data from a subset (n=190) of known-aged ducklings to evaluate the influence of hatch date and conspecific density on prefledging growth to help identify the mechanisms by which carry-over effects may operate. There was clear support for negative effects of conspecific density on prefledging growth rates, and suggestive evidence that these effects carried over to the postfledging period reducing apparent survival. There was also support for annually varying detection rates for juvenile (but not adult) scaup – likely representing decisions to delay breeding and not return to or remain at

the study site in their first year. As with apparent survival, there was suggestive evidence that a negative prefledging density COE was operating on this process. In contrast to previous research, there was not strong evidence that negative impacts of late-hatching carried over to influence survival or breeding probability. This is despite clear evidence that it influenced prefledging growth rates, albeit less so than density. The winter ENSO index was not strongly predictive of either vital rate, perhaps because of poor ability to characterize local conditions experienced by postfledging scaup. A large body of research indicates that the breeding season is almost universally important in the population dynamics of ducks. Beyond the production and survival of ducklings through this period, my data demonstrate a likely density-dependent pathway for prefledging conditions to carry over into subsequent life-history stages. If this pattern generalizes to other systems this COE may have important implications for our understanding of population dynamics and reaffirms the importance of breeding habitats in conservation planning for ducks.

4.2 Introduction

The recruitment rate of juvenile females into breeding populations is a critical component of population dynamics in most avian species, and this is particularly true for short-lived ones such as ducks (*Anatidae*; Koons et al. 2014). For ducks, survival in the first year of life typically is low and highly variable as juveniles learn to navigate a harsh and competitive environment. During the prefledging period (hatch to ~60 days), ducklings must procure the food resources needed to grow— a >15-fold increase in body mass (Lokemoen et al. 1990) — while simultaneously avoiding predators and coping with inclement weather, parasites, and diseases. Unsurprisingly, survival during this period can be very low and depend on environmental conditions (Mauser et al. 1994, Dawson and Clark 1996, Guyn and Clark 1999). Survival of

juveniles during the postfledging period, (fledging until the following breeding season) is higher, but still believed to be lower and fluctuate more than survival of adults during the same period. Unfortunately, the postfledging period is poorly understood in ducks, although this survival rate has important impacts on subsequent breeding population sizes.

Although limited, studies of the postfledging period in ducks have a) estimated survival rates (Regehr 2003), b) identified the proximate causes of mortality (Longcore et al. 1991), or in a few cases, c) attempted to identify correlates of annual variation in postfledging survival, such as the direct effects of winter weather (Gunnarsson et al. 2012) or ‘carry-over’ effects from the prefledging period (Dzus and Clark 1998, Anderson et al 2001, Blums et al. 2002). Indeed, there is a small but increasing body of evidence that events or experiences from early life-history stages can impact fitness in subsequent periods. These effects are termed carry-over effects (COEs) and may have an important role in population dynamics (Harrison et al. 2011, O’Connor et al. 2014). For example, timing of hatch and early-life environmental conditions have been documented to affect postfledging survival in some avian taxa (Brinkhof et al. 1997, Hepp and Kennamer 2012, Blomberg 2014), although evidence is mixed in ducks (Poysa et al. 2017). Below, I discuss pathways by which carry-over effects from hatch date and early-life environment may impact juvenile survival.

Hatch date is an important factor in prefledging survival across many bird taxa and in waterfowl the benefits of early-hatching seem to carry-over to the postfledging period as well (Dzus and Clark 1998, Dawson and Clark 2000). In ducks, offspring of early-laying females (i.e., early relative to conspecifics) are generally more likely to survive their first-year and return to the breeding area (Dzus and Clark 1998, Dawson and Clark 2000, LePage et al. 2000, Anderson et al. 2001, Blums et al. 2002, Clark et al. 2014). Whether this is a result of parental

quality (high quality parents breed earliest), competition from conspecifics, or seasonal deterioration of environmental quality is unclear (but see Brinkhof et al. 1997, Harriman et al. 2017). A closely related question is whether annual variability in environmental phenology mediates this relationship. For example, do early-hatched ducklings recruit at a higher rate in years with earlier spring phenology? This question has come under increasing scrutiny in the context of climate change, with the possibility for trophic mismatches (Dunn and Winkler 2010). While some bird species seem to be flexible in nest initiation dates and have advanced egg-laying in response to warming spring climates (Dunn and Møller 2014), others seem to have less flexibility or experience a de-coupling of phenological cues along their migration paths. This can lead to a mismatch between hatching of young and peak food availability or favourable weather, particularly for long-distance migrants (Both et al. 2010, Visser et al. 2012). Therefore, evaluation of hatch date COEs should also include tests for interactions with seasonal phenology.

In addition to hatch date COEs, there is potential for density related COEs in ducks. Many individuals occupying the same foraging niche can result in competition for resources resulting in the need for longer foraging bouts and slower growth (Pehrsson and Nystrom 1988, Blums et al. 2002, Gunnarsson et al. 2006). Indeed, density dependence in annual population growth rates are of substantial interest to waterfowl managers (Gunnarsson et al. 2013, Osnas et al. 2014) and identifying the mechanisms of density-dependent population regulation is an important topic in waterfowl ecology (Koons et al. 2014). At the population level, density-dependent recruitment is apparent in ducks (Kaminski and Gluesing 1987), although the period of the life cycle where it operates is poorly understood.

Finally, there is the potential for direct effects of environmental conditions on postfledging survival via thermoregulatory demands and food availability. A number of studies

have quantified the variation in non-breeding season survival of juvenile ducks (Hohman et al. 1995, Haramis et al. 1986), but fewer have evaluated the environmental correlates of variation across years (but see Bergan and Smith 1993, Blums et al. 2002). It is not trivial to quantify the conditions experienced by highly mobile and widely distributed migratory birds, but large-scale climatic indices can provide some context as to prevailing weather faced on wintering and migration areas and thereby provide some potential to evaluate within-season effects of weather (Stenseth et al. 2003, Gunnarsson et al. 2012). The El Nino-Southern Oscillation (ENSO) is one such index, related to large-scale ocean-atmosphere interactions, which have impacts on weather patterns over a substantial portion of the scaup wintering range. During positive phases of the winter ENSO, wetter-than-average conditions are typical across much of the southern USA and Gulf of Mexico region and warmer-than-average temperatures are common across western and central Canada and the USA (Ropelewski and Halpert 1986, Wang et al. 1999, Smith and Sardeshmukh 2000). These conditions could positively influence habitat conditions for ducks during both migration and wintering periods.

Here, I evaluate the relative role of the direct and carry-over effects on postfledging apparent survival of female lesser scaup ducklings (*Aythya affinis*) captured and marked in late summer just prior to fledging at Red Rock Lakes National Wildlife Refuge in southwestern Montana, USA. I hypothesized that COEs would likely operate through reduced growth during the prefledging period, so I also evaluated direct effects of these variables on prefledging growth in a subsample of ducklings for which I had prefledging growth data. Lesser scaup are the most abundant diving duck (genus *Aythya*) in North America with core breeding abundance in the western boreal forest, but also breeding throughout the prairie pothole region, and the intermountain west. While the study site lies near the southern extent of lesser scaup range, due

to its elevation the climate and seasonal phenology are similar to more northern regions where most scaup breed (Gurney et al. 2011).

While my primary focus is survival, the factors discussed above may have sub-lethal effects which could be manifested in first-year breeding propensity. Juvenile scaup will sometimes forgo breeding their first year if environmental conditions are unfavourable (Afton 1984). If they delay breeding and do not return to or remain at the study area their first year, this would result in reduced detection probability. Because adults rarely forgo breeding (Afton 1984), differences in detection probability between juvenile and adult age classes (where a methodological explanation is unlikely) implies the detection parameter contains information on breeding probability. Several researchers have recognized this and used variation in detection probability as an index to breeding probability (Lebreton et al. 1990, Clobert et al. 1994, Anderson et al. 2001, Arnold et al. 2002). I therefore evaluated alternative models where first-year detection probability is a function of some of these same factors as I considered for survival. Specifically, my research questions were:

- 1) Does hatch date relative to conspecifics influence prefledging growth and postfledging survival or breeding probability? Is this relationship mediated by timing of spring? I predicted that earlier hatched ducklings will have greater prefledging growth and higher postfledging survival or breeding probability because the highest quality parents breed earliest and because these older ducklings will have competitive advantages to conspecifics and possibly go into fall migration having had more time to grow and accumulate fat reserves. I hypothesized that positive effects of hatching early may be moderated by later spring phenology, and vice versa – a positive interaction.

- 2) Does conspecific density influence prefledging growth and postfledging survival or breeding probability? I predicted a negative COE of density, because competition for limited food resources may impact growth during the prefledging period.
- 3) Do winter weather conditions have an impact on postfledging survival or breeding probability? I predicted an index of winter weather conditions, the El Nino Southern Oscillation (ENSO), would be positively related to postfledging survival because generally wetter conditions across winter and migration areas could lead to improved wetland habitat conditions which favor higher survival and better body condition increasing likelihood of first-year breeding.

4.3 Study site

Work was conducted on Lower Red Rock Lake in southwest Montana, USA (44.59° N, 111.80° W) at an elevation of 2014 m (Figure 4.1). The lake is approximately 2,300 ha (depending on water-level) and protected as part of Red Rock Lakes National Wildlife Refuge. The lake is composed of 2 core habitat types; about half of the lake's area is open water (<1.5m deep) interspersed with hardstem bulrush (*Schoenoplectus acutus*) islands, and the remainder is seasonally flooded Northwest Territory sedge (*Carex utriculata*) that contains a scattering of small (<2 ha) open water areas. Average annual precipitation is 49.5 cm with 27% occurring during May and June. Annual average temperature is 1.7°C. Despite a harsh climate for its latitude, the study area supports a high density of breeding Lesser Scaup (i.e., >7.7 breeding pairs km²; J. Warren, USFWS personal communication).

4.4 Methods

4.4.1 Field Methods

Postfledging survival

Scaup were captured via drive-trapping during the 3rd week of August and the 2nd week of September, 2010–2018. Females were banded with a U.S. Geological Survey (USGS) aluminum leg band and fitted with a unique nasal marker (juveniles with a head length ≥ 70 mm and adults). Nasal markers were nylon pieces attached through the nares using 1.6 mm 316L stainless steel welding wire and stainless steel washers (Lokemoen and Sharp 1985); a small (ca. 3 mm diameter) piece of epoxy (WaterWeld, J-B Weld Co., Sulphur Springs, TX) was put on the distal crimped ends of the steel wire to reduce marker loss. Although my analysis was focused on juvenile females, I also included adult females fitted with nasal-markers to increase sample size (and hence precision) for estimating detection probability. Adults were captured and marked during August and September drive-trapping sessions, as well as via spotlighting in May and June. Adults captured in May and June would have a ~3.5 month longer mortality risk than adults marked in August adult, however because the emphasis of this study is juvenile survival and adults are included only to help with estimation of annual detection rates, I did not attempt to separately estimate survival for adults with different exposure periods.

Pre- and post-breeding season (May and late August/early September, respectively) resight surveys were conducted each year for marked female lesser scaup beginning May 2010. The study area was divided into 16 survey blocks of approximately equivalent open water area. Each block comprised 1 to 4 750m x 750m plots that were visited twice during a resight survey session. Each visit to a survey block was 4 hours long, beginning at sunrise for morning visits and 4 hours prior to sunset for evening visits. If a block was visited in the morning during the

first visit, it was visited in the evening on the second visit, and vice versa. Visit order was randomly established during the initial resight survey, and that order was maintained for subsequent surveys. In addition to resightings of nasal-marked females, nasal-marked adults were occasionally recaptured during night-lighting and drive-trapping.

Prefledging growth

As part of a separate study, ducklings were web-tagged at hatch in a sample of scaup nests within the study area (Stetter 2014). Some of these ducklings were subsequently recaptured during drive-trapping sessions ($n = 8, 1, 23, 73, 37, 26$, and 23 for 2010-2018, respectively), providing information on growth rates. Sex was determined via cloacal examination and mass (± 5 g), head length (± 0.1 mm), and tarsus length (± 0.1 mm) recorded.

4.4.2 Covariates

Hatch date

To enable estimates of hatch date for all ducklings, first I estimated duckling age at capture during drive-trapping as a function of sex, morphometrics, capture date, and cohort (i.e., year) based on relationships estimated from a sample of known-age ducklings ($n = 191$). To estimate the relationship with age, I ran all subsets regression of the model:

$$age_{i,j} = cohort_j + mass_{i,j} + mass_{i,j}^2 + head_{i,j} + head_{i,j}^2 + sex_{i,j} + encounter\ date_{i,j} \\ + mass_{i,j} \times encounter\ date_{i,j} + \varepsilon_{i,j}$$

$$\varepsilon_{i,j} = N(0, \sigma^2)$$

The best ranking models (those with Akaike's information criterion corrected for sample size (AIC_c) within 4 of the best approximating model) included terms for cohort, sex, mass, capture

date, the interaction of mass and capture date, and a quadratic effect of head length; the model-averaged $R^2 = 0.93$. The remaining 7% of unexplained variance likely reflects measurement error and individual heterogeneity. I calculated model-averaged predictions of age for each unknown-aged duckling captured during drive-trapping and marked with a nasal-marker, and then derived hatch date by back-calculation from known or estimated age. For the 2011 cohort, for which there were too little data to reliably estimate a year-specific intercept, I simply predicted age from models without the cohort effect. I then standardized hatch dates within years such that the hatch date variable was relative to the cohort rather than the absolute date of hatch.

Spring phenology

Satellite-derived normalized difference vegetation index (NDVI) has seen broad use in ecology since the 2000s (e.g., Pettorelli et al. 2011). The index is derived from near-infrared (NIR) and red wavelengths reflected from earth surfaces, computed as $(\text{NIR} - \text{Red}) / (\text{NIR} + \text{Red})$. NDVI provides an index of “greenness” that is sensitive to photosynthetic canopy and ground cover. I used 16-day composite, 500m resolution Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI dataset (MOD13A1; accessed at https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod13a1, January 31, 2018) summarized as a single average value within a hand-drawn polygon around the study area. The polygon was drawn to include the valley floor that the lake and surrounding sedge meadow and grasslands occupy, but excluding sandhills to the north and foothills and mountain range to the south. I modeled the seasonal NDVI curve for the study area using a double logistic function in program TIMESAT 3.1.1 (Jönsson and Eklundh 2004), such that phenology variables could be

extracted at 1-day resolution. From these modeled NDVI curves I derived the season start date, the date when modeled NDVI reaches 25% of that year's maximum amplitude.

Water level and foraging habitat availability

A capacitance probe water level and temperature data logger (model WT-HR 1500; TruTrac, Christchurch, New Zealand) were deployed each year in April at the western outflow of Lower Lake. Water levels (± 0.1 mm) and temperatures ($\pm 0.1^\circ\text{C}$) were recorded hourly throughout the breeding season. I summarized mean water levels for the month of August, which roughly corresponds to the early-to-mid brood-rearing period for scaup.

Area available as foraging habitat varies non-linearly with water levels due to the irregular topography of the lake bottom. I created an elevation map of the lake bottom using water depths measured across a systematic grid as part of a separate vegetation monitoring program (Jeffrey M. Warren, U.S. Fish and Wildlife Service, unpublished data). I subtracted these depth measurements from concurrent lake-level to estimate elevation and interpolated between stations with inverse distance weighting to produce a continuous surface of lake bottom elevation (similar to O'Neil et al. 2014). For each year of the study I calculated the area of the lake with depths suitable for duckling foraging. I considered 2 minimum depth thresholds, 0.35m and 0.5m, based on previous research of habitat selection on the lake (Austin et al. 2017) and other locations (Fast et al. 2004). Because lake depth does not exceed 1.5m in an average year and submerged vegetation may reduce the effective depth, I did consider an upper threshold for suitability.

Duckling density

I estimated population of size (\hat{N}) of lesser scaup ducklings in mid-August by parsing the 5-day August drive-trapping session into 5 separate sampling periods and fitting closed capture population models (Otis et al. 1978). For each year, I fit 4 models for closed populations in program MARK version 8.2 (White and Burnham 1999), which variously allowed constant and time-varying detection probability, first-capture probability, and individual heterogeneity in detection probability). I model-averaged the estimates of \hat{N} from each model weighted by their level of support (AIC_c). No August drive-trapping occurred in 2016 so I interpolated this value based on the linear relationship between August and September \hat{N} estimates ($R^2 = 0.68$). Because foraging area available in the lake varies with water level, I also adjusted the duckling abundance estimate by dividing it by the area of the lake which provided suitable habitat for ducklings (discussed above).

El Nino Southern Oscillation (ENSO)

I acquired the bivariate ENSO time series data produced using the method of Smith and Sardeshmukh (2000; <https://www.esrl.noaa.gov/psd/data/correlation/censo.data>, accessed Jan 31, 2018). I averaged values for the non-breeding season months of October to April in each year of the study and used these as a large-scale index to prevailing migration and wintering weather conditions.

4.4.3 Data analysis

Prefledging growth

I evaluated models for prefledging growth using mixed-effects implantation of the Gompertz growth model fit using the package lme4 (Bates et al. 2015) in Program R (R Version 3.5.1, www.R-project.org, 2 Jul 2018). To estimate the effect of the hypothesized covariates

duckling density and cohort-relative hatch date I fit the Gompertz regression model to growth data from 190 ducklings captured >1 time after web-tagging at nest:

$$\log (mass)_{i,t} = \alpha + ID_i + \log (mass)_{i,t-1} + age_{i,t} + age_{i,t}^2 + sex_{i,t} + hatch\ date_{i,t} + duckling\ density_{i,t} + \varepsilon_{i,t}$$

$$ID_i = N(0, \sigma^2)$$

$$\varepsilon_{i,t} = N(0, \sigma^2)$$

Where ID_i is a random intercept adjustment for each individual. Although Gompertz models are often used to fit regularly collected duckling growth data (Lightbody and Ankney 1984, Blais et al. 2001), the sparseness and irregular intervals between duckling measurements in my data (74% were only caught 1 time after web-tagging at nest) necessitated including a quadratic age term to inform the model of the amount of time passed between measurements and eliminate patterns in the residuals. I estimated both covariates of interest in the same model and interpret the estimate and 95% confidence intervals as evidence for the effects on prefledging growth. Results were similar using measurements of mass or tarsus as a proxy to growth, so I present only the mass models.

Postfledging survival

I completed survival analysis using Cormack-Jolly-Seber (CJS) models fit in Program MARK version 8.2 (White and Burnham 1999) through Program R via the interface package RMark Version 2.2.5 (Laake 2013). All covariates were z-scored (mean = 0, SD = 1) prior to analysis to aid in estimation and interpretation. Between 2010–2018, 643 nasal-marked juvenile birds were released, of which 107 were re-encountered alive in a subsequent session (some over

multiple years, for a total of 241 re-encounters in unique sessions) and 61 were reported shot by hunters. Although pre- and post-breeding resight sessions were ~3 months apart I combined these into a single encounter period because there were too few observations each year (mean = 14, range = 6-24) to separately estimate survival for the September-May and Sept-Aug periods and further, most (77%) juveniles were re-encountered in the pre-breeding session (or in both sessions). Additional information came from voluntary reporting of the location and date of birds shot and recovered by hunters via contact information on metal tarsal bands to the USGS banding laboratory, primarily during September to February. While hunter recoveries can provide information about site fidelity, most (53 of 61) occurred in the first winter before scaup had an opportunity to either return to the site or emigrate elsewhere, and of the remaining 8 harvested after the first winter, only 3 had not been previously resighted on the study site. Therefore, hunter recoveries provided too little information to consider fitting models with a parameter for fidelity. Due to this limitation, permanent emigration and mortality are confounded and survival estimates reflect 'local' or 'apparent' survival.

Because juvenile scaup may delay breeding and hence not return to or remain on the breeding area as yearlings (Afton 1984, Martin et al. 2009), I evaluated models that allowed for lower detection probability in their first year of life. I also tested biological mechanisms that could be correlated with postfledging detection probability; 1) current habitat conditions (indexed by May water levels) because ducks may forgo breeding when water conditions are poor (Afton 1984, Anderson et al. 2001) and 2) via carry-over effects from prefledging (hatch date, duckling density in the previous year) and winter weather conditions indexed by the ENSO index. To aid in estimation of year-specific detection probabilities I included female scaup that were nasal-marked as adults as part of a separate study (n = 609). While not providing direct

information on postfledging survival, adult data increased precision of detection probability estimates which can result in more precise estimates of juvenile survival.

4.4.4 Model fitting

I tested goodness-of-fit on a model with full time-varying apparent survival (ϕ) and detection (p) probabilities for the juvenile and adult groups; $\phi(\text{Juvenile} \times \text{Year} + \text{Adult} \times \text{Year})$ $p(\text{Juvenile} \times \text{Year} + \text{Adult} \times \text{Year})$. I used the median \hat{c} procedure implemented in program MARK, where median $\hat{c} \sim 1$ reflects good model fit (Cooch and White 2011), and values substantially >1 require an adjustment of AIC_c values used for model ranking (Burnham and Anderson 2002). The above model had a median $\hat{c} = 1.09 \pm 0.01$ SE, therefore I did not adjust AIC_c values from subsequent models.

I first evaluated the detection portion of the model. I fit simplified versions of the full time- and age-varying (2 ages: juvenile and adult) detection probability (p) model above, including models where juvenile p varied with a covariate (Table 4.1). I fit each of these detection models with the following survival models; i) age-varying (juvenile and adult), ii) time-varying with a constant offset for the adult group, and iii) full time- and age-varying, to ensure similar detection models would be selected regardless of the survival model. I retained the detection model(s) within 2 AIC_c of the best fitting model, which were not simply hierarchically more complex versions of a model with an added uninformative parameter (Arnold et al. 2010), to be used in the subsequent fitting of the apparent survival portion of the model representing the biological hypotheses of interest (Table 4.2). Although adult survival was not of interest in this study, I fit models with both constant and time-varying adult survival to allow for the most accurate estimates of detection probability which could influence juvenile survival rates.

4.5 Results

4.5.1 Observed range of covariates

There was substantial variation in the covariates recorded during the study period. The date of 25% seasonal amplitude of the NDVI curve ranged from March 12 in 2015 to May 17 in 2011 (mean = April 20, SD = 20 days). August water levels ranged from 2013.6 m above mean sea level in 2013 to 2014.2 m in 2011 (mean=2013.8, SD= 0.2). This 0.6 m difference between the highest and lowest August water levels represents an approximate halving of mean water depth in the lake which was accompanied by the estimated proportion of the lake >0.5m decreasing from 100% to 7%. The index of duckling density (i.e., \hat{N} / area of lake >0.5m deep) varied from as few as 0.3 ducklings/ha in 2011 to 11/ha in 2013 (mean = 4.1, SD = 5.4). Winter ENSO varied from -2.1 in 2011 to 1.6 in 2015 (mean=-0.1, SD=1.1); these minimum and maximum values are nearly the same in the full 1948-2018 time series from which I acquired the data, indicating the study period captured substantial winter ENSO variation.

4.5.2 Prefledging growth rates

Consistent with predictions there was a clear negative effect of hatch date on growth rate of prefledging ducklings during the study period (standardized coefficient used here and throughout; $\beta_{\text{Hatch Date}} = -0.08$, 95% CI: -0.11, -0.05), although this did not appear to be mediated by an interaction with spring phenology ($\beta_{\text{Hatch Date} \times \text{NDVI SOS}} = -0.03$, 95% CI: -0.07, 0.01). There was a similarly predicted negative effect of conspecific duckling density on growth, although support for the effect depended on how density was measured; the effect was strongest when the August duckling population estimate was divided by the estimated area of the lake >35cm deep ($\beta_{\text{Density 35cm}} = -0.12$, 95% CI: -0.16, -0.08), similar when unadjusted for area ($\beta_{\text{Density}} = -0.10$,

95% CI: -0.14, -0.06), and weakest when adjusted for area of the lake >50cm ($\beta_{\text{Density } 50\text{cm}} = -0.03$, 95% CI: -0.06, 0.01).

4.5.3 Postfledging breeding probability and survival

The best approximating detection model allowed for juvenile detection probability (p) to differ each year with constant adult p . Allowing juvenile p to vary with covariates (i.e., May water levels, winter ENSO, lag-1 duckling density, hatch date relative to cohort) rather than being estimated separately for each year reduced AIC_c substantially (Table 4.3), however there was some suggestive evidence for some covariate effects despite their imprecise estimates (Figure 4.2). As predicted, there was an estimated negative effect of duckling density on p , although, as with prefledging growth, the support depended on the way in which density was measured. The effect of unadjusted \hat{N} ($\beta_{\text{Density}} = -0.66$, 95% CI: -1.41, 0.10) and $\hat{N} / \text{area} > 35\text{cm}$ ($\beta_{\text{Density } 35\text{cm}} = -0.73$, 95% CI: -1.70, 0.24) had the most support, whereas $\hat{N} / \text{area} > 50\text{cm}$ had very little ($\Delta\text{AIC}_c = 3.7$ from the best density model). My index of spring habitat conditions, May water level, had an estimated positive effect on p as predicted ($\beta_{\text{May}} = 0.29$, 95% CI: -0.18, 0.76), as did winter ENSO, although both of these variables had comparatively little support (Table 4.3). Hatch date had an estimated negative effect as predicted ($\beta_{\text{Hatch date}} = -0.26$, 95% CI: -0.67, 0.14), however, this model also received little support compared to the density models.

Overall, while I used several age and time-varying ϕ models in the assessment of the detection structure, there appeared to be relatively little support for time variation in ϕ with the best supported time-varying model $\Delta\text{AIC}_c = 7.96$ from the best approximating model in the set. In the next modeling step I used the best supported detection probability structure $p(\text{Juv} \times t + \text{Adult})$, and evaluated ϕ models with time-varying environmental and individual-level covariates.

There was evidence for a negative effect of duckling density on postfledging survival and, as with juvenile detection probability and prefledging growth, the strength of evidence varied with the way in which density was measured (Table 4.4, Figure 4.3). The variable which had the strongest support and whose model resulted in a decrease in AIC_c over the simple age-varying model (Table 4.4) was duckling density measured as \hat{N} / estimated area of the lake >50cm ($\beta_{\text{Density } 50\text{cm}} = -0.29$, 95% CI: -0.59, 0.01; Figure 4.4). Surprisingly, this measure of density was the least supported in previous analyses. The most supported variable from prefledging growth analysis, \hat{N} / area >35cm, had an estimated negative effect on postfledging survival although its estimate was lower and less precise (Figure 4.3). Similar to the detection probability models, I did not detect a hatch date effect substantially different from 0 (Figure 4.3), and the estimated winter ENSO effect was in the opposite direction than I predicted.

4.6 Discussion

Although it is rarely quantified, juvenile female survival is frequently a critical parameter in avian population dynamics. For lesser scaup, it appears to have been particularly important during a period of major population decline, yet the causes of these fluctuations remain unexplained (Koons et al. 2017). The primary hypotheses for variation in juvenile (postfledging) survival relate to direct effects of weather, predators, or habitat conditions, including availability of food (Longcore et al. 1991, Fleskes et al. 2007, Guillemain et al. 2010, Gunnarson et al. 2012) and carry-over effects (COEs) from the prefledging period (Anderson et al. 2001, Blums et al. 2002, Blomberg et al. 2014). I evaluated support for several hypotheses to explain variation in postfledging apparent survival and breeding probability (indexed via detection probability) in juvenile female lesser scaup, specifically COEs of hatch date and conspecific density during the prefledging period, and the direct effect winter weather conditions (indexed via ENSO).

There was clear support for negative effects of conspecific density on prefledging growth rates, and suggestive evidence that these effects carried over to the postfledging period reducing both survival and breeding probability. These results are consistent with the hypothesis that high competition or poor environmental conditions in early-life can result in reduced growth prior to fledging (Cox et al. 1998) and lower postfledging survival or breeding propensity. Although they did not obtain data on prefledging growth, Blums et al. (2002) also documented negative COEs of duckling density and recruitment in several species of ducks, including the closely related tufted duck (*Aythya fuligula*). Within the Anatidae family, research in black brant geese has shown a similar pathway to density COEs as documented here. Density of goslings on brood-rearing areas were negatively related to gosling growth and body condition, which subsequently lead to reduced survival during the postfledging period (Sedinger et al. 1998, Sedinger and Chelgren 2007). Sedinger and Alisauskus (2014) pointed out that a similar mechanism operating in duck populations could help explain why large-scale predator removal treatments have increased nest success (and hence duckling densities), but not local population sizes in subsequent years (Pieron and Rowher 2010, Amundson et al. 2013).

There was clear support for annual variation in juvenile detection probabilities, whereas adult detection rates appeared relatively constant and on average higher than juvenile's (average $p_{\text{juvenile}}=0.50$, 95% CI: 0.39, 0.61, $p_{\text{adult}}=0.61$ 95% CI: 0.54, 0.67). I cautiously interpret this as evidence for annually varying breeding probability because there is no obvious methodological reason why observers would have higher success locating and reading nasal markers of adult females. Further, variation in juvenile breeding probability has previously been documented in lesser scaup (Afton et al. 1984) and is common in other *Aythya* species (Johnson and Grier 1988, Anderson et al. 2001, Arnold et al. 2002). This variation has been linked to spring habitat

conditions (particularly wetland inundation) on the breeding grounds (Afton 1984, Anderson et al. 2001) and COEs from hatch date (Anderson et al 2001), however my index of spring conditions, May lake level, had little power to explain variation at the study site, and similarly, there was little support for a hatch date effect. The strongest candidate explanation seemed to be a density COE using the same measurement of density that was most strongly supported for impacts on prefledging growth (\hat{N} /area of lake >35cm deep).

The lack of hatch date COEs in my study was surprising. Prefledging growth analysis showed a clear negative effect of hatch date on growth rate and late hatch dates have been linked to reduced recruitment in ducks several times (Anderson et al. 2001, Blums et al. 2002, Clark et al. 2014). Similarly, prefledging duckling survival has been documented to decrease with hatch date at my study site (Stetter et al. 2014) and many others (Rotella and Ratti 1992, Dzus and Clark 1998, Krapu et al. 2000). A possible source of bias is that we did not place nasal-markers on scaup with head-to-bill measurements <70 mm, thereby excluding some birds from my sample that either had a very slow growth rate, or else hatched relatively late. Another interpretation is that because the hatch date effect on prefledging growth was ~33% smaller than the that of conspecific density, I simply did not have the power to detect its COE. This could have been exacerbated by having to estimate hatch dates for most birds in the postfledging analysis, whereas the prefledging analysis used only known-aged ducklings. Otherwise, it is possible that late-hatched birds were able to overcome this early-life disadvantage despite the relatively early onset of fall and winter-like conditions in my high-elevation study site.

Finally, there was little evidence for direct effects of the index of winter weather (winter ENSO) on postfledging survival or breeding probability. While weather conditions produced by the North Atlantic Oscillation and large-scale oceanic regimes in the north Pacific appear to

influence sea duck populations (Jónsson et al. 2009, Flint 2013), it may be that these indices are simply more informative of conditions experienced by those populations than ENSO is for widely distributed wintering lesser scaup. For instance, other studies have found locally measured conditions more informative of survival than large-scale climate indices (Szostek and Becker 2015). Alternatively, it may be that lesser scaup are robust to variations in winter weather, as seems to be the case in the limited studies of over-winter survival in other duck species (Bergan and Smith 1992, Dugger et al. 1994).

Overall, survival rates of juvenile female scaup in my study area were lower than those reported elsewhere. The constant survival model estimated juvenile apparent survival at 26.2% (95% CI: 21.2, 32.0), which is lower than long-term estimates for the continental population of scaup ~50% (Koons et al. 2017), and other site-specific estimates for diving duck species (Anderson et al. 2001, Arnold et al. 2002). Other concurrent research at the study site indicate that this low survival rate is driven in part by the use of nasal-markers which lowered survival among juvenile scaup by ~20 percentage points compared to tarsal-banded only ducks (Deane 2017). These depressed survival rates could obscure COEs by creating a selection pressure even stronger than the carry-over effects, leaving an unnaturally fit sample population. On the other hand, it may be equally plausible that a nasal-marker effect could be additive to, or even antagonistically interact with, environmental effects. Unfortunately, other methods of estimating postfledging juvenile survival, such as radio-telemetry, may have similar adverse effects (Barron et al. 2010) and less obtrusive markers such as metal tarsal bands suffer from very low re-encounter rates.

In addition to low apparent postfledging survival, there was little support for models with annual variation - point estimates ranged from 18 to 33% but were estimated with poor precision.

Adult waterfowl generally have low variation in annual survival rates over time (Franklin et al. 2002), and while juveniles have been believed to be more variable, my findings of low variation are like those of other diving ducks in studies <7 years in duration (Anderson et al. 2001, Arnold et al. 2002). While variation is apparent in long-term continental-scale data for female lesser scaup juveniles (1975-2015; Koons et al. 2017), survival may simply fluctuate less over short time intervals. Alternatively, site-specific studies of apparent survival may underestimate true variation if permanent emigration from a site is density dependent. Again, as above, nasal-marker effects could conceivably moderate variation in apparent survival by artificially culling less-fit individuals whom may have otherwise survived in years with more favorable conditions.

I conclude that there is suggestive evidence of density COEs in female postfledging survival and breeding probability and this is supported by mechanistic evidence of reduced growth rates of ducklings hatched in years with high conspecific densities at the study site. However, covariates for both COE processes were estimated with low precision, and I therefore cannot ignore the hypothesis of no relationship. Similarly, by only estimating apparent survival I cannot exclude the alternative explanation that juveniles are simply more likely to permanently emigrate following years of high duckling density. The Red Rock Lakes study system may also be a poor system to generalize from given its unusually high density of breeding scaup (7.7 / km²; Jeffery M. Warren, U.S. Fish and Wildlife Service, unpublished data), however breeding densities may simply be commensurate with the quality of the site with similar ‘ducks per unit resource’ as other less productive wetland systems (Gunnarsson et al. 2004). A final consideration may be the “creching” behavior of lesser scaup in this system, whereby females amalgamate broods into large, loose rafts, sometimes exceeding several hundred ducklings. The adaptive consequences of this behavior are not well understood in scaup, but it could possibly

accentuate density effects by concentrating ducklings into a smaller space and thereby further increasing competition.

I recommend future research should find ways to estimate postfledging survival without introducing biases such as those associated with nasal-markers. Because there was little variation in juvenile survival, I suggest high-power (i.e., large sample size) and long-term studies (i.e., >10 years) or experimental manipulations may be necessary to better understand COEs of early-life environment in ducks. Further, local measurements of the environment experienced by migrating and wintering juveniles would help elucidate the relative roles of direct and COE effects in this important life-history stage. Continued improvements in GPS-transmitters could eventually provide ideal methods for obtaining unbiased location and survival data necessary to confirm results presented here and address important unknowns and assumptions.

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4.8 Tables and Figures

Table 4.1. Candidate models for detection probability of female lesser scaup at Lower Red Rock Lake, Montana, 2010-2018. Each model was fit with either a time-varying by age (juvenile or adult) or constant by group survival model. Duckling density was evaluated as support for 3 different variables; unadjusted \hat{N} , or \hat{N} divided by area of lake >50cm or 35cm deep. The $\Delta AIC_c < 2$ detection model(s) from this table were then carried forward and tested with each model in Table 4.2.

Detection (p) models for female scaup	Hypothesis
	(COE = carry-over effect)
$p(.)$	Constant detection for juvenile and adult ages.
$p(t)$	Detection varies with time equally for both ages.
$p(\text{Juv}+\text{Adult})$	Constant detection over time but differs by age.
$p(\text{Juv}+\text{Adult}+t)$	Detection differs by age but varies in parallel with time.
$p(\text{Juv}+\text{Adult}\times t)$	Time-varying detection for adults only.
$p(\text{Juv}\times t+\text{Adult})$	Time-varying detection for juveniles only.
$p(\text{Juv}\times t+\text{Adult}\times t)$	Full time-varying detection for each age.
$p(\text{Juv}\times \text{May Water Level}+\text{Adult})^a$	Juvenile detection varies with spring conditions at Lower Red Rock Lake via temporary emigration.
$p(\text{Juv}\times \text{Hatch Date relative to cohort}+\text{Adult})^a$	Juvenile detection varies with individual hatch date relative to cohort via temporary emigration.
$p(\text{Juv}\times \text{Duckling Density}_{t-1}+\text{Adult})^a$	COE of duckling density via temporary emigration.
$p(\text{Juv}\times \text{Winter ENSO}+\text{Adult})^a$	COE of winter ENSO via temporary emigration.

^a. Covariate models with time-varying detection for adults also evaluated.

Table 4.2. Candidate models for first-winter survival of female lesser scaup at Lower Red Rock Lake, Montana 2010-2018. Each survival model was fit with each of the $\Delta AIC_c < 2$ detection models from Table 4.1.

Apparent survival (ϕ) models	Variable description	Hypothesis
<i>(Each model fit with constant and time-varying adult survival)</i>		(COE = carry-over effect)
$\phi(\text{Juv})$	Constant	-
$\phi(t \times \text{Juv})$	Time-varying	-
$\phi(\text{Juv} \times \text{Hatch Date relative to cohort})$	Hatch date centered within cohort	Negative – Within cohorts, later hatched ducklings tend to have reduced growth during brood-rearing. COE reduces survival.
$\phi(\text{Juv} \times \text{Hatch Date} * \text{NDVI SOS})$	As above but with an interaction term for spring phenology,	Positive – Negative effects of late hatching are reduced in years with later phenology.
$\phi(\text{Juv} \times \text{Duckling Density})$	Estimated ducklings per ha of lake with depths ≥ 0.35 or 0.5m in August or simply unadjusted.	Negative – More competition for food during brood-rearing negatively impacts growth. COE decreases juvenile survival.
$\phi(\text{Juv} \times \text{ENSO} + \text{Adult} \times \text{ENSO})$	El Nino Southern Oscillation Index	Positive – Wetter conditions occur in the positive phase of ENSO which may benefit wintering scaup.

Table 4.3. Model selection table for determining the structure of the detection probability model to be used in subsequent modeling of survival (all models in table 1 were fit). Models within 8 AIC_c of the best approximating model are shown, except only covariate models which reduced AIC_c over simpler models are shown. Density effect subscripts unadjusted \hat{N} and \hat{N} divided by the estimated area of the lake >35cm.

Model	K	AIC _c	ΔAIC _c	Weight	-2LogLik
$\phi(\text{Juv}+\text{Adult}) p(\text{Juv} \times t + \text{Adult})$	11	2147.0	0	0.72	2124.8
$\phi(\text{Juv}+\text{Adult}) p(\text{Juv} \times \text{Density}_N + \text{Adult})$	4	2151.5	4.6	0.07	2143.5
$\phi(\text{Juv}+\text{Adult}) p(\text{Juv} \times \text{Density}_{N / \text{area} > 35\text{cm}} + \text{Adult})$	4	2152.6	5.6	0.04	2144.5
$\phi(\text{Juv}+\text{Adult}) p(t)$	10	2152.9	5.9	0.04	2132.7
$\phi(\text{Juv}+\text{Adult}) p(\text{Juv} \times \text{May Water Level} + \text{Adult})$	4	2153.4	6.4	0.03	2145.3
$\phi(\text{Juv}+\text{Adult}) p(\text{Juv} \times \text{Relative Hatch Date} + \text{Adult})$	4	2154.5	7.5	0.02	2146.4
$\phi(\text{Juv} \times t + \text{Adult}) p(\text{Juv} \times t + \text{Adult})$	18	2154.9	8.0	0.01	2118.5
$\phi(\text{Juv} + \text{Adult} \times t) p(\text{Juv} \times t + \text{Adult})$	18	2154.9	8.0	0.01	2118.5
$\phi(\text{Juv}+\text{Adult}) p(\text{Juv} \times \text{Density}_{N / \text{area} > 50\text{cm}})$	4	2155.2	8.2	0.01	2147.2
$\phi(\text{Juv}+\text{Adult}) p(\text{Juv} \times \text{Winter ENSO})$	4	2155.3	8.4	0.01	2147.3

K= number of parameters, AIC_c = Akaike's information criterion adjust for small samples, Weight= Akaike's weight, -2LogLik= -2×Log-Likelihood

Table 4.4. *A priori* models for apparent survival of juvenile female lesser scaup at Lower Red Rock Lake, MT, 2010-2018. Models that contained uninformative parameters were removed from the table and model weights were recalculated.

Model	K ^a	AIC _c	ΔAIC _c	Weight	-2LogLik
<i>all models: $p(\text{Juv} \times t + \text{Adult})$</i>					
$\phi(\text{Juv} \times \text{Density}_{N / \text{area} > 50\text{cm}} + \text{Adult})$	12	2145.4	0.0	0.42	2121.2
$\phi(\text{Juv} + \text{Adult})$	11	2147.0	1.6	0.19	2124.8
$\phi(\text{Juv} \times \text{Density}_{N / \text{area} > 35\text{cm}} + \text{Adult})$	12	2148.2	2.8	0.10	2124.0
$\phi(\text{Juv} \times \text{Winter ENSO} + \text{Adult})$	12	2148.5	3.1	0.09	2124.3
$\phi(\text{Juv} \times \text{Hatch Date} + \text{Adult})$	12	2149.0	3.6	0.07	2124.8
$\phi(\text{Juv} \times \text{Density}_N + \text{Adult})$	12	2149.0	3.6	0.07	2124.8
$\phi(\text{Juv} \times \text{Hatch date} * \text{NDVI SOS} + \text{Adult})$	14	2151.6	6.2	0.03	2123.3
$\phi(\text{Juv} \times t + \text{Adult})$	19	2157.0	11.6	0.02	2118.5

^a K= number of parameters, AIC_c = Akaike's information criterion adjust for small samples, Weight= Akaike's weight, -2LogLik= -2×Log-Likelihood

Figure 4.1. Study area at lower Red Rock Lake, Red Rock Lakes National Wildlife Refuge. The shaded area indicates open water areas with near-shore areas comprised of seasonally flooded sedge.

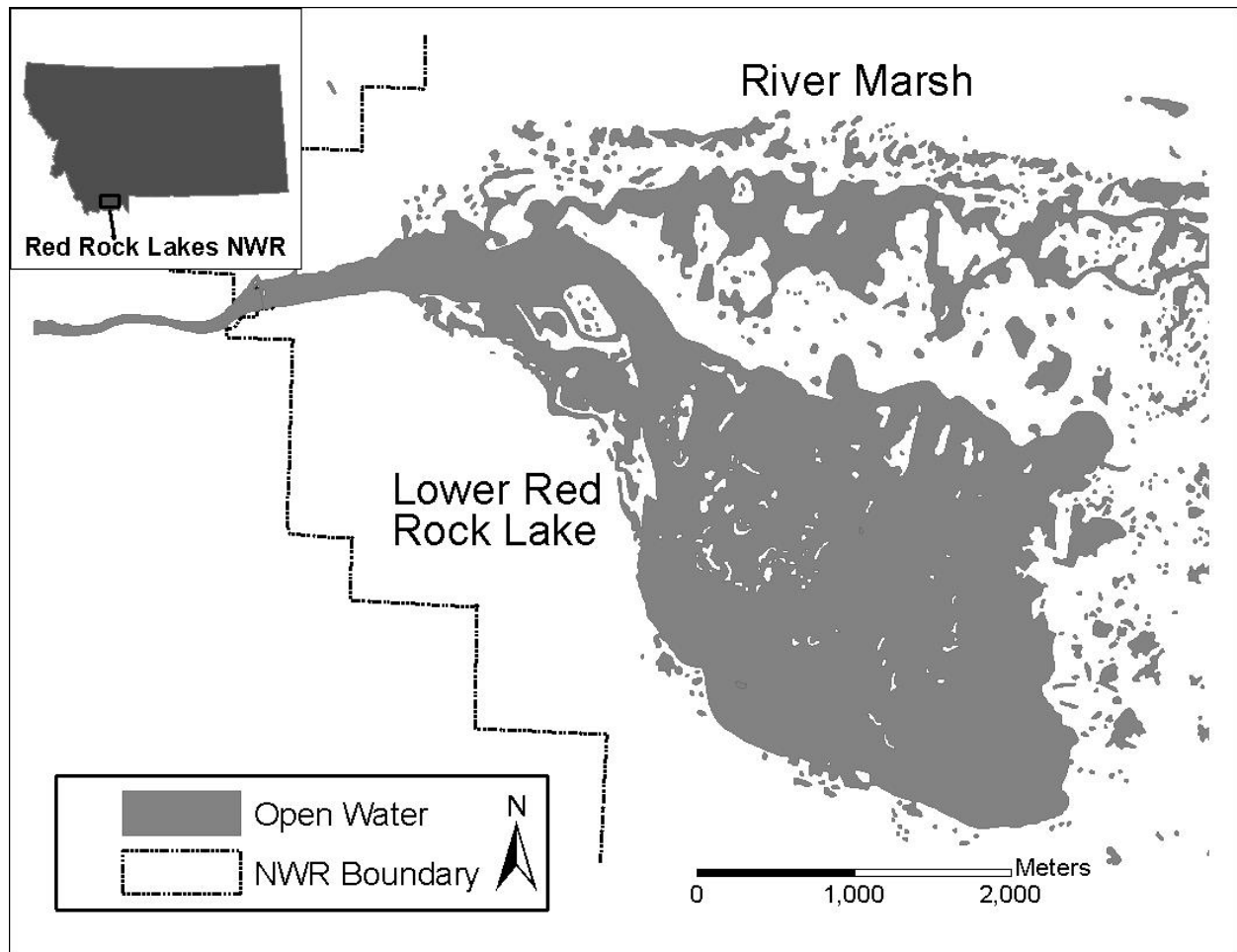


Figure 4.2. Effect estimates and 95% confidence intervals for variables representing a priori hypotheses for juvenile scaup detection probability. \hat{N} is the population estimate for lesser scaup ducklings.

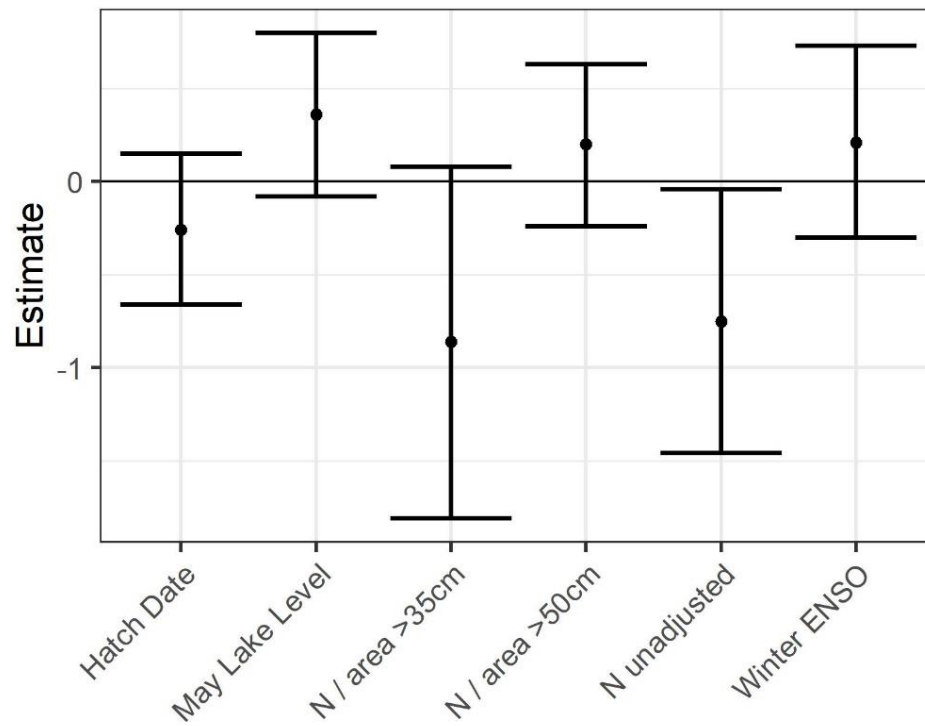


Figure 4.3. Effect estimates and 95% confidence intervals for variables representing a priori hypotheses for juvenile scaup survival. \hat{N} is the population estimate for lesser scaup ducklings.

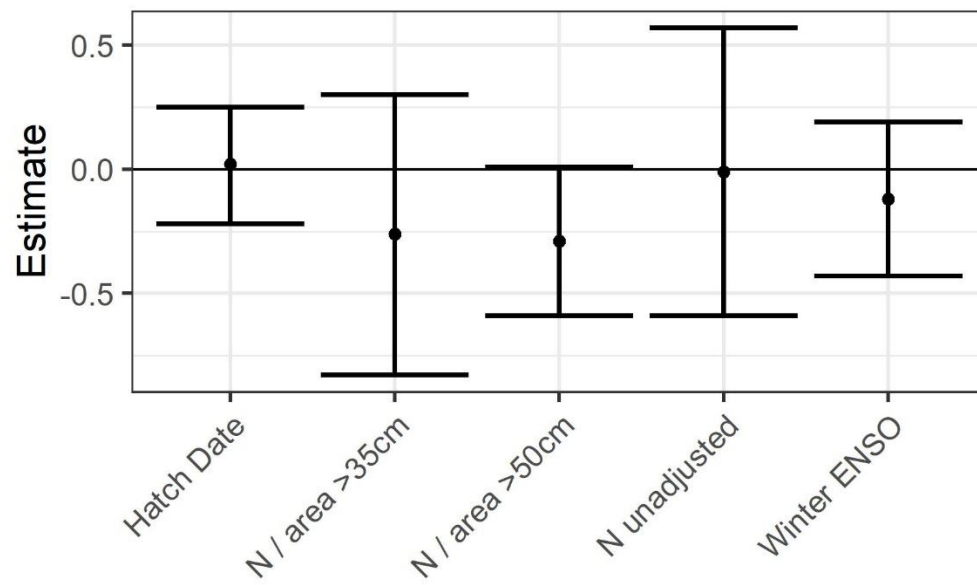
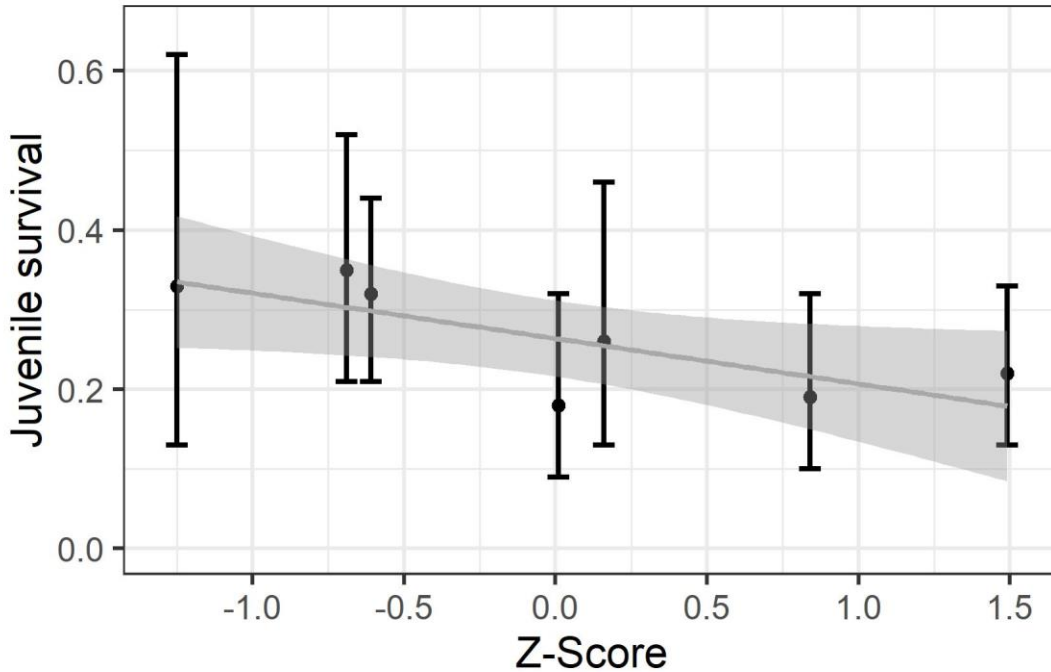


Figure 4.4. Duckling density (\hat{N} / estimated area of lake >50cm) in August against time-varying estimates of juvenile scaup apparent survival from the model $\phi(\text{Juv} \times \text{time} + \text{Adult})$ $p(\text{Juv} \times t + \text{Adult})$. Lines and shaded areas are predictions and 95% CI from a linear regression model fit to illustrate effects.



CHAPTER 5 : INTER-SPECIFIC PLASTICITY IN TIMING OF BREEDING AMONG NORTHERN HEMISPHERE DUCKS

5.1 Abstract

Relative timing and flexibility for breeding dates may influence bird species' population vulnerability to climate change via potential phenological mismatch with their environments. Despite high interest in climate-individual-population interactions, there have been remarkably few comparisons of how closely-related species respond to common phenology gradients. I acquired data on duck species spanning a wide gradient of average nest initiation dates from three long-term research sites and compared population- and individual-level plasticity to varying spring phenology and whether intraspecific variation in response exists. Early nesting species included common goldeneye (*Bucephala clangula*) and mallard (*Anas platyrhynchos*), mid-late-nesting gadwall (*Mareca strepera*), and late-nesting lesser scaup (*Aythya affinis*) and white-winged scoter (*Melanitta fusca deglandi*). I found strong evidence of plasticity to spring temperature among females of the earliest breeding duck species, whereas late-nesting scaup and scoter, did not respond. Despite this lack of response, late-breeding species exhibited annual variation in mean breeding dates, suggesting other cues may be used to time breeding. Among species that did track spring phenology there was evidence that this could be accounted for by phenotypic plasticity in goldeneye and gadwall, but not in mallard. Finally, there was evidence that individual female goldeneye and gadwall varied in the strength of their plasticity to phenology – this variation could be a source of adaptive potential to adjust for advancing spring phenology expected with climate change. Further research on the fitness consequences of

plasticity to spring phenology, including the trophic mechanisms and population consequences, are needed.

5.2 Introduction

Life-history traits such as relative timing and flexibility for breeding dates may influence bird species' population response to climate variability and change. Traits that constrain flexibility may limit the ability of birds to track changes in the phenology of their environment (Both et al. 2006). In the context of climate change and advancing spring phenology in many parts of the northern hemisphere (Schwartz et al. 2006) a lack of flexibility could produce mismatches between seasonal resource requirements and peaks in food quality or quantity with negative impacts on population viability (Jones and Creswell 2010).

In some bird species, hatch date-food resource mismatches have been linked to negative individual-level effects in some populations (Visser et al. 1998, Both and Visser 2001, Both et al. 2006), yet these negative impacts on individuals do not necessarily translate to population-level declines (Reed et al. 2013). How individuals respond to local conditions of weather and food supply can even differ between populations of the same species (Charmantier et al. 2008, Porlier et al. 2012). Phenological shifts could impact individual responses and population dynamics in distinct ways, and some research has revealed unique patterns in diverse taxa (Primack et al. 2009). Among Antarctic-nesting penguins, Lynch et al. (2012) documented interspecific differences in breeding-date responses to October mean temperatures and further hypothesized that such shifts could strengthen interspecific competition for nesting sites. Yet, despite high interest in climate-individual-population interactions, there have been remarkably few comparisons of how closely-related species respond to common phenology gradients.

In ducks there is little evidence to date of population-level impacts of advancing spring phenology (Arzel et al. 2014, Ross et al. 2015), but in arctic and sub-arctic goose populations, mismatch between the phenology of grazing lawns and gosling hatch dates have individual- and population-level consequences (Brook et al. 2015, Ross et al. 2017 & 2018). Ducklings rely almost exclusively on aquatic invertebrate food sources for growth (reviewed in Baldassarre 2014), and peaks in the abundance of some aquatic invertebrates appear tied to seasonal water temperature (Cooper 1965, Panov and McQueen 1998, Gerten and Adrian 2002), creating the possibility for trophic mismatch as in geese. It is important to evaluate variation in plasticity within and among species to better understand whether species have potential to adjust to future climate changes (IPCC 2007).

Northern hemisphere duck populations have a wide range of mean nest initiation dates, with some species having average nesting dates separated by as much as 60 days (Raquel 2016). While early-nesting species seem to readily adjust nesting dates to match the onset of spring-like conditions, it is uncertain whether late-nesting species respond similarly. For instance, Gurney et al. (2011) showed that the late-nesting species, lesser scaup (*Aythya affinis*), had similar average nest initiation dates across a wide latitudinal and growing season length gradients (44 to 65° N latitude and site-average 100 to 257 growing days, respectively), and showed little annual response to an index of spring phenology. In contrast, early-nesting species, such as mallard and goldeneye seem to adjust timing of nesting to match cues of spring phenology (Drever and Clark 2007, Oja and Pöysä 2007, Clark et al. 2014). Drever et al. (2012) hypothesized that populations of late-nesting duck species could be more vulnerable to advancing spring conditions if females did not adjust to warmer weather by nesting earlier; this hypothesis has not been tested.

I compared the degree of plasticity for breeding dates exhibited by individually-marked females of five duck species with early, mid-season and late nesting dates. In particular, I estimated 1) population- and individual-level plasticity for breeding dates, with emphasis on the response to spring phenology, and 2) the degree of within-individual variation in the adjustment to spring phenology.

5.3 Study Areas

I acquired data on species spanning a wide gradient of average nest initiation dates from three long-term research sites (Table 5.1). Early nesting species included common goldeneye (*Bucephala clangula*) and mallard (*Anas platyrhynchos*), mid-late-nesting gadwall (*Mareca strepera*), and late-nesting lesser scaup (*Aythya affinis*) and white-winged scoter (*Melanitta fusca deglandi*). Common goldeneye data were collected near Maaninka in central Finland (63° 09' N, 27° 17' E). The study area consisted of 23 lakes and ponds and the bays of larger lakes, surrounded by agricultural land and managed forests. The size of the study area increased in the first years of the study and reached its current size (*ca* 280 km²) in 1989 (Ruusila et al. 2001, Clark et al. 2014). White-wing scoter data were collected from females nesting on islands and adjacent uplands of Redberry Lake, within the Redberry Lake Migratory Bird Sanctuary (52° 41' N, 107° 11' W), in southcentral Saskatchewan, Canada. The lake is at the southern edge of the scoter breeding range and is surrounded predominately by cropland and aspen parkland forest (Alisauskas et al. 2004, Traylor et al. 2004). Data for the remaining three species were collected at the 361-ha St. Denis National Wildlife Area (52° 12' N, 106° 5' W), Saskatchewan, Canada, located ~100 km southeast of the Redberry Lake site and within a similar landscape (Clark and Shutler 1999).

5.4 Methods

5.4.1 Breeding Date

Nests were located by different methods at each site. At Maaninka, goldeneyes nested in nest boxes, checked for eggs three to four times during the breeding season, as long as boxes remained unoccupied (Clark et al. 2014). At Redberry Lake, islands and adjacent uplands were searched for nests on foot, while at St. Denis, nests were found by using a combination of foot-searches and by dragging a chain between two all-terrain vehicles (Clark and Shutler 1999, Traylor et al. 2004). At both Canadian sites, nest searches were completed three to five times per year during the nesting season. Nest initiation date was estimated by back-calculating the nest age from clutch size (assuming 1.5 eggs per day for scoter, and 1 egg per day for all other species) and estimated stage of embryonic development via the candling method of Weller (1956). I followed Clark et al. (2014) in using hatch date as the index for breeding date in the goldeneye population.

5.4.2 Spring Phenology

Ice-out has been recorded at the Maaninka site for each year of the goldeneye study and has been shown to strongly influence goldeneye breeding dates (Clark et al. 2014), but I did not have comparable observations at the Canadian sites. Therefore, I used a standard metric of spring phenology at each site based on temperature data from the nearest meteorological station. At Maaninka these data are available in a gridded format downloaded from (<http://mesi.metla.fi/>; accessed 27 February 2019; see Venäläinen et al. 2005). The nearest recording station for Redberry Lake and St Denis was Saskatoon, Saskatchewan (52° 10' N, 106° 43' W), located ~65 and 45 km from the sites, respectively (downloaded from <http://climate.weather.gc.ca/>). First, I determined the date when long-term average (1984-2018) daily temperature exceeded 0° C for

each site, which was near 1 April at both Maaninka and Saskatoon. I took the mean of the daily mean temperatures in the 30 days bounding this date (i.e., March 15 to April 15) as an indicator of the relative annual timing of spring at each site. At Maaninka mean temperatures during this window were somewhat correlated to ice-out dates ($r = -0.46$, $p = 0.006$, 34 years), but lacked the positive time-trend seen in the ice-out time series and were less predictive of goldeneye nesting dates in the models described below. I also calculated a slightly later temperature window, April 1 to April 30, which had a better correspondence with ice-out dates ($r = -0.77$, $p < 0.001$, 34 years) and which I use in the following analysis for goldeneye. I retained the earlier March 15 – April 15 window for the Canadian sites as it was more predictive of breeding dates in the models below.

5.4.3 Data Analysis

Renesting

Many ducks will attempt to renest if their first clutch is destroyed. While it is not possible to determine if a nest of a marked female is the first attempt, I attempted to reduce the impact of re-nesters on the analyses by excluding dates which occurred very late in the season. For each species and each year, I removed breeding dates deemed to be outliers by using the common Tukey boxplot definition of being >1.5 times the interquartile range of breeding dates above the 75th percentile. This resulted in removal of 16 goldeneye, 5 mallard, 6 gadwall, 1 scaup, and 15 scoter records. Potential renesting females remaining in the analysis would have the effect of weakening the observed response to spring phenology.

Population-level plasticity

For each species, I calculated the degree of population-level plasticity by estimating 1) the slope of response to the index of spring phenology in a mixed effects regression model, and 2) the amount of unexplained variation in breeding dates attributable to study-year (see below). It is well-established that older females nest earlier in ducks (Afton 1984, Rohwer 1992, Milonoff et al. 2002, Devries et al. 2008), so I accounted for female age by allowing a linear or quadratic relationship with breeding date. I included two random intercepts; 1) 'year', to account for shared but unexplained annual variation in breeding date, and 2) 'female', to account for multiple (potentially correlated) observations of breeding date for the same female and determine whether females differed in mean breeding dates. The model was:

$$Breeding\ Date_{i,t} = age_{i,t} + age_{i,t}^2 + phenology\ index_{i,t} + year_i + female_i + \varepsilon_{i,t}$$

$$year_i \sim N(0, \sigma_{year}^2)$$

$$female_i \sim N(0, \sigma_{female}^2)$$

$$\varepsilon_{i,t} \sim N(0, \sigma_{residual}^2)$$

Because species may be responding to annual cues other than my index of spring phenology, I assessed plasticity more generally by evaluating support for the 'year' random intercept. In addition to a likelihood ratio test to evaluate support for a 'year' random intercept, I also calculated the proportion of variance in breeding date associated with 'year' as $\sigma_{year}^2 / (\sigma_{year}^2 + \sigma_{female}^2 + \sigma_{residual}^2)$ from variances estimated in the model above (i.e., accounting age, and female specific differences). In this context, a high level of variance attributable to 'year' would indicate that females are responding to annual factors other than the

one I measured. For reference, I also calculated the proportion of variance explained by year without the fixed effect of phenology, i.e., the total proportion of variance attributable for year. I calculated 95% CI for these variance components using parametric bootstrapping over 1000 simulated datasets (Nakagawa and Schielzeth 2010). Only females with >1 lifetime breeding attempt were included in the analysis, and I compared results using a more restrictive criteria of >2 lifetime breeding attempts for inclusion in the analysis.

Individual-level plasticity

Population-level responses characterized as above are a result of phenotypic plasticity (i.e., individual female adjusting laying time to phenology in each year she breeds), as well as microevolutionary and other factors (Charmantier et al. 2008, Charmantier and Gienapp 2014). To more directly evaluate phenotypic plasticity I calculated the difference in breeding dates between successive breeding attempts and the corresponding difference in spring phenology (Charmantier et al. 2008). I controlled for age by associating the age at the previous breeding attempt (i.e., lag-1) in each matched pair of sequential breeding dates. I estimated the slope of response using the same model structure as above.

Within-individual variation in plasticity

Finally, I assessed evidence for individual variation in plasticity by adding a random slope for ‘phenology \times female’ to the model above, following Charmantier et al. (2008). I evaluated the level of support by comparing this random slope model to simpler versions of the model’s random effects structure using likelihood ratio tests. All models were fit in program R 3.5.2 (R Core Team 2019) using the package lme4 1.1-20 (Bates et al. 2015) and restricted maximum likelihood estimation.

5.5 Results

Sample sizes of individually-marked females with >1 nesting attempt varied by species (Table 5.1). The range of the phenology index also varied by site and time period (Canada March 15-April 15 mean temperature; -8.1 to 3.7° C and Finland April 1 to April 30 mean temperature; -1.6 to 4.9° C; Figure 5.1). Each species showed substantial annual variation in breeding dates (Table 5.1, Figure 5.2), with scoters showing the least (SD = 6.6 days) and mallards the most (SD = 19.9 days).

Separate analyses of females having a minimum of two or three nesting attempts yielded qualitatively similar results, so I present only those results from analysis of females with ≥ 2 attempts to maximize sample size (results for ≥ 3 attempts are included in electronic supplements). The population-level response of females to spring phenology was most evident among early-breeding goldeneye and mallard and, possibly, in mid-late breeding gadwall (Figure 5.3). Estimates for individual- and population-level responses were similar for all species, except mallard, implying that population-level responses are not driven by the phenotypic plasticity of individual female mallards.

Plasticity to spring phenology was not apparent in late-breeding scaup or scoter, but there was evidence for annual variation in their mean breeding dates as indicated by support for the ‘year’ random intercept (Table 5.2) and variance components analysis (Figure 5.4). This suggests that scaup and scoter adjust breeding dates to unmeasured annual cues (Figure 5.5), and that goldeneye and gadwall also respond to additional factors not accounted for by the phenology index (Figure 5.4).

Average breeding dates differed significantly among females in goldeneye, scoter, and possibly scaup (Table 5.2). Individual differences in the strength of response to spring phenology were supported only in gadwall and possibly goldeneye (Table 5.2), with some females being more plastic than others; these responses were not detected in female mallard, scaup or scoter. Results for scaup and scoter remained consistent when I evaluated female responses to other metrics of spring phenology, such as average daily temperatures from mid-May to mid-June.

5.6 Discussion

Population-level responses to spring temperature conditions have been described for several duck species (reviewed in Drever and Clark 2007) but to my knowledge this is among the first analyses of individual-level responses across avian species that differ in average breeding dates. I found strong evidence of plasticity to spring temperature among females of the earliest breeding duck species, whereas late-nesting species, scaup and scoters, did not respond. Remarkably, early-breeding female mallards did not exhibit individual phenotypic plasticity, yet at the population-level, mean breeding dates tracked phenology. While the population-level response to spring phenology is well-documented in mallards (Devries et al. 2008), the lack of individual plasticity suggests that juvenile mallard recruits could be the segment of the population which is plastic to spring phenology. A similar explanation was proposed for migration timing in Icelandic black-tailed godwits (Gill et al. 2014). In contrast, estimates of population- and individual-level plasticity of the other early-breeding species, goldeneye, were very similar, indicating population response in this population can be entirely explained by phenotypic plasticity.

Taken together, these results are consistent with hypotheses that late-breeding species may be the least able to adjust for advancing spring phenology expected with anthropogenic

climate change. Female scoter and scaup did not breed earlier in years with warmer spring conditions. Despite the non-response to the spring phenology index by these late-breeders there was evidence for year-specific variation in mean breeding dates as indicated by support for mixed effects models incorporating ‘year’ as a random intercept term (Table 5.2). This annual variation was common for all species to varying degrees, even with the model already accounting for the spring phenology index (Figure 5.4). This suggests that other year-specific factors act as cues for individuals to adjust timing of breeding, even among females of late-breeding species. In addition to breeding later in the season, female scaup and scoter arrive on breeding areas later than the other ducks (Afton 1984), so perhaps they are responding to cues occurring later in the breeding season than my March 15 – April 15 index of spring phenology. For instance, scaup and scoter rely heavily on amphipods for provisioning ducklings (Brown and Frederickson 1980, Afton et al. 1991, Fast et al. 2004), and these species seem to increase in biomass later in the season in a manner related to seasonally increasing water temperatures (Cooper 1965, Menon 1969, Hargrave 1970). Late-season water temperatures may be only poorly correlated with my early spring phenology variable. To partially evaluate the possibility that scaup and scoter may be responding to phenological cues later in the breeding season, I performed post-hoc analyses using i) mean temperatures closer to their average nest initiation dates (mean temperature May 15 – June 15), and ii) mean temperatures across a wider window of the breeding season (mean temperature April 1 – June 30) which could correspond to increased aquatic invertebrate activity as warmth accumulates in breeding wetlands. However, neither species showed a clear response to these later mean temperature windows.

The reproductive consequences of plasticity in breeding dates has not been fully established in most species, including ducks. In goldeneyes, early breeding females produced more recruited

offspring in early and late spring conditions (Clark et al. 2014), a general pattern reported in some other duck species (Blums and Clark 2004) including lesser scaup (Dawson and Clark 2000). Apparent first-year survival also appears to be higher among early-hatched female mallard and gadwall ducklings (RGC, unpubl), and while first-year survival has not been quantified in scoter, ducklings of early-hatched broods survive at higher rates (Traylor and Alisauskas 2006). So in general the ability of breeding females to respond appropriately to early onset of spring could be advantageous.

There is also the question of adaptation (i.e., microevolution) in environments where prolonged changes in mean spring phenology have been observed or are expected in the future. If breeding-resource mismatches reduce individual fitness, this creates selection pressure to adjust timing of breeding (Nussey et al. 2007). However, for adaptation to occur, there must be a genetic basis for breeding date or phenotypic plasticity thereof. While I did not have female pedigree information to directly address this question (*sensu* Nussey et al. 2007), my results for repeatability of breeding dates across years and individual variability in phenotypic plasticity provide a starting point. There was mixed support for whether an individual female's breeding dates were correlated across years. This pattern was not apparent in mallard or gadwall, yet clearly supported for early-breeding goldeneye and late-breeding scoter. While detection of this pattern only in these species may be related to their relatively larger sample sizes, it is nonetheless interesting. It implies some females consistently nest at dates that differ from the population mean. Further, among female goldeneye, there was evidence that individuals varied in their response to spring phenology, consistent with the findings of Clark et al. (2014). This intraspecific variability in plasticity was shared by female gadwall, whom despite a proclivity to mid-late season nesting, also tracked spring temperatures. The fitness consequences of this

repeatability and its heritability should be topics of future research to understand how species may be able to adapt to climate change through microevolution.

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5.8 Tables and Figures

Table 5.1. Descriptions of study site locations, study years, and timing of breeding for five duck species (SD = standard deviation). Also shown are sample sizes of individually-marked female ducks with ≥ 2 and ≥ 3 recorded lifetime breeding attempts. While hatch dates are used as the indicator of goldeneye breeding date in analysis, nest initiation dates are shown here for comparison by back-calculating initiation date as ‘hatch date – $(1.5 \times 8 + 28)$ ’, where eight is the mean clutch size and 28 the mean incubation length for goldeneye.

Species ^a	Study Site	Years	Average nest initiation date	Females with ≥ 2 nesting attempts	Females with ≥ 3 nesting attempts
Common goldeneye	Maaninka, Finland	1985-2018	4 May SD = 8.7	1812	1616
Mallard	St. Denis, Canada	1983-1998	20 May SD = 19.9	185	89
Gadwall	St. Denis, Canada	1986-2001	6 June SD = 10.6	111	41
Lesser scaup	St. Denis, Canada	1989-2000	15 June SD = 10.2	73	45
White-winged scoter	Redberry Lake, Canada	2000-2018	17 June, SD=6.6	544	348

^a Common goldeneye (*Bucephala clangula*), mallard (*Anas platyrhynchos*), gadwall (*Mareca strepera*), lesser scaup (*Aythya affinis*), white-winged scoter (*Melanitta fusca deglandi*).

Table 5.2. Comparison of models for female plasticity in breeding date by species. Likelihood ratio tests are used to sequentially test more complex models including random intercepts for ‘Year’ and ‘Female’ groupings, and random slopes for “Female \times Phenology”. Fixed effects are constant in all models, accounting for age, age², and the spring phenology index. Estimates are based on females that made at least 2 breeding attempts over their lifetime (results similar with minimum of 3 attempts).

Species	Random effects	Log likelihood	DF	Likelihood ratio	<i>p</i> -value
Mallard	None	-807.97	0		
Mallard	Year	-805.53	1	4.90	0.027
Mallard	Year, Female	-805.51	1	0.02	0.880
Mallard	Year, Female X Phenology	-805.47	1	0.10	0.755
Scaup	None	-269.80	0		
Scaup	Year	-267.89	1	3.83	0.050
Scaup	Year, Female	-266.36	1	3.05	0.081
Scaup	Year, Female X Phenology	-266.19	1	0.34	0.560
Gadwall	None	-413.39	0		
Gadwall	Year	-400.90	1	24.98	0.000
Gadwall	Year, Female	-400.24	1	1.34	0.247
Gadwall	Year, Female X Phenology	-397.78	1	4.91	0.027
Goldeneye	None	-6,095.60	0		
Goldeneye	Year	-6,031.45	1	128.30	0.000
Goldeneye	Year, Female	-5,814.46	1	433.97	0.000
Goldeneye	Year, Female X Phenology	-5,813.21	1	2.51	0.113
Scoter	None	-1,795.12	0		

Species	Random effects	Log likelihood	DF	Likelihood ratio	<i>p</i> -value
Scoter	Year	-1,773.78	1	42.67	0.000
Scoter	Year, Female	-1,765.19	1	17.18	0.000
Scoter	Year, Female X Phenology	-1,765.16	1	0.05	0.822

Figure 5.1. Average daily temperatures during March 15-April 15 for Canadian sites (1983-2018) and April 1- April 30 for the Finnish site (1983-2018).

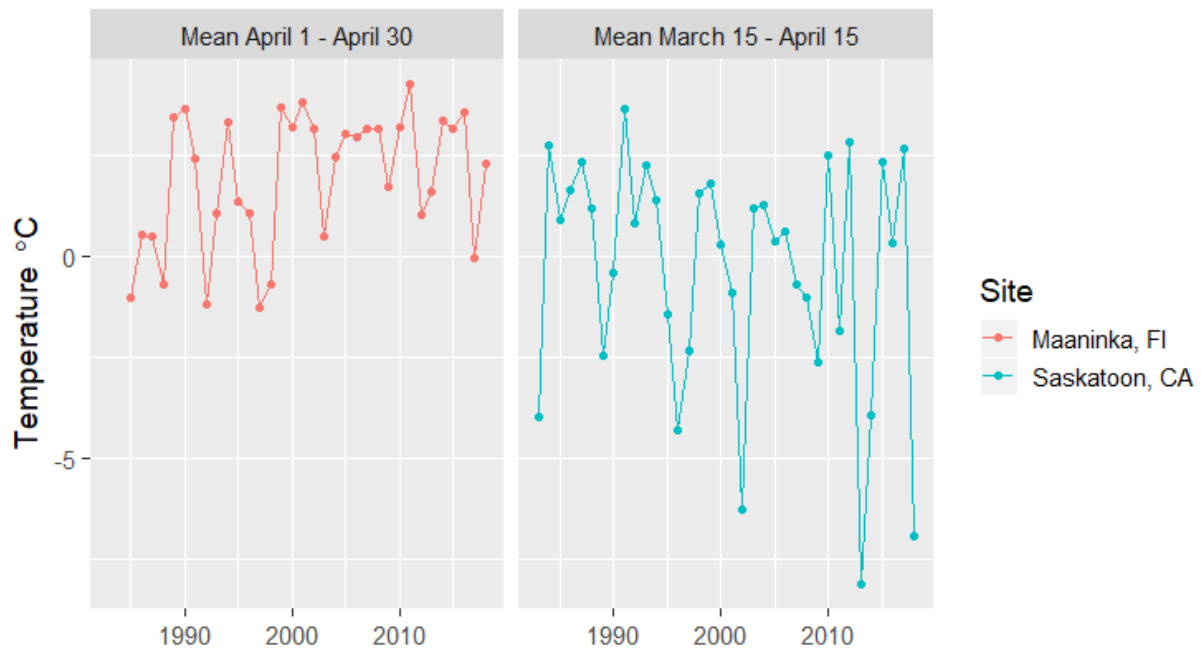


Figure 5.2. Population-level response to spring phenology index by species. A regression line is included for illustrative purposes from the model ‘breeding date ~ spring temperature’.

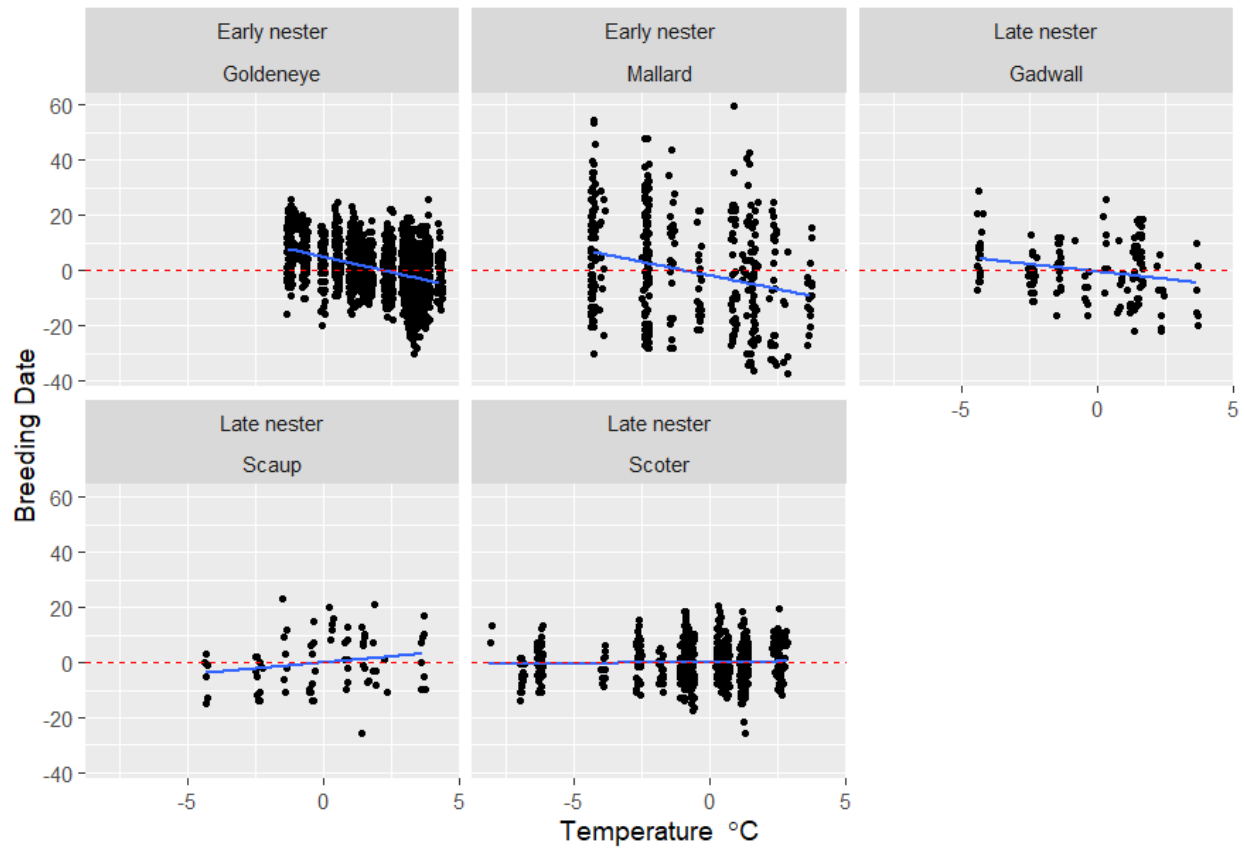


Figure 5.3. Comparison of estimates of population- and individual-level responses in breeding date (95% CI) for spring temperatures. Similar estimates at both levels indicate that population-level responses are likely due to individual phenotypic plasticity. Goldeneye and mallard are early-nesters, gadwall mid-late, and scaup and scoter are late-nesters. Responses are shown for datasets with a minimum of 2 lifetime nesting attempts per female. Results were similar with a minimum of 3 attempts. Sample sizes in Table 1.

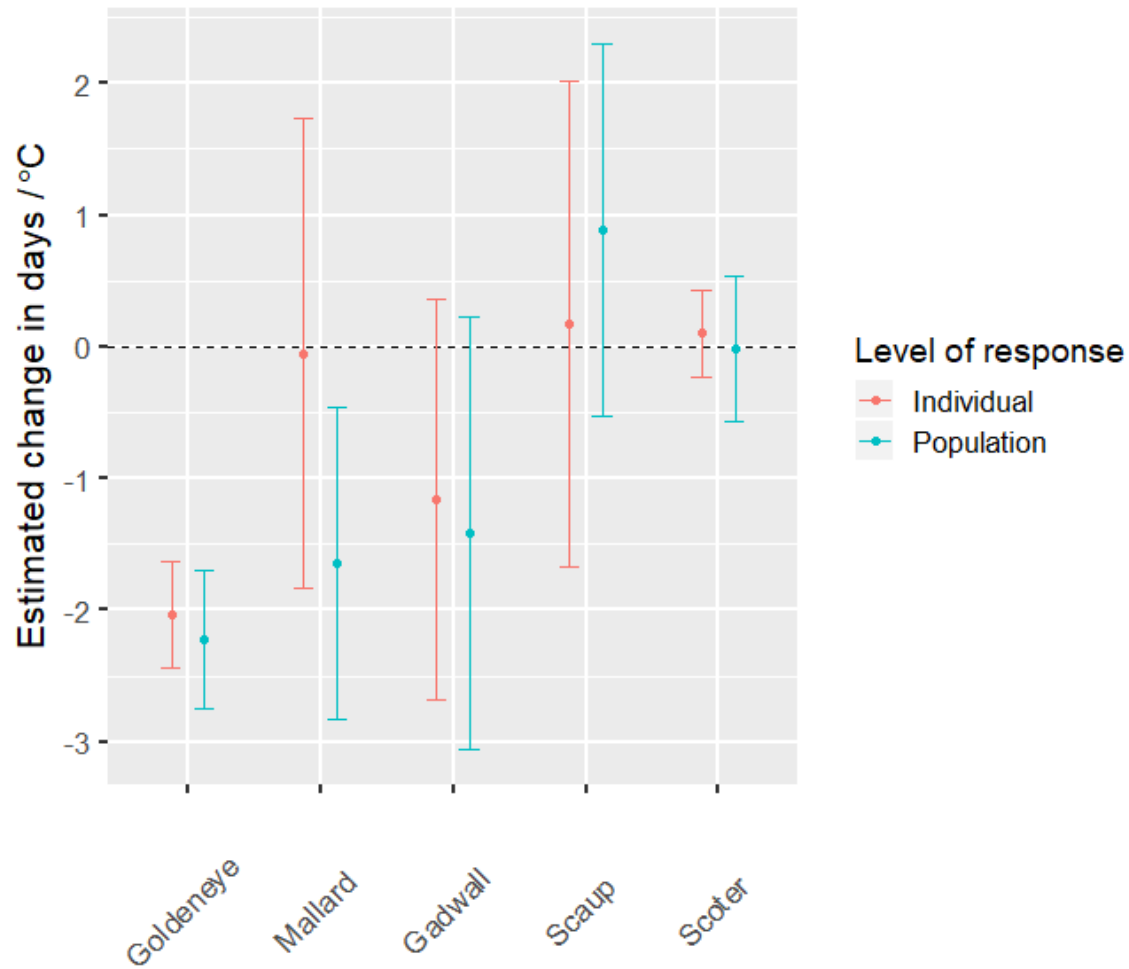


Figure 5.4. Proportion of variance in breeding date related to the random effect of year for female ducks with ≥ 2 lifetime breeding attempts. Age was controlled for in all models, however results are shown with and without spring phenology in the fixed effects. Confidence intervals are based on parametric bootstrapping ($n = 1000$ simulations). Sample sizes for each species shown in Table 1.

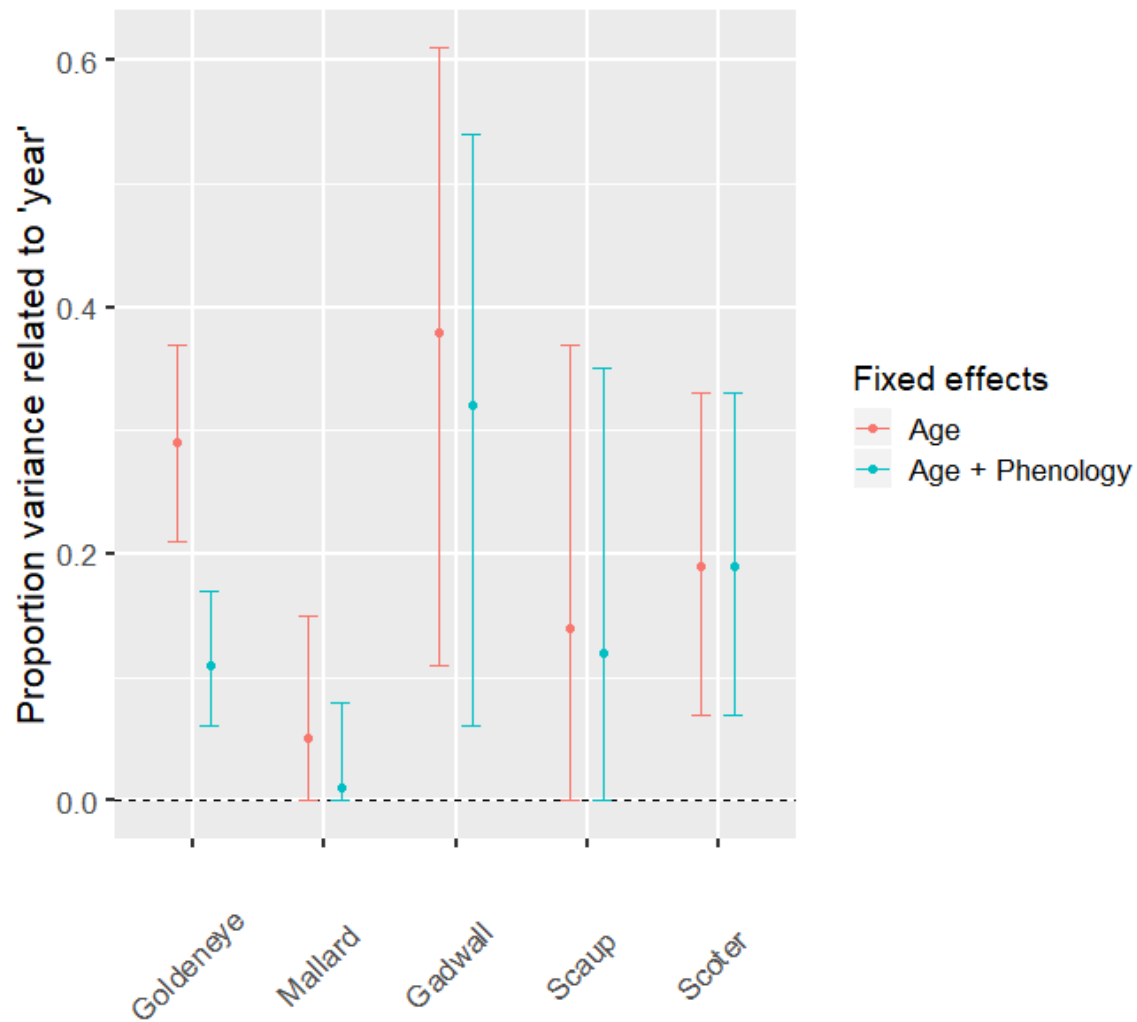
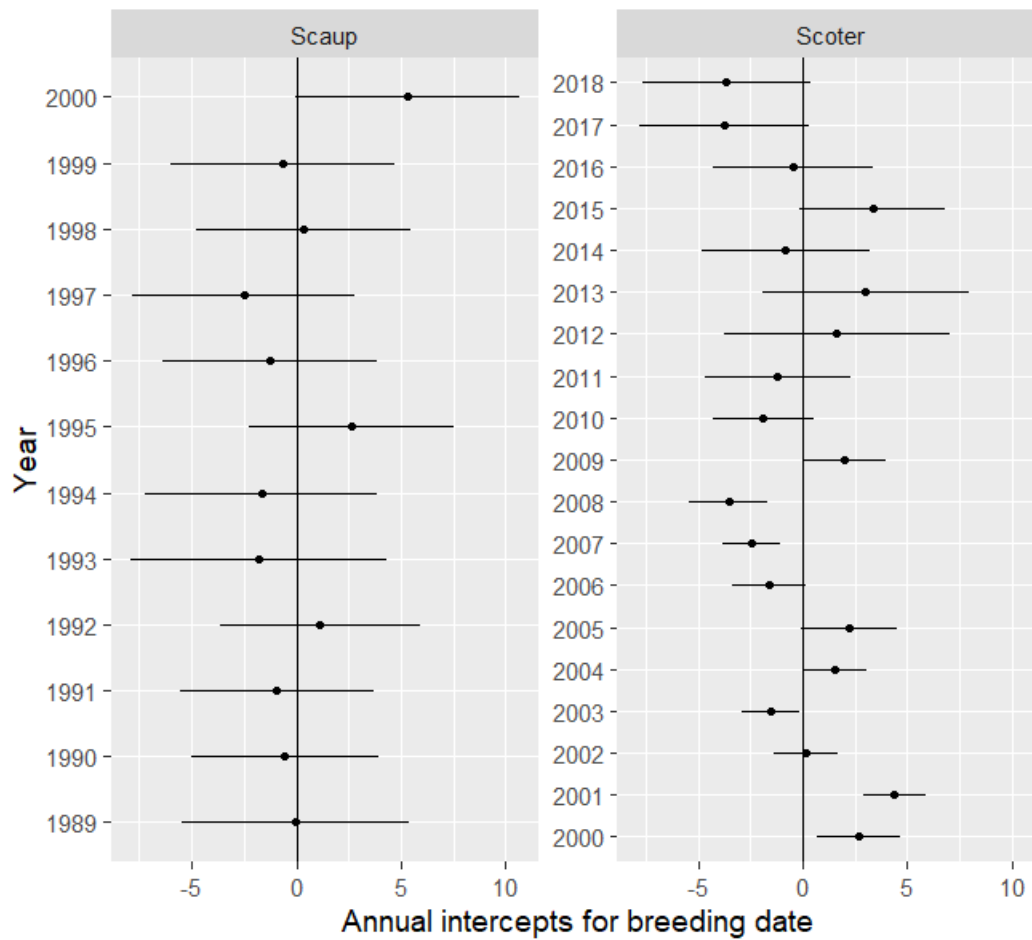


Figure 5.5. Annual deviations from the grand average breeding date in late-breeding species which did not respond to the spring phenology index. Shown are random effect estimates \pm SD for females with ≥ 2 lifetime nesting attempts, scaup $n = 73$ and scoter $n = 544$.



Electronic Supplemental material:

Tables and Figures from main text reproduced using data subset to include only females with ≥ 3 lifetime breeding attempts. Table and figure numbering from the main text are retained to facilitate comparison.

Table 5.S2: Comparison of models for female plasticity in breeding date by species. Likelihood ratio tests are used to sequentially test more complex models including random intercepts for ‘Year’ and ‘Female’ groupings, and random slopes for “Female \times Phenology”. Fixed effects are constant in all models, accounting for age, age², and the spring phenology index. Estimates are based on females that made at least 3 breeding attempts over their lifetime.

Species	Random effects	Log likelihood	DF	Likelihood ratio	<i>p</i> -value
Mallard	None	-381.89	0		
Mallard	Year	-378.54	1	6.68	0.010
Mallard	Year, Female	-378.54	1	-0.00	1.000
Mallard	Year, Female X Phenology	-378.54	1	-0.00	1.000
Scaup	None	-167.95	0		
Scaup	Year	-165.12	1	5.66	0.017
Scaup	Year, Female	-163.26	1	3.71	0.054
Scaup	Year, Female X Phenology	-163.25	1	0.03	0.858
Gadwall	None	-150.06	0		
Gadwall	Year	-142.67	1	14.77	0.000
Gadwall	Year, Female	-142.12	1	1.10	0.295
Gadwall	Year, Female X Phenology	-140.09	1	4.06	0.044
Goldeneye	None	-5,458.71	0		
Goldeneye	Year	-5,394.19	1	129.03	0.000
Goldeneye	Year, Female	-5,191.96	1	404.47	0.000

Species	Random effects	Log likelihood	DF	Likelihood ratio	<i>p</i> -value
Goldeneye	Year, Female	-5,190.64	1	2.65	0.104
	X Phenology				
Scoter	None	-1,152.60	0		
Scoter	Year	-1,146.83	1	11.55	0.001
Scoter	Year, Female	-1,140.25	1	13.14	0.000
Scoter	Year, Female	-1,139.92	1	0.66	0.415
	X Phenology				

Figure 5.S3: Comparison of estimates of population- and individual-level responses in breeding date (95% CI) for spring temperatures. Similar estimates at both levels indicate that population-level responses are likely due to individual phenotypic plasticity. Goldeneye and mallard are early-nesters, gadwall mid-late, and scaup and scoter are late-nesters. Responses are shown for datasets with a minimum of 3 lifetime nesting attempts per female. Sample sizes in Table 1.

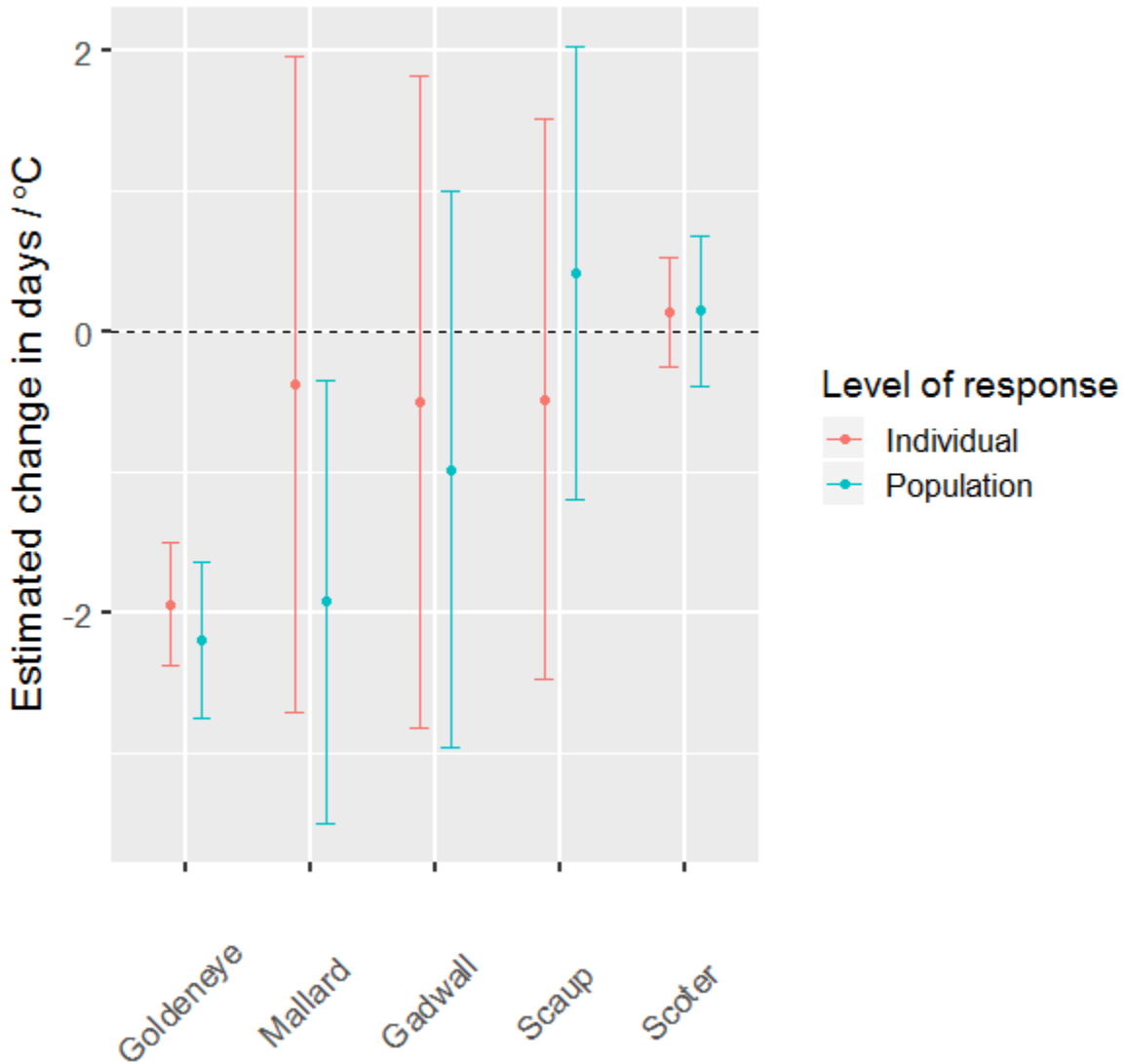


Figure 5.S4. Proportion of variance in breeding date related to the random effect of year for female ducks with ≥ 3 lifetime breeding attempts. Age was controlled for in all models, however results are shown with and without spring phenology in the fixed effects. Confidence intervals

are based on parametric bootstrapping ($n = 1000$ simulations). Sample sizes for each species shown in Table 1.

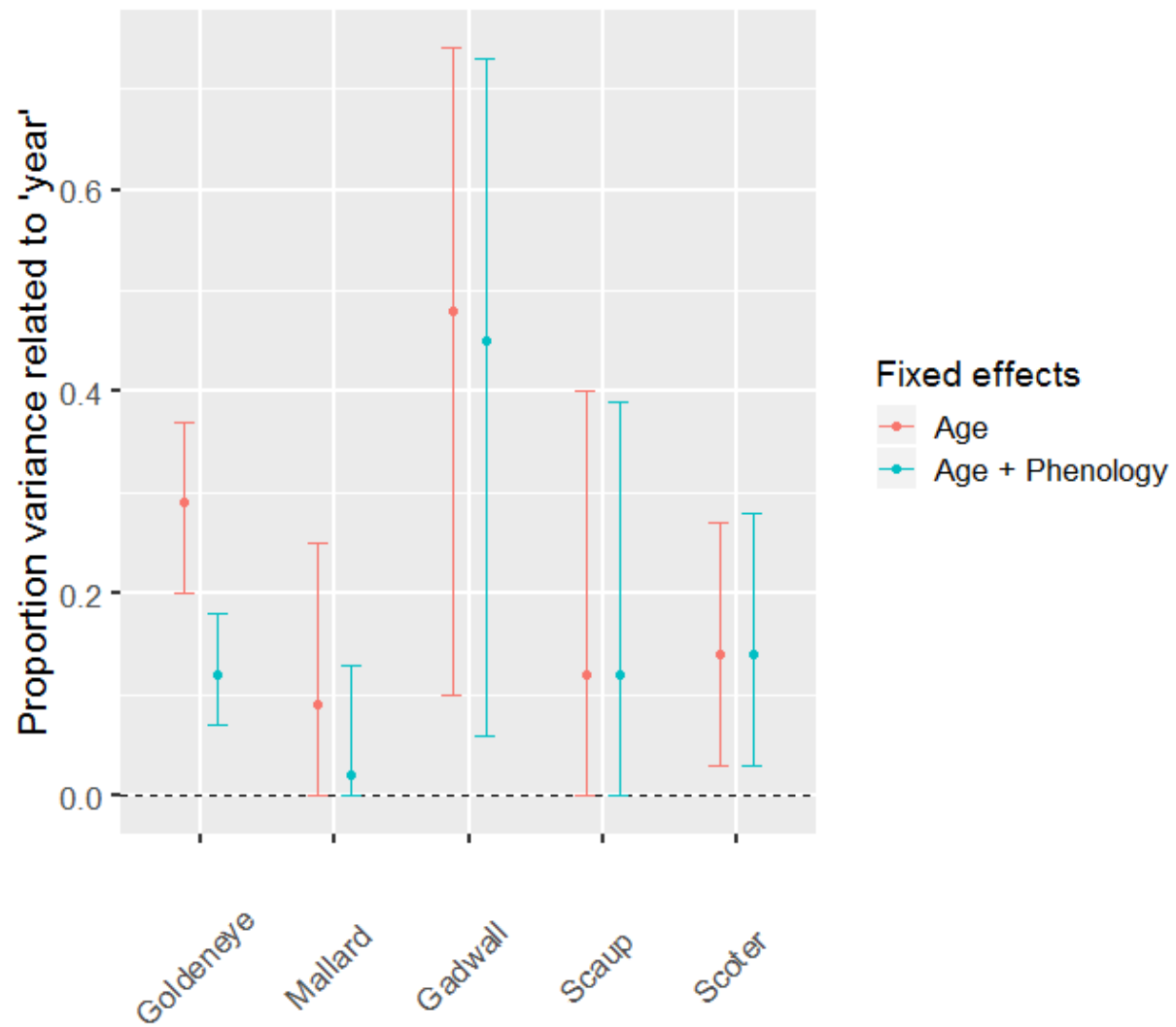
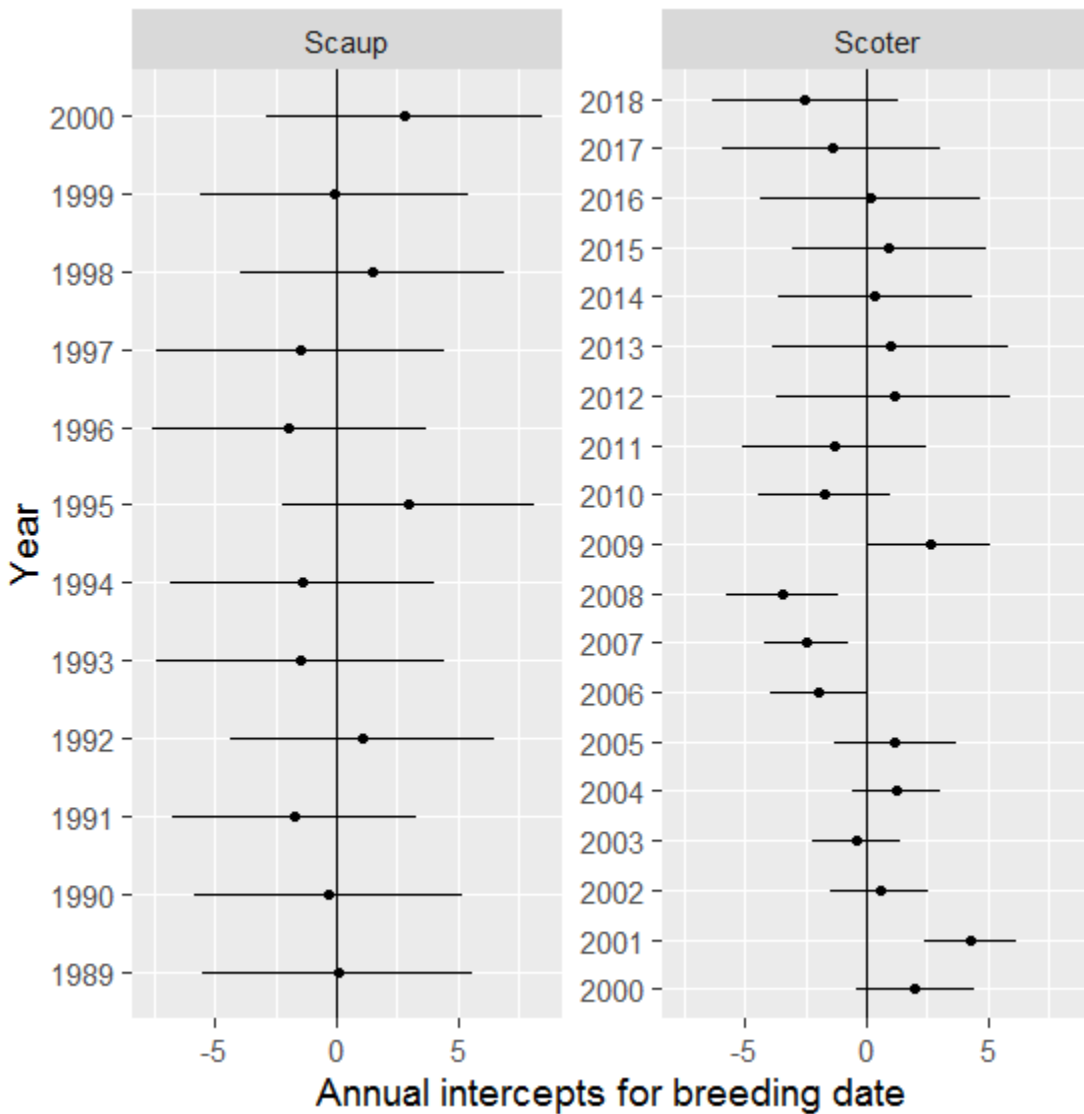


Figure 5.S5. Annual deviations from the grand average breeding date in late-breeding species which did not respond to the spring phenology index. Shown are random effect estimates \pm SD for females with ≥ 2 lifetime nesting attempts, scaup $n = 73$ and scoter $n = 544$.



CHAPTER 6 : GENERAL DISCUSSION AND CONCLUSIONS

The climate – its annual variation, cycles, and anthropogenic change – plays a central role in the distribution and abundance of bird species (Møller et al. 2010). The impact of climate change and variation on ducks is poorly understood and this continues to hinder conservation planning (Guillemain et al. 2013). Broadly, my thesis evaluated evidence for impacts of annually varying weather conditions (i.e., climate variability) and longer-term trends associated with a combination of natural climate cycles and anthropogenic climate change on ducks. I took advantage of long-term data collected at spatial scales ranging from individuals at small study sites up to large-scale populations within and across continents. I looked for climate impacts on annual population growth rates, long-term population trajectories, and individual fitness and timing of breeding. This combination of individual- and population-level analyses provides important perspective on population change and its demographic drivers. Where possible I used inter-species comparisons to evaluate whether effects were mediated by life-history strategies such as timing of breeding. Collectively, my results indicated that individual ducks and populations have been resilient to annual fluctuations in weather conditions, but that populations seemed to respond to sustained long-term trends driven by climate cycles and anthropogenic climate change.

6.1 Synthesizing individual and population level results

In Chapters 2 and 3, I evaluated the impacts of annual variation and trends in weather on ducks at the population level (Figure 6.1). In the North American (NA) boreal forest analysis (chapter 2), trends in growing season variables were not evident (during 1982-2013), so the

analysis necessarily focused on impacts of annual variation. Evidence for responses in the annual population growth rates of NA ducks were limited and frequently did not match predictions based on life-history strategy - this suggests that duck populations were resilient to considerable variability in growing season characteristics. In contrast, long-term trends in weather were evident across major breeding areas in the cross-continental analysis of chapter 3 (1976-2011). Although weather was not annually correlated on the two continents, there were shared increasing trends in temperature and precipitation which were correlated with increasing trajectories of several species. These increasing trends may be partly driven by positive cycling of the Atlantic multi-decadal oscillation or anthropogenic greenhouse gas forcing.

Taken together the analyses of chapters 2 and 3 suggest that duck populations may be able to compensate for transient variations in weather, but that long-term changes can impact populations. This differs from other studies (primarily of smaller-bodied passerines) where annual effects of weather were evident and partly accounted for observed population trends (Sillet et al. 2000, Sæther and Engen 2010, Pearce-Higgins et al. 2015). Given this lack of annual response but shared long-term trends, I posit that effects of climate trends on ducks are likely mediated by gradual multi-year effects on natural habitats and land use. This kind of indirect response is clearly illustrated by the response of North American ducks to fluctuations in mid-continent wetland abundance (Drever et al. 2006, Walker et al 2013). Wetland abundance is partly driven by precipitation and temperature patterns over multiple years (Ballard et al. 2014, LaBaugh et al 2018) and hence wetland water storage mediates the impact of weather on breeding duck populations.

From the individual-level perspective, the resiliency of populations to annual variations in weather are borne out somewhat by the findings of chapters 4 and 5 (Figure 6.1), particularly

as related to variations in spring phenology. There I found early-breeding species were directly responding to cues of spring phenology by adjusting breeding dates, and that late-breeding species also had some flexibility though it was not related to my indices of spring phenology. In chapter 4, I found that apparent survival of postfledging scaup was not related to hatch date or spring phenology and instead appeared to fluctuate with local prefledging conspecific density. Likewise, variation in an index to first-year breeding probability of scaup was most closely related to conspecific density and not phenology or spring conditions. The flexibility of duck breeding dates and the evidence for density dependent survival and breeding are potential mechanisms for the resiliency I observed at the population-level.

6.2 Future research directions

While ducks seemed resilient to annual variations in weather observed during my study periods, there was evidence that long-term trends in climate influenced duck populations (Chapter 3). A plausible mechanism is multi-year or lagged changes to habitats caused by gradually changing climate. For instance, variation in wetland area and abundance are important factors driving breeding duck populations in central North America (Drever et al. 2006, Walker et al 2013) and they are strongly influenced by precipitation over multi-year periods which affect net water storage (Ballard et al. 2014, LaBaugh et al 2018). This type of gradual change in wetland habitats is an example of a mechanism by which climate change can impact duck populations without correlated interannual variations between weather and population change (Hefley et al. 2016). I therefore recommend that research to understand how ducks are affected by climate change should transfer focus from non-lagged direct effects of weather on duck population growth to an understanding how climate affects habitat quality over many years and how this in turn influences duck vital rates or populations. For instance, there is not presently a

high-quality time series of wetland data for the North American but developing these products would help test a hypothesis that boreal and prairie duck populations are similarly impacted by wetland abundance.

Beyond quantifying climate impacts on wetland extent or abundance, future investigations should expand our understanding of impacts on wetland habitat quality. Because ducks rely on wetland invertebrate food sources to fuel reproduction and duckling growth (Krapu et al 1981, Cox et al. 1998), direct study of how aquatic invertebrate populations and communities respond to climatic variation and change would provide valuable insights. Some initial research has indicated potential for important changes in phenology of seasonal abundance (Gerten and Adrian 2002, Hansson et al. 2014) and potential for changes in communities (Burgmer et al. 2007, Corcoran et al. 2009). Experimental manipulations of wetland conditions to simulate predicted climate change would be particularly valuable because this would allow for inferences on the impacts of temperature regimes predicted, but not yet observed.

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6.4 Figures

Figure 6.1. Organization of thesis chapters according to internal and external population factors addressed.

