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ASSESSING CHANGES IN WATERFOWL POPULATION AND COMMUNITY  
DYNAMICS

by

Beth E. Ross

A dissertation submitted in partial fulfillment  
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Wildlife Biology

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UTAH STATE UNIVERSITY  
Logan, Utah

2014

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## ABSTRACT

Assessing Changes in Waterfowl Population and Community Dynamics

by

Beth E. Ross, Doctor of Philosophy

Utah State University, 2014

Major Professor: Dr. David Koons  
Department: Wildland Resources

Studying long-term ecological studies allows for a better understanding of processes driving populations and communities, and this understanding can be used to improve conservation efforts. These studies can describe how changes in the environment have led to current states of populations and communities, and indicate if the current state or trend falls within expectations based on past dynamics. Studies of long-term datasets also help ecologists predict how populations may shift with climate, water, or land-use change and determine necessary management action to maintain sustainable populations and community interactions. Serving as a “test of time,” long-term monitoring can provide insight into the influence of predation, intra- or interspecific competition, and other interactions on system dynamics. Studies need to explicitly include these drivers and sources of autocorrelation in data (e.g., spatial autocorrelation) to obtain unbiased estimates of ecological processes for guiding management. Fortunately, new statistical analyses for ecological applications are available that help ecologists make full use of the information present in long-term studies while properly accounting for sampling error and autocorrelation.

In this study, I use advanced statistical methods to analyze a long-term dataset, the Waterfowl Breeding Population and Habitat Survey, and address questions about waterfowl population and community dynamics. In Chapter 2, I use multi-state occupancy models to determine how the presence of lesser and greater scaup (*Aythya affinis* and *A. marila*)

has changed on their breeding grounds in North America since 1955. In Chapter 3, I use a Bayesian hierarchical model to determine the drivers of the breeding scaup population in the Northwest Territories of Canada. Lastly, in Chapter 4 I incorporate more waterfowl species into the hierarchical model from Chapter 3 to determine the drivers of the pochard duck community, along with the role of species interactions. My results indicate that the occupancy of scaup has decreased in the boreal forest of Canada and increased in the prairie parklands. Additionally, scaup in the Northwest Territories are largely influenced by density dependence and snow cover extent. Finally, the pochard community in the Northwest Territories is regulated more by environmental drivers than intra- or interspecific interactions. These results indicate that management of the species through hunting regulations likely deserves further study, as scaup likely exhibit some sort of compensation in response to hunting.

(111 pages)

## PUBLIC ABSTRACT

Assessing Changes in Waterfowl Population and Community Dynamics

by

Beth E. Ross

Studying long-term ecological studies can help ecologists understand what causes populations and communities of wildlife to change. Understanding these causes can help guide conservation efforts. Additionally, results from long-term datasets allow ecologists to predict how populations may shift with global change. Ecologists can then determine necessary management action to maintain sustainable populations in the future. However, there can be a large amount of “noise” in a long-term dataset. If ecologists fail to account for this noise, they may make incorrect management decisions. For example, samples taken in two nearby locations will likely be more similar than samples taken from two distant locations. Closely related data points such as this can cause mistakes in the analysis that lead to flawed decisions. Fortunately, new statistical analyses for ecologists are able to make full use of the information present in long-term studies while properly accounting for these biases.

In this study, I use advanced statistical methods to analyze a long-term dataset, the Waterfowl Breeding Population and Habitat Survey. This aerial survey counts the number of ducks in upper North America each summer, and I will use it to answer questions about duck populations and communities. In Chapter 2, I estimate how the population of lesser and greater scaup (*Aythya affinis* and *A. marila*) has changed since 1955. These species are of interest because their population is thought to be declining. I conclude that the proportion of breeding scaup has remained the same, which means that some other portion of their migration cycle is the cause of the decline. In Chapter 3, I compare environmental effects on scaup in the Northwest Territories of Canada to see which might be the most important. My results indicate that the average annual snow cover, summer drought conditions, and density dependence have the most influence on the population in this location. Lastly, in

Chapter 4 I include more species of ducks in my analysis to determine how they might be affected by changes in the environment. These results imply that the pochard community is affected the most by the environmental conditions in the NWT rather than interactions, such as competition, among members of the community.

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I continue to believe that the network of graduate students at USU is relatively unique, and I am grateful for all of the interactions and support I received from this group.

My parents, Bob and Lu Ross, have always supported my decisions and encouraged my continued (and continued...) education. Without their support and example, I would not have made it this far. Thank you.

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Beth Ross



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## CHAPTER 1

### INTRODUCTION

Studies of long-term ecological studies allow for a better understanding of processes driving populations and communities, and by doing so, can be used to improve conservation efforts (du Toit 2010). These studies can describe how changes in the environment have led to current states of populations and communities, and indicate if the current state or trend falls within expectations based on past dynamics (Lovett et al. 2010). Long-term datasets can also allow ecologists to predict how populations may shift with climate change and determine necessary management action to maintain sustainable populations and community interactions. Serving as a “test of time,” long-term monitoring can provide insight into the influence of predation (Colchero et al. 2009), intra- or interspecific competition (Viljugrein et al. 2005, Péron and Koons 2012), and other interactions on system dynamics, and how these processes might be affected by climate, water, and land-use change. Studies need to explicitly include drivers like these and various sources of autocorrelation in data (e.g., spatial autocorrelation, Beguin et al. 2012) to obtain unbiased estimates of ecological processes (Auer and Martin 2013, Viljugrein et al. 2005) for guiding management in the right direction. Fortunately, new statistical analyses for ecological applications are able to make full use of the information present in long-term studies while properly accounting for sampling error and autocorrelation.

In this study, I use advanced statistical methods to analyze a long-term dataset, the Waterfowl Breeding Population and Habitat Survey (BPOP), and address questions about waterfowl population and community dynamics. Several studies have used the BPOP dataset to address questions regarding density dependence (Sæther et al. 2008, Murray et al. 2010), or the effects of climate on waterfowl population (Drever et al. 2012), and community dynamics (Bethke and Nudds 1995). However, I am unaware of any study that has addressed the relative effect of all of these drivers simultaneously.

The BPOP survey is especially useful for understanding the drivers causing the spatio-temporal changes in the abundance of scaup (lesser and greater scaup combined, *Aythya*

*affinis* and *A. marila*). Scaup abundance in North America has declined to levels that are  $\sim 33\%$  below the North American Waterfowl Management Plan goal (Zimpfer et al. 2013), but greater scientific information is needed before sound management actions can be implemented. There is not a consensus on the underlying mechanisms that may have caused the decline (Austin et al. 2006), which appears to be greatest in the western boreal forest of Canada (Ross et al. 2012). Global change and increased drought (Sorenson et al. 1998) could be partly causing this decline through a decrease in wetland abundance and quality. In fact, some of these changes may already be occurring; Drever et al. (2012) found that decreasing snow cover extent in the boreal forest is negatively correlated with regional population growth rates in scaup, presumably through bottom-up impacts on wetland availability and quality for breeding scaup.

A leading hypothesis for the underlying cause of scaup decline is decreased food availability during spring migration, thus scaup are arriving on the breeding grounds in poor body condition (i.e., the Spring Condition Hypothesis; Austin et al. 2000, Anteau and Afton 2004). Long-term declines have been observed in body condition and nutrient reserves during spring migration, which could have a significant impact on reproductive effort and success (Anteau and Afton 2004). Moreover, Anteau and Afton (2008) found a long-term decline in consumption of their preferred food (*Amphipod spp.*) in the upper Midwest. Recent studies in the boreal forest, however, suggest that scaup in 2003 and 2004 had a similar body condition relative to historically collected scaup (DeVink et al. 2008a). Scaup on the Great Lakes and other migratory stopover locations are also known to contain high levels of toxins, particularly selenium (Anteau et al. 2007). However, DeVink et al. (2008b) and others (Fox et al. 2005, Matz and Rocque 2007) concluded that selenium and mercury levels are low in boreal scaup, and not likely responsible for the population decline in this important breeding region. Conflicting findings and a variety of other explanations (e.g., change in North American climate, altered trophic interactions, and anthropogenic developments in the boreal forest) illustrate the complicated nature of the decline in scaup abundance. Several factors are likely impacting scaup, and perhaps no single hypothesized

cause can explain the decline entirely, presenting the need for a thorough analysis that can address several hypotheses simultaneously.

A hierarchical model is one statistical method able to simultaneously quantify potential factors related to the decline of scaup. Hierarchical models have recently received a great deal of attention in ecology (Royle 2008), as have a unique type of hierarchical model called an occupancy model (MacKenzie et al. 2002). Both of these methods allow ecologists to incorporate hypotheses about population or community drivers while accounting for potential biases in long-term datasets (MacKenzie et al. 2003, Kery et al. 2009). Occupancy models estimate the probability of presence in a given area conditional on the probability of detecting presence at a site if it occurs (MacKenzie et al. 2002). A benefit of occupancy studies is that they only require presence and absence data, which can be easier to collect than information about abundance.

Here, I use the BPOP survey to better understand the drivers of the decline of scaup on their breeding grounds. In Chapter 2, I use multistate occupancy models (Nichols et al. 2007) to determine how scaup presence and pairing for breeding have changed since 1955. I then incorporate estimates of pairing probability as a measure of breeding propensity, defined as the probability a sexually mature adult will breed in a given year, in population models to determine how changes in scaup breeding propensity might be impacting their population dynamics. By comparing to spatio-temporal trends in abundance from my M.S. thesis in Statistics (Ross et al. 2012), I assess if changes in breeding propensity could have possibly driven the decline of the scaup population, or if other factors must have been more instrumental. If female scaup are in poor body condition when they arrive on the breeding grounds, they may delay or forgo breeding, both of which would appear as a drop in breeding propensity in the survey data.

In Chapter 3, I use a Bayesian hierarchical model to estimate specific drivers of scaup abundance in the Northwest Territories (NWT) of Canada, an important breeding area (Chapter 2, Ross et al. 2012). When applied to long-term datasets, hierarchical models can greatly increase our knowledge about ecological processes affecting abundance, species



richness, and other metrics of interest. Additionally, hierarchical models separate sampling and process variation and can incorporate random effects (Royle 2008). My hypothesized drivers of scaup in the NWT were density dependence, climate, and predator abundance, which may also affect scaup elsewhere (Sæther et al. 2008, Drever et al. 2012, Beauchamp et al. 1996).

In Chapter 4, I expand on the hierarchical model in Chapter 3 to address drivers of diving duck community dynamics in the NWT, of which scaup are included. I incorporate snow cover extent and total fox abundance, as in Chapter 3, but also include parameters to address how species covary in a community. This approach allows me to gain insight into the potential importance of waterfowl species interactions while explicitly accounting for environmental effects in the fixed-effect terms of the model. This study may be the first to incorporate a dynamic model with an effect for species autocorrelation while also accounting for observation error. However, other studies have addressed species interactions separately in the fixed terms (Adler and HilleRisLambers 2008). Including more waterfowl species in the model from Chapter 3 allows me to determine if the same factors driving scaup populations affect the diving duck community at large, or if scaup are a special case in the community, and declining because of factors only affecting them.

## CHAPTER 2

### SCAUP OCCUPANCY PATTERNS

#### 2.1 Introduction

To better understand the drivers of population dynamics, it is important to first understand how survival and reproduction in local spatial regions contribute to metapopulation dynamics (Runge et al. 2006). Decreases in survival and reproduction can indicate ecological “sinks” (Pulliam 1988), and sensitivity analysis of these parameters can provide insight into the best management actions available to reverse population declines (Caswell and Takada 2004). Making use of long-term datasets, especially those maintained over broad spatial extents, allows ecologists to better understand how the demography of a species has changed through time relative to habitat changes.

Worldwide, there are now a variety of long-term index surveys of avian abundance that provide a wealth of information for demographic research. For example, the North American Waterfowl Breeding Population and Habitat Survey (BPOP) provides a rich source of demographic data on 10 focal duck species dating back to 1955, and covers a large portion of each species’ breeding range (Zimpfer et al. 2013). Since 1978 the continental scaup (lesser scaup, *Aythya affinis*, and greater scaup, *A. marila*, collectively) population has declined to levels that are ~33% below the North American Waterfowl Management Plan goal (Zimpfer et al. 2013). This decline has sparked concern amongst hunters, management agencies, and conservation groups alike (Afton and Anderson 2001). The greatest decline in abundance of scaup appears to be occurring in the western boreal forest (Ross et al. 2012), where populations may have depressed rates of reproductive success (Martin et al. 2009), survival, or both (Afton and Anderson 2001, Walker and Lindberg 2005, Hobson et al. 2009). However, the specific vital-rate processes responsible for the decline are not known (Koons et al. 2006).

Three main hypotheses have been proposed for the scaup decline: 1) the Spring Condition Hypothesis concurrent with 2) an increased uptake of toxins during spring migration,

and 3) other factors such as climate change affecting wetland availability and quality. The Spring Condition Hypothesis states that scaup are experiencing decreased food availability during spring migration, thus arriving on the breeding grounds in poor body condition (i.e., the Spring Condition Hypothesis; Austin et al. 2000, Anteau and Afton 2004). Studies tracking body condition and nutrient reserves throughout the scaup migration have observed a long-term decline in both body condition and nutrient reserves that could have a significant impact on reproductive effort and success (Anteau and Afton 2004). Moreover, Anteau and Afton (2008) found a long-term decline in consumption of their preferred food (Order *Amphipoda*) in the upper Midwest. Recent studies in the boreal forest, however, suggest that scaup in 2003 and 2004 had a similar body condition relative to historically collected scaup (DeVink et al. 2008a). Scaup on the great lakes and other migratory stopover locations are also known to contain high levels of toxins, particularly selenium (Anteau et al. 2007). However, DeVink et al. (2008b) and others (Fox et al. 2005, Matz and Rocque 2007) concluded that selenium and mercury levels are low in boreal scaup, and not likely responsible for the population decline in this important breeding region. Conflicting findings and a variety of other explanations (e.g., change in North American climate, altered trophic interactions, and anthropogenic developments in the boreal forest) illustrate the complicated nature of the decline in scaup abundance. Several factors are likely impacting scaup, and perhaps no single hypothesized cause can explain the decline entirely.

While studies making use of multistate capture-mark-recapture models have been used for decades (Arnason 1973), developments of multistate occupancy models are relatively new (Nichols et al. 2007, MacKenzie et al. 2009). Without requiring unique knowledge of the individuals, multistate occupancy models focus on a given site's state of occupancy by an organism; such as species presence and successful reproduction, species presence without successful reproduction, or species absence (Nichols et al. 2007). Across both sites and surveys, one can estimate the proportion of sites in a particular occupancy state, which can be quite useful for guiding cost-efficient conservation and management plans at a landscape

scale. Accounting for the probability of detecting a species at a site is also a key component of these models, reducing bias and underestimation of occupancy rates (Nichols et al. 2007). Moreover, careful thought about the states considered could provide insight into underlying vital-rate drivers of population dynamics. Because occupancy models are relatively new and are still undergoing development, few studies have quantitatively determined how occupancy rates affect the dynamics of population abundance. As the two are closely related and of great importance to conservation and management, further research is needed in this area of occupancy modeling.

The BPOP assesses more than total abundance; it also monitors whether birds are observed in groups, as breeding pairs, or not observed at all along a survey segment (i.e., multiple states of occupancy among segments). By using the spatial hierarchy of the BPS survey, these data could be analyzed using recent multistate occupancy models to gain insight into spatial differences and temporal changes in “pairing propensity,” the probability scaup will form a pair bond, while concurrently accounting for an observer’s ability to detect scaup and properly classify the state variable. Such analyses could at least clarify whether changes in pairing and breeding propensity, the probability a female will breed, could be responsible for regional declines in scaup abundance. Previous work in Alaska has indicated that breeding propensity of female lesser scaup is low, which could be contributing to their decline (Martin et al. 2009). If changes in pairing or breeding propensity are responsible for the decline, researchers could focus on elucidating the mechanistic links between migratory habitat, food availability, scaup body condition, and demography. If not, then it would be warranted to focus greater attention on drivers related to other demographic pathways (e.g., predation on nests and breeding females, harvest during the non-breeding season, and other hypotheses).

Using long-term BPS data in a multistate occupancy framework, my objectives were to: 1) estimate probabilities of site occupancy and detection for breeding pairs relative to non-breeding groups on the breeding grounds, 2) quantify temporal changes in site-specific occupancy of the North American scaup population, and 3) determine the implications of

such changes on the dynamics of both spatial distribution and population growth.

## 2.2 Methods

### 2.2.1 Study Area and Survey Methods

I utilized data collected by the US Fish and Wildlife Service (USFWS) and Canadian Wildlife Service (CWS) during the North American Waterfowl Breeding Population and Habitat Survey (BPOP, Smith 1995). The BPOP has been flown every May and June since 1955 in the Traditional Survey Area (TSA), which encompasses the north-central United States, central and western Canada, and a large portion of Alaska (Fig. 2.1). This region is thought to represent the primary breeding grounds for a large proportion of North American waterfowl, including scaup. Moreover, the TSA consists of strata divided by similar habitats and duck densities (Smith 1995). Within each stratum pilots flew multiple transects, each comprised of 28.8 km strip-segments. The number of segments sampled in a transect ranged from 1 to 35, and varied through time. For my analysis, I treated the survey transect as the site (analogous to the individual in traditional capture-recapture analysis) and the segment as the basal sampling unit representing an encounter occasion. Because the majority of transects contained 12 or fewer segments, I broke the few long transects with greater than 12 segments into 2 or 3 ‘sites’, resulting in 427 total sites with 636 encounter occasions from 1955 to 2007. Dividing transects allowed me to reduce the number of non-surveyed or missing encounter occasions on short transects. This was a reasonable method because many transects are flown immediately adjacent to the last segment of the previous transect. The TSA encompassed several different habitat types (e.g., boreal forest, prairie parkland, and tundra). These broad regions are divided into 9 smaller crew areas for ground surveys based on geographical and political boundaries.

Throughout the survey, pilots counted the number of paired, single, and grouped ducks of each species to the left of the plane; accompanying biologists recorded the same information on the right side; the pooled counts by pilots and observer were used to assess occupancy state of the segment. I was interested in the delineation of scaup recorded in

mixed-sex groups (non-breeding or not yet paired) as opposed to breeding pairs; I did not utilize data regarding single drakes due to the skewed sex ratio in scaup (Afton and Anderson 2001). Fixed-wing aerial surveys such as this may yield biased estimates of naïve occupancy state (Green et al. 2008), and the probability of detecting ducks likely varied with observer and other factors (Koneff et al. 2008), which highlights the importance of accounting for heterogeneity in detection probability across the broad range of habitats encompassed throughout the TSA.

### 2.2.2 Model Descriptions

I developed a multistate model to estimate variation in scaup occupancy across space and through time (Nichols et al. 2007), but did not formally account for transition rates between alternative occupancy states over time (i.e., I did not utilize the robust design model because data were insufficient). For all models, I considered three observable states of scaup occupancy at a segment: unoccupied (0), occupied but not paired (i.e., grouped birds: 1), and occupied with paired scaup (2). The models consisted of 5 parameters: occupancy of a site by scaup, regardless of breeding state ( $\psi^1$ ), occupancy of a site by pairs, given the transect is occupied ( $\psi^2$ ), scaup detection probabilities for sites with ( $p^2$ ) or without pairs ( $p^1$ ), and the probability that evidence of pairing is found, given that a pair occurs at a site and is detected ( $\delta$ ). If a survey occurs in four segments, one example of an encounter history may be  $h_i=(1,0,2,1)$ , where non-paired scaup are detected in the first segment, no scaup are detected in the second, paired scaup are detected in the third, and non-paired scaup are detected in the last segment. The probability of this encounter history is then specified as  $\Pr(h_i) = \psi_i^1(1 - \delta_{i,1})p_{i,1}^2(1 - p_{i,2}^2)\psi_i^2p_{i,3}^2\delta_{i,3}p_{i,4}^2(1 - \delta_{i,4})$ . The likelihood for all encounter histories,  $\mathbf{h}$ , over all transects,  $S$ , is:

$$(1) \quad L(\boldsymbol{\psi}^1, \boldsymbol{\psi}^2, \mathbf{p}^1, \mathbf{p}^2, \boldsymbol{\delta}|\mathbf{h}) \approx \prod_{i=1}^S \Pr(h_i)$$

I developed a suite of models within the multistate framework using time (represented as either annual or decadal variation, as well as a model based on a change point at 1974

when the method for recording groups changed (Boomer and Johnson 2007), and crew area as covariates for the parameters just described (Table 2.1). I then used maximum likelihood to estimate model parameters (Nichols et al. 2007). Models with different covariates for detection probability were examined first, while holding occupancy parameters constant. Once the best covariates were selected for detection probabilities, I included these covariates in models to evaluate the best covariate structure for occupancy probabilities. The multistate occupancy framework is based on a conditional binomial model, where the probability of pairing (state 2) is conditional on the transect being occupied by scaup, and I assume that spatial sampling of segments without replacement adequately fits the binomial model (addressed in Discussion).

I compared models using Akaike’s Information Criterion adjusted for sample size (AICc; Akaike 1973; Tables 2.1 and 3.1). Models were implemented in the RMark package (Laake 2008) within R (R Core Team 2013).

### 2.2.3 Impact of Changes in Pairing Propensity on Population Dynamics

The conditional probability that paired scaup occupy a site,  $\psi_2$ , essentially represents a site-level pairing propensity, or the probability that a given site contains pairs of scaup. While it is possible that some paired scaup do not breed (Martin et al. 2009), the site-level pairing propensity is likely closely tied to the probability that an individual will breed (Afton 1984). For the following population model, I assume that scaup identified as paired will eventually breed. To heuristically address how changes in breeding propensity affect population dynamics, I parameterized the location and time-specific estimates of  $\psi_2$  from the best multistate occupancy model as breeding probabilities ( $bp$ ) in region-specific population models developed by Koons et al. (2006); a meta-analysis of demographic research studies. Koons et al. (2006) developed a population model for scaup based on survival and fecundity estimates from research in both the boreal forest as well as the prairie parklands, but based on different data than the BPOP survey. By incorporating estimates of breeding propensity from my occupancy analysis, I can determine how estimated changes have impacted population growth. The steps of going from a single  $\psi_2$  value to stage-specific

breeding probabilities were calculated as:

$$(2) \quad bp_{1(t,i)} = \frac{\psi_{2(t,i)}}{n_1 + bpratio \times n_2}$$

$$(3) \quad bp_{2+(t,i)} = bp_{1(t,i)} \times bpratio$$

where  $t$  represents time,  $i$  represents crew area,  $n_1$  is the age-1 component of the projected stage distribution at time  $t$  (see below),  $n_2$  is the age-2+ component of the projected stage distribution at time  $t$ , and  $bpratio$  is a constant based on estimates in Koons et al. (2006) that depicts the likelihood of breeding for females of age 2 or older relative to age-1 birds.

I projected population dynamics for a given crew area using the respective boreal forest or prairie parkland population models from Koons et al. (2006), which are based on a two-stage matrix model for female scaup:

$$(4) \quad \mathbf{A}_t^k = \begin{bmatrix} F_{1,t} & F_{2+,t} \\ P_1 & P_{2+} \end{bmatrix}$$

$$(5) \quad \mathbf{n}_{t+1} = \mathbf{A}_t^k \mathbf{n}_t$$

where  $k$  represents the region in which a crew area resides,  $t$  represents year, and  $F$  and  $P$  represent fertility and survival probabilities, respectively. Numerical subscripts on  $F$  and  $P$  represent stage classes (age-1 and age-2+ females). Additionally, fertility for a given stage  $s$  is given by:

$$(6) \quad F_s = 0.5 \times bp_s \times BS \times (CS_s \times NS + (1 - NS) \times RP_s \times CS_s \times NS) \times DS \times JS$$

where  $bp_s$  is the breeding propensity of females in stage  $s$  (see above);  $BS$  is the breeding-season survival for both age-1 and age-2+ females;  $CS_s$  is the estimate of clutch size of



females in stage  $s$ ;  $NS$  is the nest success;  $RP_s$  expresses the renesting probability for females in stage  $s$ ;  $DS$  is survival of the ducklings; and  $JS$  represents survival of juvenile scaup from fledging until the first birthday. All other estimates for the fertility parameters are taken from Koons et al. (2006). Population projection was initiated from the modeled stable stage distribution (Koons et al. 2006), but modified by crew area and time-specific estimates of  $\psi_2$ . While  $\psi_2$  was used to calculate stage-specific breeding probabilities for each crew area and time step, all other vital rates were held constant according to the levels reported in Koons et al. (2006). The projection modeling is thus more akin to sensitivity analysis, in that it assesses the effect of breeding propensity on population growth rate, given observed spatio-temporal variation in  $\psi_2$ , while holding all other vital rates constant. The results could nevertheless be used to see if changes in breeding propensity could have been responsible for observed changes in the abundance of breeding pairs over time and across space (Ross et al. 2012).

## 2.3 Results

### 2.3.1 Parameter Estimation

My results from  $AIC_c$  model selection indicate that one model far out-performed all others (Table 2.1), and it contained an interaction between year and crew area for occupancy of scaup,  $\psi^1$ , and condition occupancy of paired scaup,  $\psi^2$ . Additionally, the model indicated  $p_1$  was different before 1974 compared to after 1974,  $p_2$  varied by decade, and  $\delta$  varied by crew area (Table 2.1; Appendix, Table 6.1). I constrained parameter estimates for crew areas 1 and 2 to be similar due to convergence issues with models for separate estimates (point estimates obtained from the model with a full year by crew area interaction indicated that occupancy estimates for crew areas 1 and 2 were nevertheless biologically similar).

My top model indicated that the estimate of  $p^1$  was significantly higher before 1974, though the detection probability was low for both periods (0.064 before 1974 and 0.038 after 1974). Estimates of  $p^2$  were highest during the first decade of the study, and ranged from

0.511 to 0.59 throughout the duration of the study (Appendix, Fig. 6.1). Regardless of state, site occupancy by scaup ( $\psi_1$ ) decreased in crew areas 3 and 9, but increased or remained relatively constant in all other crew areas (Fig. 2.2). The conditional site-occupancy of paired scaup ( $\psi^2$ ) decreased in 4 crew areas, increased in 2, and remained stable in 2 (Fig. 2.3). Crew area 8 in the eastern prairies experienced a relatively large increase in occupancy by paired scaup (from approximately 0.5 to 0.9), while the largest decreases were in crew area 9 in the eastern portion of the TSA boreal region (from approximately 0.96 to 0.75) and crew area 7 in the prairie parkland region (from approximately 0.82 to 0.63). Crew area 1 had the highest estimate of  $\delta$  at 0.95 and crew area 9 had the lowest at 0.72 (Appendix, Table 6.2).

### 2.3.2 Impact of Changes in Pairing Propensity on Population Dynamics

Overall, changes in projection of the relative population growth rate reflected changes in estimates of  $\psi^2$ . The temporal changes in  $\psi^2$  for each crew area resulted in large and small changes in relative population growth rates in both the prairie parkland and boreal forest regions. Of particular note was the dramatic projected increase in growth in crew area 8 within the prairie parkland (increase of 0.18 since 1955); crew area 3 in the boreal forest region exhibited an increase in modeled growth rate as well (increase of 0.03 since 1955; Fig. 2.4). The largest decrease in both  $\psi^2$  and relative  $\lambda$  was in crew area 7 (decrease of 0.10 since 1955; Fig. 2.3) with crew areas 5, 6, and 9 also showing a decrease (decrease of 0.035, 0.035 and 0.06, respectively).

## 2.4 Discussion

I found that occupancy rates of scaup ( $\psi^1$ ) in all prairie-parkland crew areas increased since 1955; indicating that scaup have expanded their use of this eco-region. In contrast, rates of occupancy have recently decreased in the central and eastern boreal forest regions of the TSA (Fig. 2.2); suggesting that recent population decline has simultaneously resulted in range contraction, especially in crew areas 3 and 9 (Fig. 2.2). While the boreal forest was nearly completely occupied for the greater part of the study, the highest levels of transect

occupancy are now in the prairie parkland region, perhaps driven by underlying differences in the birth-death balance.

Additionally, it appears that the occupancy of paired scaup has changed throughout their range in different ways, and my results for the conditional occupancy of pairs were more spatially heterogeneous than those for the simple presence of scaup. There was a large decrease in  $\psi^2$  in the Western U.S. prairies (i.e., crew area 7), but large increases in the Eastern U.S. prairies (crew area 8). The decrease in  $\psi^2$  in crew area 7 coincides with an increase in  $\psi^1$ , indicating that the scaup occupying this area are now primarily not paired. Scaup may have shifted their breeding areas to the east as the western prairies became drier, and the eastern prairies saw an increase in precipitation, as well as an expansion of land enrolled in the Conservation Reserve Program (Reynolds et al. 2006). Indeed, it appears that nesting scaup have increased in the Dakota prairies (Stephens et al. 2005), and that population counts have increased as well. In the Canadian prairie-parklands,  $\psi^2$  has decreased slightly; however, the negative impact on modeled population growth (Fig. 2.3) is not large enough to explain the magnitude of observed population declines in the parkland region (Fig. 2.5). Thus, rather than low reproductive effort, poor reproductive success and female breeding season survival may have been more responsible for localized decline within the parklands (Koons and Rotella 2003).

At the eastern edge of the boreal TSA, however, the precipitous drop in  $\psi_2$  preceded the drop in  $\psi_1$ , indicating that reduced breeding propensity in this region may have driven local population decline and reduced use of the region. Yet, throughout the northern and northwestern boreal forest,  $\psi^2$  has either increased or remained stable near 100%, thus suggesting that breeding propensity has not been a causal factor of significant population decline found in other studies (Ross et al. 2012, Fig. 2.6). Using stable isotopes, Hobson et al. (2009) found that northern boreal habitats produce fewer scaup offspring per adult than southern prairie-parkland habitats. By comparing these results to the current study, it is likely that demographic factors other than breeding propensity, such as lower nesting success, duckling survival or female breeding season survival (Brook and Clark 2005), are

responsible for the low productivity of scaup in boreal Canada, thus leading to the decline in the population (Ross et al. 2012). The contribution of scaup pairing and breeding propensity to changes in projected population growth display a spatially heterogeneous signature. Changes in breeding propensity may have contributed greatly to both increases (crew area 8) and decreases (crew areas 7 and 9; Fig. 2.3) in population growth at the edge of the breeding range, but did not likely cause population decline within the important core breeding areas (parkland and boreal Canada) or in crew area 7 (Fig. 2.5).

Although my occupancy results illustrate the population-level implications of potential changes in scaup breeding propensity, or lack thereof, they may also be indicative of changes in migratory patterns, breeding phenology, or decisions of individuals that once bred at the edge of the range to disperse towards the core. Commensurate with temporal changes in the availability of preferred foods (Anteau and Afton 2006, 2008), scaup may have been forced to delay their spring migratory and breeding phenology since the 1950s in order to meet energetic demands. If scaup are migrating and breeding later, the surveys of the southern crew areas may be capturing birds that are now staging rather than breeding at the surveyed location (Naugle et al. 2000). Such a shift has been suggested by the Spring Condition Hypothesis, which states that female scaup are acquiring fewer nutrients during northward migration, thus arriving on the breeding grounds later and in poorer body condition (Anteau and Afton 2004). The BPOP survey design limits my ability to differentiate between true changes in breeding propensity as opposed to changes in phenology. Nevertheless, a shift in breeding phenology could be equally detrimental to the population. Birds breeding at a later date would have less time to raise a successful brood (Dawson et al. 2000), and surviving ducklings would have less time to acquire the necessary resources needed to migrate southward in the fall. For example, young hatching later would miss the main flux of invertebrates they rely on for food, causing further limitations in their development (i.e., the mismatch hypothesis; Visser et al. 1998, Drever and Clark 2007). However, if scaup are migrating later as suggested by the Spring Condition Hypothesis, then I would expect an increase in  $\psi_2$  in southern locations, which was observed, but I would also expect

a mirrored decrease at the most northern latitudes, which I did not find. Thus, it is more likely that  $\psi_2$  measures breeding propensity rather than changes in migratory and pairing phenology.

The multistate occupancy methodology lends itself nicely to a wide variety of data, such as occupancy of a particular territory (Nichols et al. 2007, MacKenzie et al. 2009), differing intensities of amphibian calls (MacKenzie et al. 2009), or types of indirect sign left by wildlife (Wilson et al. 2010). To my knowledge, my study is the first to use BPOP data to address questions regarding state-specific habitat occupancy of a waterfowl species. Although I was primarily interested in occupancy dynamics of scaup, the methods used here can easily be used to help gain insight into declines and range contractions of other waterfowl species (e.g., northern pintails; Miller and Duncan 1999), and help explain changes in breeding-season habitat use of waterfowl populations. The BPOP could also be combined with the 4-square mile pair surveys in the Dakotas or the historical brood surveys to address more detailed occupancy questions (Cowardin et al. 1995). Use of 2-species occupancy models could additionally illustrate any potential competition occurring between waterfowl species on the breeding grounds (MacKenzie et al. 2004).

The occupancy modeling framework used in this study assumes that transects are closed to changes in the state of occupancy during the survey period. Due to the large geographic area covered in the BPOP survey, this assumption may have been violated, especially given that surveys are conducted while scaup could still be migrating to their northern breeding grounds (Naugle et al. 2000). Additional surveys timed to better coincide with the scaup migration could prove useful for obtaining further information about the reproductive ecology of scaup and other late-nesting species.

In addition to closure assumptions, the BPOP sampling design violates an important sampling distribution assumption of occupancy models. Because the segments are flown systematically in one direction down a transect, and not selected randomly from the total area of the survey, my encounter occasions (segments) were sampled without replacement. Outcomes of sampling without replacement generally follow a hypergeometric distribution.

Occupancy models, however, are based on binomial distributions for encounter occasions that are sampled with replacement (MacKenzie et al. 2003). Consequently, substituting replications across space (without replacement) for replications over time (with replacement) can produce inherent bias in occupancy estimates (Kendall and White 2009). Yet, probability theory states that with a large sample space, and a small probability of selecting any particular outcome, the hypergeometric distribution approximates the binomial (Rice 2007). Given the large area encompassed by the TSA region (roughly 3.4 million km<sup>2</sup>) and the small total area of the flown segments (roughly 22000 km<sup>2</sup> in a given year), the probability of scaup selecting a given segment is approximately 0.006. Given this small probability, my estimates should have little if any bias from sampling spatially without replacement because the sampling outcomes are expected to closely approximate a binomial distribution.

By utilizing BPOP data within a recently developed occupancy modeling framework, I found strong evidence for a spatio-temporal shift in scaup occurrence (Fig. 2.2). Moreover, by integrating spatio-temporal changes in pairing propensity ( $\psi_2$ ; Fig. 2.3) into population models (as breeding propensity), I was able to heuristically investigate the role spatially heterogeneous breeding propensity may have played in regional population change. When combined with other studies and datasets (e.g., Hobson et al. 2009), it seems that breeding propensity is not the causal mechanism of population decline within core scaup breeding areas (parkland and boreal Canada, Ross et al. 2012), but it is still difficult to make such a judgment in other locales. However, Ross et al. (2012) concluded that these particular areas were the only areas exhibiting significant population decreases or increases (Figs. 2.5 & 2.6). Additionally, Koons et al. (2006) determined that breeding propensity had a low elasticity, therefore, relatively large changes in this parameter cause only a small change in population dynamics. The benefit of my multi-tiered modeling approach is that I was able to use existing datasets and the comparative method to gain insight into the likely, and unlikely, factors most responsible for changes in scaup population dynamics. Hopefully, connecting multiple modeling techniques such as this will help streamline future research efforts as we

work toward the common goal of understanding and managing declining populations.

Future work with occupancy models and the BPOP could involve several different outlets. The incorporation of broad-scale climatic indices, such as the Palmer Drought Severity Index, Pacific Decadal Oscillation, as well as snow cover extent, and predation could prove useful in describing population changes (see Chapter 3). Additionally, recently developed models for occupancy might also be of use. For example, the incorporation of a Markovian detection process into the model would likely be useful in controlling for spatial autocorrelation among segments on transects (Hines et al. 2010). Also, new Bayesian hierarchical models developed for single sampling occasions (Dail and Madsen 2013) may prove useful for the BPOP data, as these data have no sampling replicates due to the design of the survey. Occupancy models that explicitly incorporate changes in habitat in parallel with changes in occupancy (Breininger et al. 2009) could also be useful in areas of the prairie parklands, where changes in pond count and habitat enrollment programs (e.g., CRP) could be modeled at the same time as changes in occupancy.

TABLE 2.1. Top-ranked models based on differences in  $AIC_c$  ( $\Delta AIC_c$ ). Crew area and year or decade were used as covariates in the models. A parameter with no covariates is indicated by (.), and the number of parameters in a given model is indicated by ‘No. Par.’

Model	No. Par	$AIC_c$	$\Delta AIC_c$
$\psi(\text{year} \times \text{crew area}), \delta(\text{crew area}), p_1(1974), p_2(\text{decade})$	49	162551	0
$\psi(\text{crew area, 1\&2 separate}), \delta(\text{crew area}), p_1(1974), p_2(\text{decade})$	35	162811	259.4
$\psi(\text{decade}), \delta(\text{crew area}), p_1(1974), p_2(\text{decade})$	29	164970	2418.7
$\psi(\text{year}), \delta(\text{crew area}), p_1(1974), p_2(\text{decade})$	21	164985	2433.2



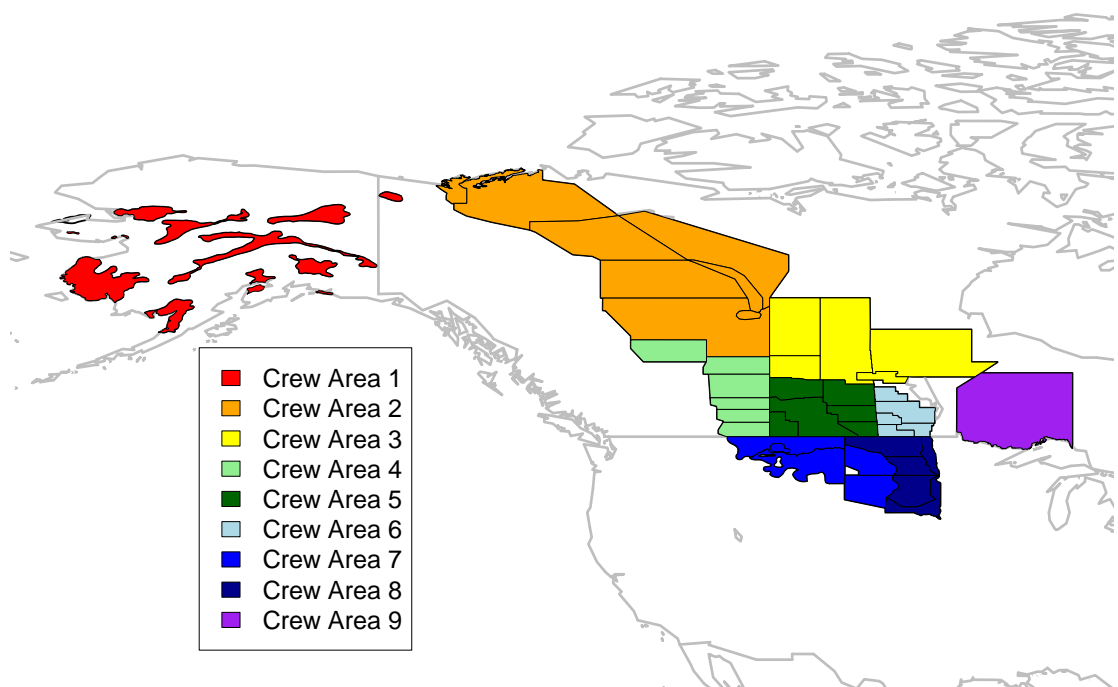


FIG. 2.1. Traditional Study Area for the North American Waterfowl Breeding Population and Habitat Survey with crew areas. Crew Areas 1-3 and 9 are in the boreal forest habitat, while the rest are considered prairie parklands.

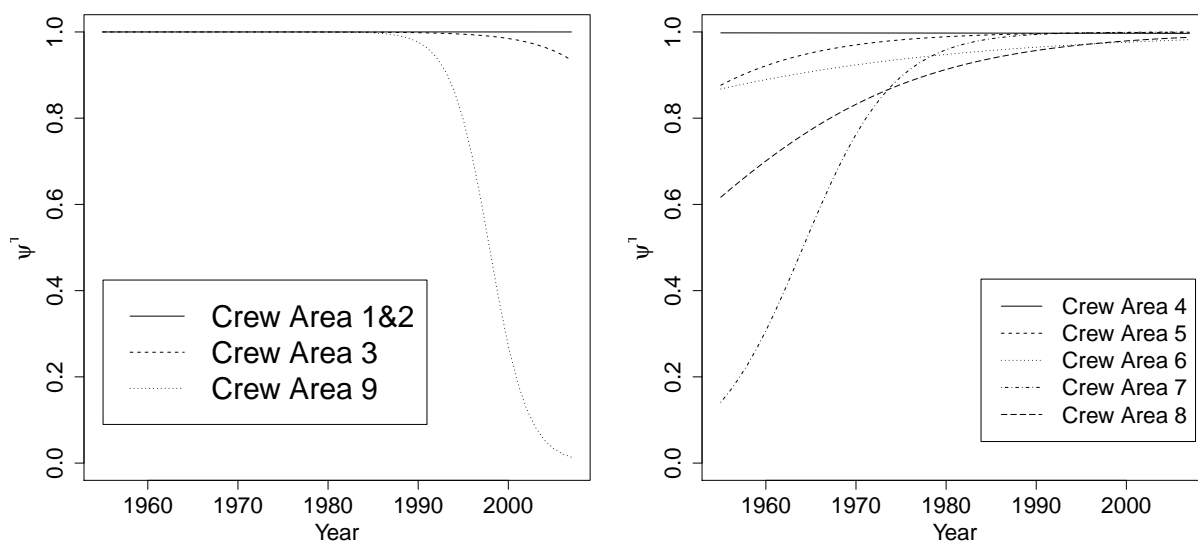


FIG. 2.2. Occupancy estimate of scaup ( $\psi_1$ ) for each crew area in the Traditional Survey Area of the North American Waterfowl Breeding Population and Habitat Survey. Occupancy estimates are given for 1955-2007 for boreal forest (A) and prairie parkland (B) habitats.

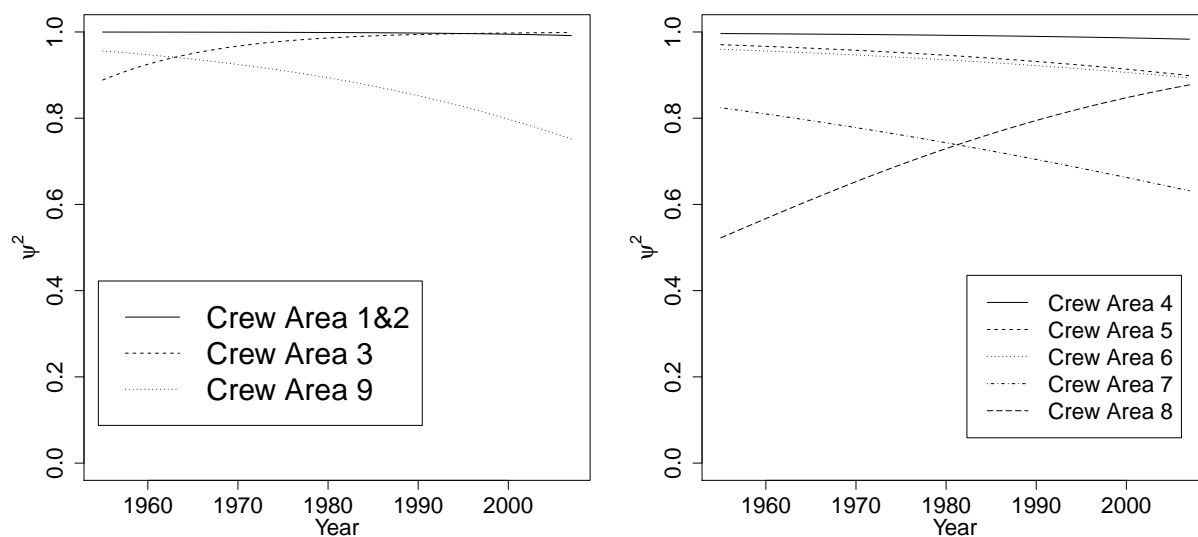


FIG. 2.3. Conditional occupancy of paired scaup ( $\psi_2$ ) in the boreal forest (A) and prairie parkland (B) regions of the Traditional Survey Area of the North American Waterfowl Breeding Population and Habitat Survey. Occupancy estimates are given for 1955-2007.

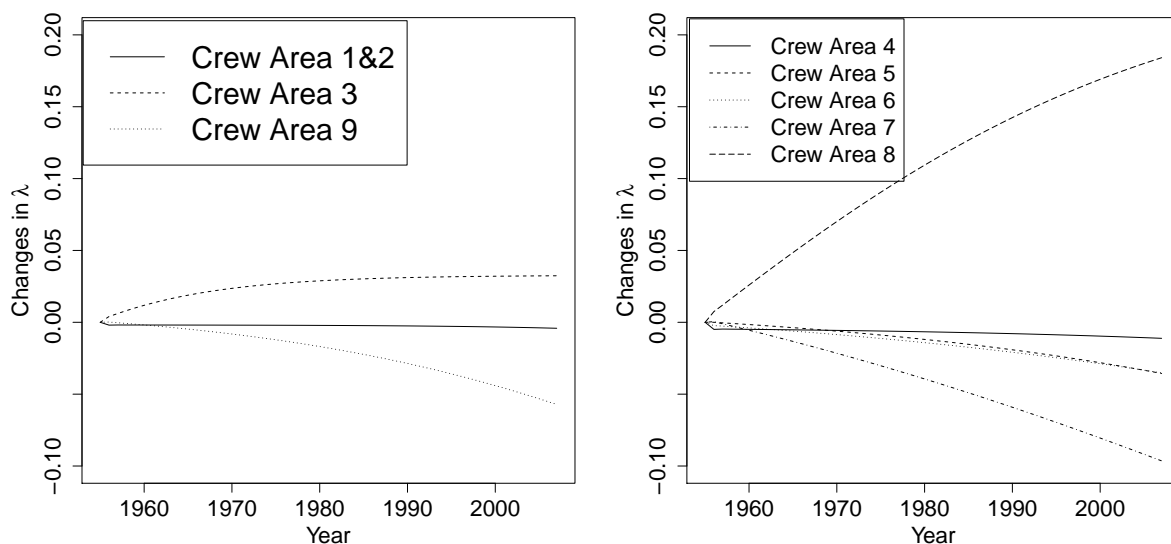


FIG. 2.4. Changes in the relative population growth rate since 1955 using the boreal forest (A) and prairie parkland (B) population models and the spatio-temporal estimates of  $\psi_2$  as breeding propensities.

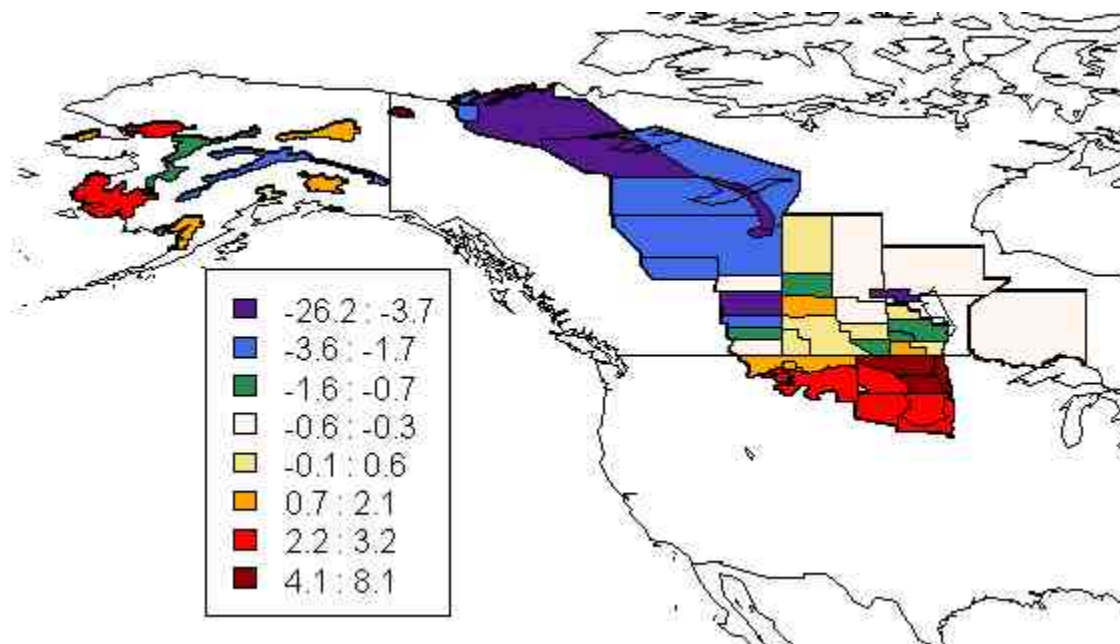


FIG. 2.5. Changes in counted breeding pair abundance since 1957. Negative numbers indicate pairs lost and positive numbers indicate pairs gained. Note that not all differences are estimated to be statistically different from zero. Figure recreated from (Ross et al. 2012)

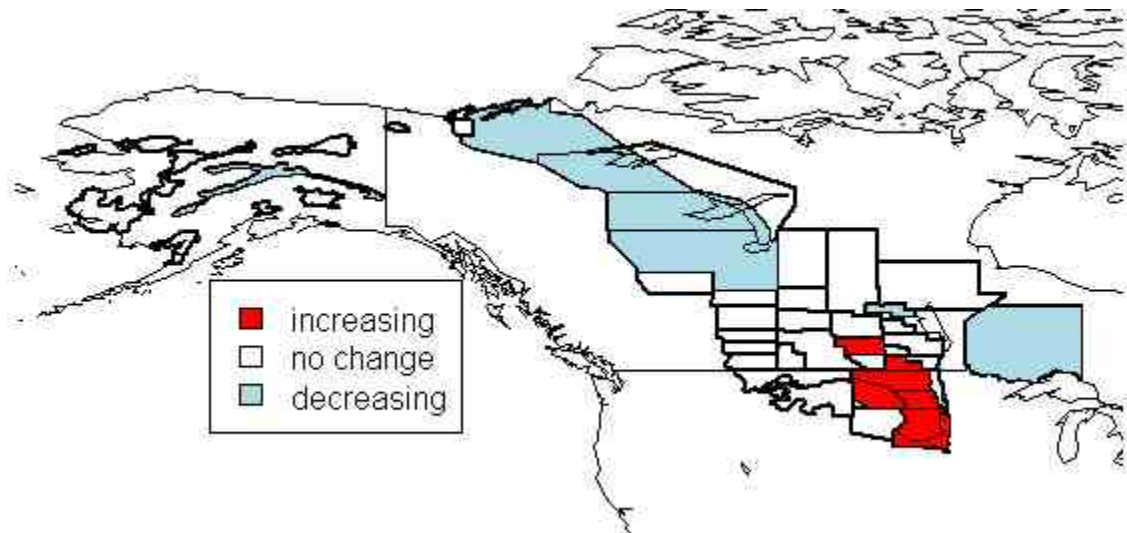


FIG. 2.6. Increases and decreases in the abundance of breeding pairs since 1957. Highlighted areas show a 95% chance of a population increase (red) or decrease (blue) in the area since 1957. Figure recreated from (Ross et al. 2012)

## CHAPTER 3

### DRIVERS OF SCAUP POPULATION DYNAMICS

#### 3.1 Introduction

Climate change is occurring more rapidly than during past global warming cycles (Rahmstorf et al. 2007), and worst-case scenarios predict a loss of biodiversity that would constitute the sixth major extinction (Bellard et al. 2012). Yet few studies address how climate change will alter species interactions (e.g., competition, predation), and shift resulting population dynamics (Rockwell et al. 2011, Zarnetske et al. 2012). Without fully understanding how climate affects populations in parallel with species interactions and other population drivers, effective management and conservation in the era of global climate change will be difficult (Hulme 2005).

In addition to direct effects on populations, e.g. through thermoregulatory effects on demography, climate can indirectly affect populations via changes to food web dynamics (Russell and Ruffino 2012) through predator-prey interactions (Wilmers et al. 2007) or resource availability (McCaffery et al. 2012). Moreover, changes in climate can intensify mechanisms related to density dependence (e.g., intraspecific competition, disease transmission, prey switching, etc., Lima and Berryman 2006). While work on small mammals (Lima et al. 2002) and ungulates (Forchhammer et al. 2002) has highlighted the interaction of density dependence, climate, and predation, many studies on population dynamics fail to incorporate multiple drivers into population models. Rarely are density dependence, climate, and trophic interactions examined simultaneously, which can lead to spurious conclusions about the regulators of population dynamics (Viljugrein et al. 2005).

In this chapter, I use a long-term, broad-scale dataset of scaup (lesser, *Aythya affinis*, and greater scaup, *Aythya marila*, combined during surveys because of their similar appearance) abundance to evaluate the influence of climate variables, indices of predator abundance, and density dependence on scaup population dynamics in the western boreal forest of Canada, the core of their breeding range. Scaup in North America have declined to

levels that are  $\sim 34\%$  below the North American Waterfowl Management Plan goal (Zimpfer et al. 2013), and the most precipitous declines have occurred in their preferred western boreal forest habitat in Canada (Ross et al. 2012). Although there is not a consensus on the underlying mechanisms causing the population decline (Austin et al. 2006), climate seems to be playing an important role (Drever et al. 2012), but an understanding of how climate, predation, and density dependence interact to drive population dynamics is lacking.

I propose, and test, several possible drivers of the scaup decline in their core breeding range. Climate change, for example, could directly affect waterfowl populations through a decrease in wetland abundance and quality via increased drought (Fig. 3.1; Sorenson et al. 1998). In fact, some of these changes may already be occurring. Decreasing winter snow cover duration on the boreal breeding grounds is related to reduced regional scaup population growth rates, presumably through impacts on summer wetland availability and quality for breeding scaup (Drever et al. 2012). In addition to direct effects on wetland habitat and associated food resources, climate could also indirectly alter predation on scaup through changes in alternative prey (Fig. 3.1). If predators preferentially feed on alternative prey species (e.g., small mammals) rather than a focal species (e.g., scaup), climate change can result in indirect effects on the focal species through changes in the alternative prey and a shared predator response to those resources (e.g., apparent competition; Oliver et al. 2009). For example, if predators experience increased survival and fecundity from an abundance of small mammals in year  $t$ , scaup would be negatively impacted through increased predation in year  $t+1$ . In such cases, I might expect lagged temporal effects of climate on a focal species as it can take time for numerical and functional responses to percolate through a food web (Walker et al. 2013).

In addition to indirect interactions and apparent competition, predators could also directly affect waterfowl through predation. Through direct interactions with the predator community, an increased predator abundance should negatively affect the abundance of a focal prey species via increased prey mortality, but handling time and prey switching can mitigate the intensity of such effects (van Leeuwen et al. 2013). Both climate and

predation can thus change the density of a focal population through a number of non-mutually exclusive trophic interactions. In turn, these effects should adjust the strength and ability to detect the presence of density dependence (Turchin 2003, Viljugrein et al. 2005).

Given the precipitous decline of the once abundant North American scaup population, and the evidence that climate may be playing a role in this decline (Drever et al. 2012), my objective was to simultaneously address how density dependence, climate, and predators all affect scaup population dynamics at the core of their breeding range. To better elucidate the factors that may be influencing the dynamics of this declining species, I used a state-space modeling approach that controls for observation error (de Valpine and Hastings 2002), the latter of which can lead to erroneous conclusions about the role of density dependence and environmental variation in regulating population dynamics (Freckleton et al. 2006). By simultaneously considering climate variables and other potential drivers of population dynamics, and using a rigorous estimation framework, future research and management can be based on more robust science for guiding conservation and policy decisions aimed at mitigating and reversing the deleterious response of scaup, and other species, to global climate change.

## **3.2 Methods**

### **3.2.1 Survey Methods**

Every year since 1955, the U.S. Fish and Wildlife Service and Canadian Wildlife Service conduct the North American Waterfowl Breeding Population and Habitat Survey (BPOP), which provides a rich source of demographic data for > 10 duck species, including scaup. The BPOP includes over 3.3 million square kilometers in the north-central United States, much of western Canada, and Alaska; purposefully covering a large portion of each species' breeding range (Fig. 3.2, Zimpfer et al. 2013). Surveys are conducted every May through June using aerial transects (Smith 1995), and flown at 145-170 km per hour at an altitude of 30-50 m. Multiple 28.8 km segments are combined to form strata, the main spatial unit

of the survey defined by ecozones and political boundaries. Observers survey 200 m on each side of the segment and record by species the number of lone drakes, flocked drakes (2 or more), pairs, mixed sex groups (3 or more), but not lone hens. My focus was on the delineation of scaup recorded as breeding pairs, rather than total scaup abundance, because pairs best represent the breeding potential of the population. I did not use data regarding single drakes because the skewed sex ratio in scaup means that males are not limiting in the population (Afton and Anderson 2001). I chose the Northwest Territories region of Canada (NWT) because of the substantial declines in regional scaup abundance (Afton and Anderson 2001, Ross et al. 2012) and the nature of available data regarding predators. Pelt harvest in this territory is conducted more for subsistence trapping, and the trends of furbearer harvest are likely more reflective of true furbearer demography than in other territories and states where trapping has become a hobby.

### 3.2.2 Model for Population Dynamics

My statistical model for the scaup population in the NWT is motivated by Gompertz density dependence (Turchin 2003, Dennis et al. 2006). Under discrete-time Gompertz growth, the population at time  $t$  ( $y_t$ ) is defined mathematically as

$$(7) \quad y_t = \lambda y_{t-1}^\theta$$

where  $\lambda$  is the population growth rate,  $y_{t-1}$  is the population at the previous time period, and  $\theta$  represents density dependence in the system. Taking the log of both sides and incorporating a term for stochasticity ( $\epsilon$ ) yields

$$(8) \quad \log(y_t) = z_t = \alpha z_{t-1} + r + \epsilon_t$$

where  $r = \log(\lambda)$ , the intrinsic rate of population growth from low density and  $\alpha$  is the effect of dependence on the log of population size at time  $t - 1$  ( $z_{t-1}$ ).

My basal unit of data was the total number of scaup pairs  $y_{i,j,t}$ , summed for each



segment  $i$ , in stratum  $j$ , in year  $t$ . The BPOP scaup data are overdispersed and contain a disproportionately high number of zeros along with a high variance relative to the mean (Ver Hoef and Boveng 2007, Ross et al. 2012). Thus, I considered two potential data models for statistical estimation of population dynamics, a model where  $y_{i,j,t} \sim \text{NegBinom}(\mu_{j,t}, \phi)$ , and a zero-inflated negative binomial model where

$$y_{i,j,t} \sim \begin{cases} 0, & \text{with probability } \psi \\ \text{NegBinom}(\mu_{j,t}, \phi), & \text{with probability } (1 - \psi) \end{cases} \quad (9)$$

for segments  $i = 1, \dots, n_j$  in stratum  $j = 1, \dots, m$  during observation period  $t = 1, \dots, T$  (e.g., years 1957-2012). The  $\mu_{j,t}$  parameter is related to the average number of counted pairs across segments in stratum  $j$  and year  $t$ , and  $\phi$  is an overdispersion parameter. The parameters related to the observation error,  $\psi$  and  $\phi$ , account for random under- and over-counting but do not account for any systematic bias in the counts.

Using  $\mu_{j,t}$  from the data model (Eq. 9), the process model was specified as

$$(10) \quad z_{j,t} = \log(\mu_{j,t}) = \alpha z_{j,t-1} + \beta_{0,j} + \mathbf{x}_{j,t}' \boldsymbol{\beta} + \epsilon_{j,t}$$

where  $\alpha$  is the degree of density dependence (as in Eq. 8), the  $\beta_{0,j}$  parameters are stratum-specific growth rates (analogous to  $r$  from Eq. 8) adjusted by  $\boldsymbol{\beta}$ , the vector of parameters to be estimated for  $\mathbf{x}_{j,t}$ , the vector of potentially time-varying and spatially-explicit covariates. A population then exhibits density dependence for values of  $\alpha < 1$ . The  $\boldsymbol{\beta}$  parameters thus directly add to or subtract from the population growth rate in each stratum,  $\beta_{0,j}$ , when covariate values differ from 0. Unstructured, spatial, or temporal stochasticity was modeled with random effects  $\epsilon$ .

To estimate the multiple processes that could have affected scaup population dynamics in the NWT during a  $> 50$  year time span, and to formalize my hypotheses about the underlying mechanisms affecting scaup population dynamics, I arranged covariates into three groups: 1) density dependence, 2) climate, and 3) predation. Models were then compared using the negative mean of the log of conditional predictive ordinate (CPO)

values (Held et al. 2010), ranking the models by their predictive ability using a form of leave-one-out cross-validation. I then combined variables from the best models of each group to simultaneously quantify effects of density dependence, climate, and predation.

### **Density-Dependent Effects**

I chose the Gompertz form of density dependence because it performs well in studies of waterfowl population dynamics (Sæther et al. 2008) and other species (Dennis et al. 2006, Knappe and de Valpine 2012; Eq. 7), and because it is difficult to statistically identify alternative models for density dependence from one another (Dennis and Taper 1994). In addition, the estimated intensity of density dependence can be biased when studies fail to separate sampling and process error, leading to incorrect conclusions about the role of density dependence in a system (Freckleton et al. 2006). I therefore used hierarchical models to separate sampling and process error and reduce bias in the estimation of key focal parameters, such as density dependence and other drivers of population performance (de Valpine and Hastings 2002, Knappe and de Valpine 2012). I estimated density dependence using the entire duration of the study from 1957-2012 in order to gain insight into the strength of density dependence in the absence of covariates. I also used this same time period to determine which random effects to include in the process model (i.e., spatial, temporal, or unstructured error) and which data model to use for further models (i.e., the negative binomial or zero-inflated negative binomial).

### **Climate Effects**

Scaup arrive on the breeding grounds and nest later than many other waterfowl species (Austin et al. 1998). Because of this unique life-history characteristic, they may be especially sensitive to environmental changes. To examine how climate impacts scaup population dynamics in the NWT, I considered an array of climate variables that could affect environmental conditions for scaup on their breeding grounds. These included broad-scale climate circulation indices as well as more fine scale variables. Each chosen climate variable had previously been shown to affect the population dynamics of avian species (Papineau 2001,

Drever et al. 2012, Smith and Gaston 2012). Because of differences in data availability, I quantified the effects of climate for two time periods: 1967-2010, the time period when snow extent data were available, and 1958-2010, the time period when all other climate variables were available. Unless otherwise stated, each covariate was averaged over the current “scaup year,” from the beginning of June in year  $t-1$  to the end of May in year  $t$  (because the BPOP survey in the NWT tends to occur in early June each year). I chose this time frame to incorporate effects of environmental conditions and trophic mismatches (Drever et al. 2012) on duckling survival from year  $t-1$  to year  $t$  when populations are counted. I also considered lag-1 effects for climate variables on the breeding grounds because climate during June  $t-2$  to May  $t-1$  can affect primary productivity and the abundance of alternate prey (e.g., microtine rodents for foxes Elmhagen et al. 2000 or fish for mink Zschille et al. 2014), potentially eliciting a numerical response in predators that could in turn affect waterfowl nest success and offspring survival in the following year (Walker et al. 2013).

In addition to the broad-scale Arctic Oscillation (AO) and Pacific Decadal Oscillation (PDO) circulation indices that could influence overall wetland dynamics and food resources in the NWT (Papineau 2001, Morrison and Hik 2007, Smith and Gaston 2012), I also considered more fine-scale climate variables to gain deeper insight into spatio-temporal processes. Palmer Drought Severity Index (PDSI) data were available in a 2.5 degree grid over the study area (Dai et al. 2004). The center of each stratum was calculated, and the grid value that corresponded to this center was used as an estimate for the stratum. Rather than calculate PDSI for the entire scaup year, I used specific time periods related to the time of breeding as the covariate. I calculated PDSI for the following three seasons: the early (the month of May just before  $t-1$  and June of year  $t-1$ ), late (July and August of year  $t-1$ ), and total breeding season (the month of May just before  $t-1$  through August of year  $t-1$ ). The response of scaup to PDSI during the breeding season would then affect surveyed abundance in year  $t$ . The lag-1 effects of PDSI were calculated in the same fashion but relative to year  $t-2$ , which could capture complex trophic interactions among PDSI, alternative prey, and predators that eventually affect scaup.

The spring melt of winter snowpack may have a greater effect on wetland dynamics than other forms of precipitation, and decreased snow cover duration has a negative impact on scaup abundance (Drever et al. 2012). Snow cover extent duration was averaged over the current scaup year, from June of year  $t-1$  to May of year  $t$ . Data on snow cover extent were in a grid-based format (Robinson and Frei 2000), and aligned in the same manner as the PDSI data. The measure of snow cover extent in the current scaup year would primarily affect surveyed abundance at time  $t$  in stratum  $j$  primarily through settling and habitat-selection decisions (e.g., through wetland and icepack conditions upon arrival to the breeding grounds). The lagged effect would be indicative of impacts on demography in the previous breeding season that in turn affect surveyed abundance at time  $t$ . Thus, to capture any impacts snow extent might have on complex trophic interactions that take time to percolate through the food web to scaup, I also considered lag-2 effects.

I chose the climatic indices above for their relationship to high latitudes and boreal forest habitat. Changes in climate along migratory routes could have a direct impact on migratory phenology, and because the BPOP survey is not designed for the scaup life cycle, such processes could in turn affect the abundance of scaup counted on the breeding grounds (i.e., through an availability bias; Austin et al. 2002). To account for such processes to the best of my abilities, I used the El Niño Southern Oscillation (ENSO) and the abundance of ponds in the prairies in the current scaup year as covariates because each might affect the availability of habitat and food resources during scaup migration northward to the NWT (Naugle et al. 2000, Stenseth et al. 2003); yet I note that changes in migratory phenology could also be affected by other variables that are difficult to measure at broad scales.

### **Predator Effects**

I also evaluated the relationship between scaup population dynamics and indices of predator abundance: red fox, *Vulpes vulpes*, total fox (red and arctic fox, *Vulpes lagopus*), and mink, *Neovison vison*, which are known to prey heavily on scaup nests, ducklings (Talent et al. 1983, Pietz et al. 2003) and reproductive females (Afton 1984, Koons and Rotella 2003). An index to predator abundance for each species, or group of species, was developed

based on furbearer data from Statistics Canada for 1958-2012. The number of furbearer pelts harvested was reported collectively for the Northwest and Nunavut territories until 1999 (when the territories divided). To estimate the proportion of fox pelts harvested in the boundaries of the current NWT alone until 1999, I calculated the average proportion of pelts harvested from each territory using data available from 2000-2006. The proportion of fox pelts harvested from the NWT during 2000-2006 was applied to past data to obtain estimates of the fox pelts harvested in the NWT from 1970-1999. Since nearly all mink (> 90%) were collected within the current NWT border, and not Nunavut, no proportional adjustment was made for the mink data and the collective counts were used.

Because furbearer harvest could be influenced by socio-economic factors related to fur trapping, I first used the price per pelt adjusted for inflation and the lag-1 adjusted price per pelt as predictor variables in a linear regression model for furbearer abundance. Quadratic parameterizations of the predictor variables were also considered, accounting for non-linear responses to changes in fur harvest, and all models were fit using maximum likelihood. The best model for socio-economic drivers of annual pelt numbers was selected using Akaike's Information Criterion adjusted for sample size ( $AIC_c$ ; Akaike 1973). The standardized residuals from the best model for each predator species were then used as a covariate in the process model for scaup population dynamics for 1958-2012 (Eq. 10).

### **Model Implementation**

I considered additive and plausible interactive models with the variables that performed best in the preceding topical analyses. Typically, the state-space model above (Eqs. 9 and 10), with or without covariates, would be fit using Markov Chain Monte Carlo estimation of posterior distributions, usually using a combined Gibbs sampler and Metropolis-Hastings algorithm after solving for the full-conditional distributions where closed-form solutions exist (Banerjee et al. 2004). Instead, I used integrated nested Laplace approximation (INLA) to approximate the marginal posterior distributions of the parameters of interest (Rue et al. 2009, Ruiz-Cárdenas et al. 2012). By making use of latent Gaussian models, INLA is capable of approximating the posterior distribution with high accuracy at a much faster

computational rate than Markov Chain Monte Carlo estimation of posterior distributions of the parameters (Rue et al. 2009). I implemented INLA using the R package (INLA; Rue et al. 2009, R Core Team 2013) and provide annotated code pertaining to my models (Appendix). Priors were set using default values and distributions in the INLA package (Rue et al. 2009, Ruiz-Cárdenas et al. 2012). Additional background on a related model and implementation can be found in previous work (Ross et al. 2012).

### 3.3 Results

#### Density-Dependent Effects

The strength of density dependence was significant (95% credible intervals for  $\alpha$  were  $< 1$ ) when implemented in a model without covariates for climate or predator abundance. I then considered density dependence in further models (referred to as the null model) with climate or predator covariates (or later both) because the effect of density dependence can change in the presence of environmental variability and resource limitation (Viljugrein et al. 2005). A process model with an unstructured random effect was the only form of random effect that converged for all models and was used in subsequent models with climate and predator covariates along with a negative binomial data model ( $-\text{mean}(\log(\text{CPO}))$ ) of 5.045 vs. a zero-inflated model, 5.051).

#### Climate Effects

When I compared climate-effect models for 1967-2010 (when snow extent data were available) using the  $-\text{mean}(\log(\text{CPO}))$ , a model with snow cover extent with both an immediate and a lag-2 effect ranked better than models with other effects of snow extent, as well as models with AO, PDO, and PDSI covariates, though a model with lag-1 July-August PDSI ranked second best (Appendix, Table 6.3). The lowest  $-\text{mean}(\log(\text{CPO}))$  indicates that snow cover extent in the winter and spring immediately preceding surveyed abundance at time  $t$  along with a delayed effect from time  $t-2$  are better at predicting scaup population dynamics than other covariates. When eliminating snow extent from the analysis and

expanding the time frame to 1958-2010, a model with a lag-1 and current effect of July to August PDSI ranked best (Appendix, Table 6.4), indicating that drought severity during the late breeding season better predicts changes in scaup population dynamics than other climate covariates available during the 1958-2010 time period. The models with climate and habitat covariates hypothesized to influence scaup population dynamics in the NWT through changes in migratory phenology (ENSO and pond counts) were not well supported in either analysis (i.e., they performed worse than models with more localized climate on the breeding grounds).

### **Predator Effects**

The best socio-economic model from the set of furbearer regressions included a linear effect for the price of pelts in the previous year for red fox and total fox, and quadratic effect of price of pelts in the current year for mink (Appendix, Tables 6.5, 6.6, & 6.7). Residuals from these models were z-standardized and used as covariates in the process model for scaup population dynamics (Appendix, Fig. 6.2).

In the group of models for predator index effects on scaup population dynamics, total fox abundance (with a quadratic effect) had the best ability to predict scaup population dynamics in the NWT relative to other predator abundance indices. All other models for predator index effects on scaup population dynamics performed worse than the null model with just density dependence (Appendix, Table 6.8).

### **Combined Effects**

For both time periods (1958-2010 and 1967-2010), models with covariates related to local climate (July-August PDSI + lag-1 July-August PDSI, or snow cover + lag-2 snow cover extent, respectively) were retained in the best-ranking model among those allowing for various combinations of the density-dependence, climate, and predator variables that performed best in the preceding analyses. For the 1958-2010 time period, interactions between a quadratic effect of total fox abundance and the immediate and lagged effects of July-August PDSI were additionally supported (Tables 3.1). Of particular note, the interactive

effect for lag-1 July-August PDSI by total fox abundance was positive and statistically significant (i.e., 95% CI did not overlap 0; Table 3.2). During times of drought (i.e., negative values of lag-1 July-August PDSI), the index for total fox is concave down, with the highest predicted abundance of scaup pairs at intermediate levels of total fox abundance (Fig. 3.3). With wetter conditions, and positive values of lag-1 July-August PDSI, the effect of total fox abundance switches to concave up, and predicted scaup abundance is greatest at either high or low levels of total fox abundance. Overall, the largest predicted values of scaup pair abundance are in years with wet conditions and high total fox abundance (Fig. 3.3), though the majority of observed conditions occur in mid-ranges of fox abundance and values of lag-1 July-August PDSI.

A much simpler model with only the lag-2 and immediate effect of snow cover extent performed best for 1967-2010 (Table 3.2). An increase of snow cover in the winter and spring immediately preceding scaup abundance surveys at time  $t$  resulted in statistical and biologically significant reductions in scaup population abundance in a given stratum at the time of survey (Table 3.4, Fig. 6.1). Alternatively, snow cover extent in winter and spring two years prior did not have a statistically significant effect on scaup population dynamics in year  $t$ . All estimates of the intrinsic growth rate for each stratum from the top models ( $\beta_{0,j}$ , Eq. 10) were less than 0, indicating a decreasing population in each stratum at covariate levels of 0 (Tables 3.2 & 3.4). When considered simultaneously with climate and/or predator effects, density dependence ( $\alpha < 1$ ) was present during both time periods (Tables 3.2 & 3.4).

### 3.4 Discussion

Several studies have evaluated the effects of predation (Sargeant et al. 1984, Beauchamp et al. 1996) and abiotic drivers (Drever et al. 2012, Almaraz et al. 2012) on waterfowl population dynamics, yet none that I am aware of have simultaneously evaluated predation and climatic effects and how they may interact. I show that breeding pair dynamics of scaup in the Northwest Territories were correlated significantly with climatic variables, and my results suggest that the effects of predation shift with climatic intensity (i.e., drought),



though this interaction was poorly estimated for 1967-2010.

For the years when snow data were available, snow cover from the winter and spring prior and two years prior to the beginning of the breeding season in May of year  $t$  were the most important climatic variables. The importance of snow cover seems to primarily relate to the immediate effects of snow cover, which likely affect settling decisions of scaup as they arrive in the NWT, and less through trophic cascades related to alternative prey. While not statistically significant, the lag-2 effect was also included in the top model from the climate analysis, indicating that the lag-2 effect of snow cover may be important relative only to more immediate effects. While my results indicate a negative associate with increased average snow cover extent, other studies have shown a positive relationship with total snow cover extent (Drever et al. 2012), though the analysis framework differed between studies. Still, other results from my study also indicate a negative response to drought indices, consistent with the findings from Drever et al. (2012).

The intensity of drought in the NWT was also important for scaup population dynamics, and additionally supported my hypothesis that trophic interactions affect scaup population dynamics. The best ranking climate variable during the 1957-2010 time period (for which snow data were not available) was the July-August PDSI and lag-1 effect. The effect of July-August PDSI suggests that scaup demography responds most strongly to changes in water availability during the late breeding season, likely through mechanisms affecting predation on ducklings and food resources that could affect both duckling and juvenile survival (Dawson et al. 2000, Walker and Lindberg 2005). Although not the vital rates with the greatest potential to affect population growth, changes in scaup duckling and juvenile survival can have important impacts on population dynamics (Koons et al. 2006). Additionally, the interaction of the lag-1 effect of July-August PDSI with total fox abundance suggests impacts of July-August PDSI on alternate prey for foxes, and related numerical response by foxes might eventually affect scaup population dynamics as well. Although not conclusive, my findings suggest that future studies of the effects of interactions between climate, predators, and alternative prey on scaup are needed.

The southern (ENSO) climate oscillation index was a poor predictor of scaup dynamics in the Northwest Territories, as were fluctuations in pond counts in the PPR. Some researchers have hypothesized that scaup may have changed their timing of migration (Austin et al. 2002), which could be related to variation in temperature on their early-spring staging areas (Naugle et al. 2000). The lack of an ENSO effect on counts of scaup pairs in the Northwest Territories suggests that such changes have not occurred, or are not related to the ENSO averaged over the scaup year. In addition, changes in wetland numbers in the PPR driven by drought, drainage, or tiling that creates deeper wetlands (which in turn support fish that compete with scaup for food resources) could affect forage availability in this important staging area for scaup migrating northward to the boreal forest (Anteau and Afton 2006, 2008). The Spring Condition Hypothesis (Afton and Anderson 2001, Anteau and Afton 2004, 2008) proposes that scaup may be migrating later because of a) insufficient food resources on the critical prairie pothole region staging area, or b) the need to regain body condition during staging because of insufficient food resources and body condition in more southern locales, in turn resulting in fewer scaup arriving on the breeding grounds in time to be counted (Anteau and Afton 2006). If this process is occurring, variation in the PPR wetland numbers does not appear to be a good surrogate for identifying such cross-seasonal effects on scaup pairs in the boreal forest. I found no evidence for an effect of PPR pond conditions on scaup abundance further north in the NWT.

Other long-term, large-scale studies of population dynamics in waterfowl species (Viljugrein et al. 2005, Sæther et al. 2008, Murray et al. 2010) found marginal support for density dependence in some diving duck populations, including scaup. My results indicated that density dependence is an important driver of scaup pair abundance, at least in the NWT. An important aspect of my study was the reduction in bias by separately estimating sampling and process error (Freckleton et al. 2006). Previous analyses I conducted that did not properly account for this bias through state-space modeling yielded results that suggested density dependence was not an important driver of scaup population dynamics in the NWT (results not shown), highlighting the importance of this state-space model-

ing approach. While I did not explicitly test interactions between climatic variables and density dependence, the strength and significance of density dependence did not change with the inclusion of climate and predation effects, and was a significant driver of population dynamics with or without other covariates. Density dependence could be affecting the population through competition for resources throughout their migratory cycle, density-dependent predation of nests, increases in disease transmission (Lima and Berryman 2006), or a combination of factors that requires further research targeted at identifying density-dependent mechanisms.

There are several ways that my results can be used to help guide management actions. For example, determining the relative influence of predation and climate on population dynamics can fundamentally change directives of management actions taken to influence a population most efficiently (e.g., predator control during drought, habitat management, or broader-scale policies directed at mitigating the impacts of climate change). Moreover, the effect of local density dependence on the breeding grounds indicates the potential for compensatory effects of harvest, though the mechanism for any such compensation is still unknown (e.g., mortality compensation, reproductive compensation). These processes are of high management concern (Austin et al. 2006) and deserve additional study using modern quantitative methods that can take advantage of available data.

In conclusion, changes in abundance of breeding scaup in the NWT seems to be most greatly tied to density dependence, climate, and to some extent predator abundance, specifically an interaction between predators and climate for some time periods. Scaup population dynamics do not seem to be driven by potential changes in migratory phenology, as climate and pond conditions in the south do not seem to be as important as snow cover and drought in the north. Although exploration of other variables that could be affecting migratory phenology, and the potentially related effects on surveyed counts, deserve further study. My results highlight the benefits of comparing multiple environmental and intrinsic population drivers when studying species of management and conservation concern to best elucidate how future changes in climate may affect populations through both direct and indirect

pathways. Although the results might not yet be clear enough to guide on-the-ground management actions, my findings build upon the work of Drever et al. (2012) and provide insight into where future research on scaup population dynamics should be conducted.

TABLE 3.1. Comparison of models from the combined analysis of scaup pair abundance in the Northwest Territories from 1958-2010. Covariates from the top model within each group are abbreviated as “fox” for the predator group (a model with total fox + (total fox)<sup>2</sup>) and “PDSI” for the climatic group (a model with an effect of  $\text{PDSI}_{\text{July-August}} + \text{PDSI}_{\text{July-August,lag-1}}$ ). “Null” indicates a model with no covariates, but all models contain an unstructured random effect and Gompertz form of density dependence in the process model. Models are ranked by the negative mean of the log of the CPO values.

Model	-mean(log(CPO))
Fox $\times$ PDSI	5.0317
PDSI	5.0424
Null	5.0460
Fox + PDSI	5.0463
Fox	5.0511

TABLE 3.2. Parameter estimates from the top model shown in Table 1 for the combined analysis of scaup pair abundance in the Northwest Territories during 1958-2010, including mean, standard deviation (SD) and 95% credible intervals (0.025 quantile and 0.975 quantile). The  $\beta_{0,j}$  parameters represent the stratum-specific ( $j^{th}$ ) growth rates, ‘Fox’ represent the beta estimates for the linear or quadratic index of total fox abundance, ‘PDSI<sub>July–Aug</sub>’ represents the beta estimate for July-August PDSI, ‘PDSI<sub>July–Aug,lag–1</sub>’ represents the beta estimate for the lag-1 July-August PDSI, and  $\alpha$  represents the strength of density dependence.

Parameter	Mean	SD	0.025 quantile	0.975 quantile
$\beta_{0,13}$	-0.4792	0.18	-0.7863	-0.1404
$\beta_{0,14}$	-0.6938	0.26	-1.1258	-0.2097
$\beta_{0,15}$	-0.4598	0.18	-0.7607	-0.1298
$\beta_{0,16}$	-0.4510	0.18	-0.7501	-0.1222
$\beta_{0,17}$	-0.5908	0.22	-0.9505	-0.1905
$\beta_{0,18}$	-0.4904	0.19	-0.8095	-0.137
PDSI <sub>July–Aug</sub>	0.0136	0.01	-0.0117	0.0389
PDSI <sub>July–Aug,lag–1</sub>	-0.0312	0.01	-0.0587	-0.0037
Fox	-0.0064	0.02	-0.0403	0.0288
Fox <sup>2</sup>	-0.0027	0.01	-0.0212	0.0162
PDSI <sub>July–Aug</sub> × fox <sup>2</sup>	-0.0019	0.0056	-0.0128	0.009
PDSI <sub>July–Aug,lag–1</sub> × fox <sup>2</sup>	0.0150	0.007	0.0013	0.0286
PDSI <sub>July–Aug</sub> × fox	-0.0088	0.012	-0.0324	0.0148
PDSI <sub>July–Aug,lag–1</sub> × fox	-0.0050	0.0157	-0.0359	0.0258
$\alpha$	0.8931	0.043	0.8099	0.9761

TABLE 3.3. Comparison of models from the combined analysis of scaup pair abundance in the Northwest Territories from 1967-2010. Covariates from the top model within each group are abbreviated as “Fox” for the predator group (a model with total fox + (total fox)<sup>2</sup>) and “Snow” for the climatic group (a model with an immediate and lag-2 effect of snow cover extent). “Null” indicates a model with no covariates, but all models contain an unstructured random effect and Gompertz form of density dependence in the process model. Models are ranked by the negative mean of the log of the CPO values.

Model	-mean(log(CPO))
Snow	5.0066
Fox + Snow	5.0166
Null	5.0247
Fox × Snow	5.0195
Fox	5.0387

TABLE 3.4. Parameter estimates from the top model in the combined analysis of scaup pair abundance in the Northwest Territories during 1967-2010, shown in Table 3, including mean, standard deviation (SD) and 95% credible intervals (0.025 quantile and 0.975 quantile). The  $\beta_{0,j}$  parameters represent the stratum-specific ( $j^{th}$ ) growth rates, ‘Snow<sub>lag-2</sub>’ represents the beta estimates for snow cover extent in the winter and spring preceding scaup abundance surveys at time  $t-2$  and its effect on scaup population growth between  $t-1$  and  $t$ , ‘Snow’ represents the beta estimates for snow in the winter and spring preceding scaup abundance surveys at time  $t$ , and  $\alpha$  represents the strength of density dependence.

Parameter	Mean	SD	0.025 quantile	0.975 quantile
$\beta_{0,13}$	-0.6877	0.2128	-1.0548	-0.3081
$\beta_{0,14}$	-0.943	0.3019	-1.4601	-0.4038
$\beta_{0,15}$	-0.833	0.2316	-1.2399	-0.4154
$\beta_{0,16}$	-0.7508	0.2155	-1.1223	-0.366
$\beta_{0,17}$	-0.8924	0.262	-1.3372	-0.4263
$\beta_{0,18}$	-0.7815	0.2294	-1.1762	-0.3725
Snow <sub>lag-2</sub>	0.0294	0.0346	-0.0386	0.0972
Snow	-0.1124	0.0346	-0.1805	-0.0445
$\alpha$	0.83	0.05	0.73	0.93

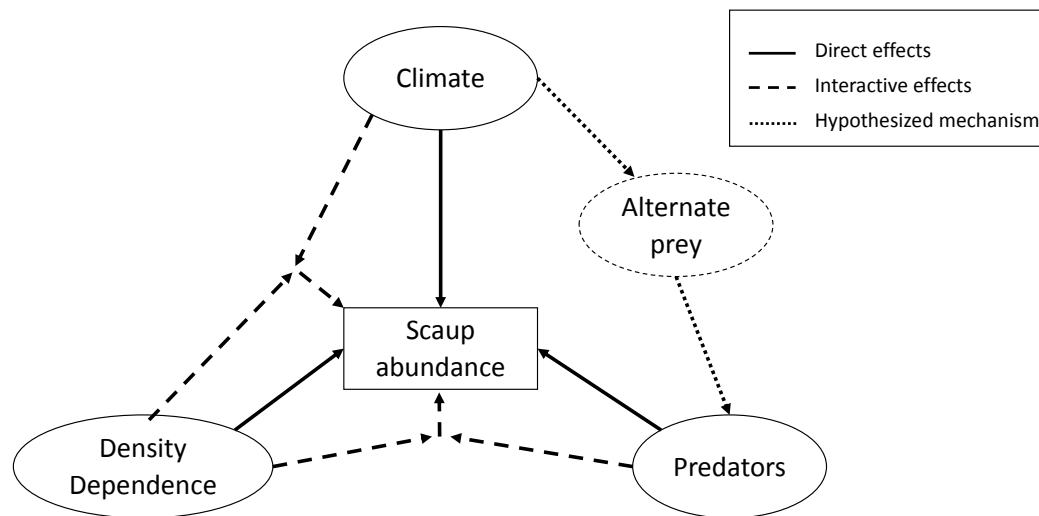


FIG. 3.1. Proposed direct and indirect drivers affecting scaup on their breeding grounds. Dotted arrows and circles indicate hypothesized indirect mechanisms influencing population drivers incorporated into the model, solid arrows indicate direct effects, and dashed arrows indicate interactions between effects.



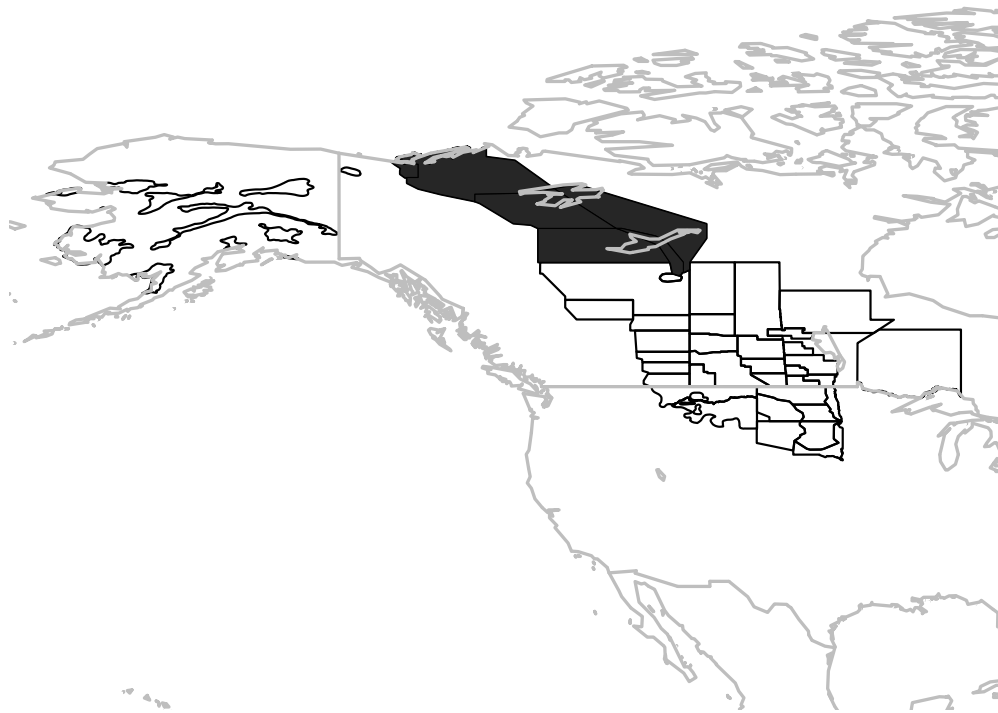


FIG. 3.2. Traditional study area for the North American Waterfowl Breeding Population and Habitat Survey. Area for the Northwest Territories portion of the study shown in black and includes strata 13 through 18, covering  $\sim 713,000 \text{ km}^2$ .

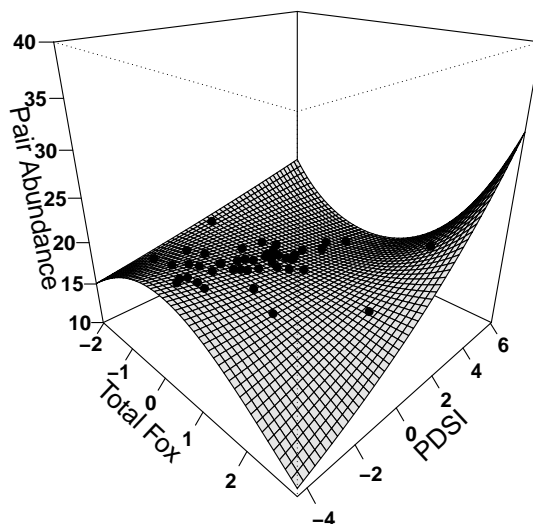


FIG. 3.3. The interactive effect of  $PDSI_{July-August,lag-1}$  with the index for total fox abundance on annual scaup pair abundance for Stratum 13 (relationships hold for Strata 14-18). Points are provided for predictions across 90% of the range of  $PDSI_{July-August,lag-1}$  and total fox abundance.

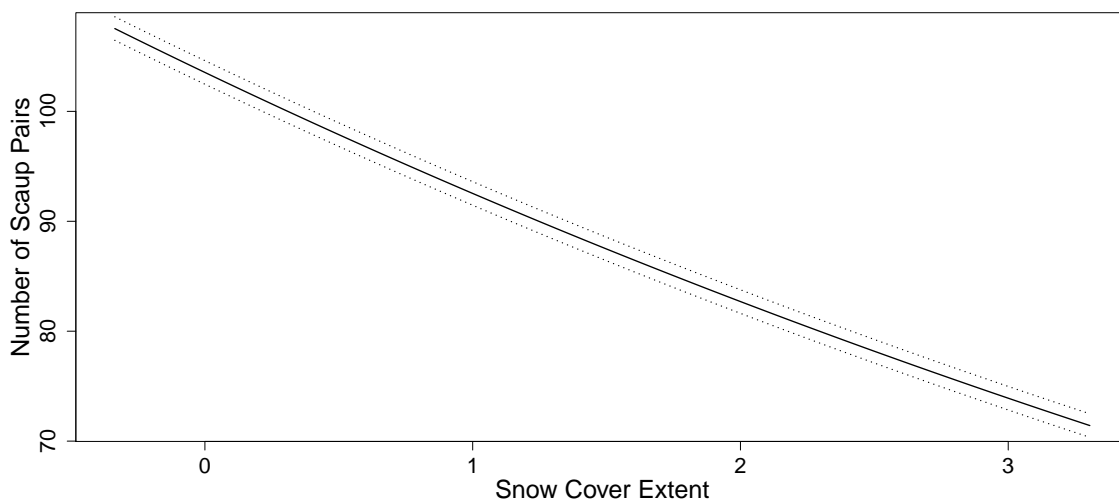


FIG. 3.4. The predicted effect of snow cover from winter to spring prior to sampling in year  $t$  on annual scaup pairs in the NWT in stratum 13 with 95% upper and lower credible intervals.

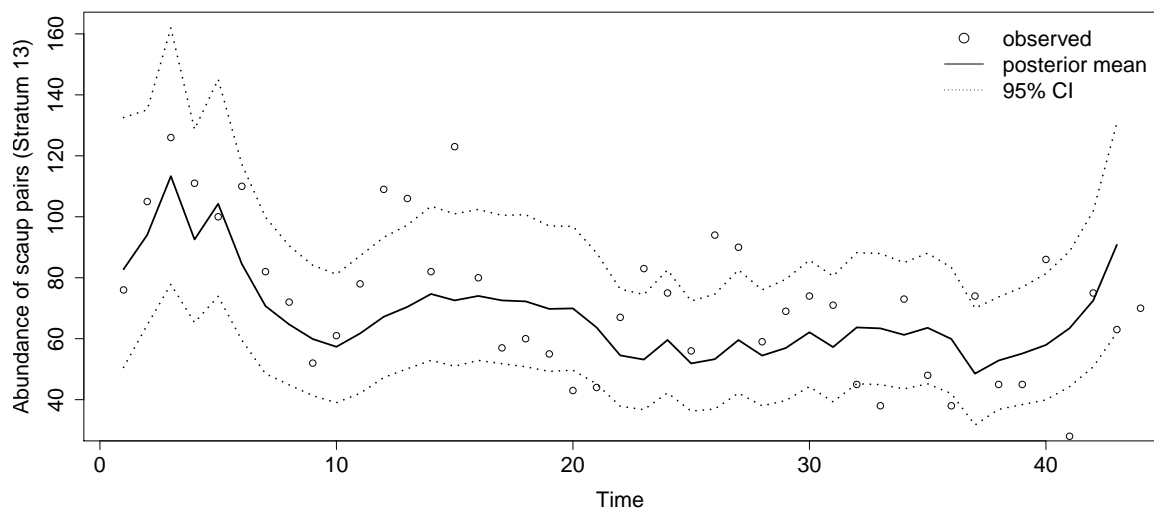


FIG. 3.5. Predicted (solid line with 95% credible interval in dotted line) and observed abundance (open circles) of scaup pairs in stratum 13 of the Northwest Territories.

## CHAPTER 4

## WATERFOWL COMMUNITY DYNAMICS IN THE NORTHWEST TERRITORIES

**4.1 Introduction**

A major question in community ecology is whether the interactions among species sharing a similar trophic niche are more important in regulating community dynamics than shared environmental drivers (Houlahan et al. 2007). When species exhibit similar responses to environmental variables, the relationships among species abundances in a community can exhibit positive covariation, or synchrony (Houlahan et al. 2007), which might also be influenced by facilitation or mutualism. Alternatively, competition for resources causes species to negatively covary. The difficulty of determining if a community is regulated by competition, compensation (e.g., filling of a niche following independent effects of the environment on another species), or concordant dynamics is that the mechanisms are often intertwined. If species are closely related, environmental factors will likely impact them in similar ways. Yet, related species will likely also compete for resources within a shared niche space (Pimm 1994).

Understanding community drivers is important for determining the relative effects of internal regulation of the community through species interactions compared to extrinsic factors (Adler and HilleRisLambers 2008, Adler et al. 2009). When species in a community respond similarly to dominant environmental factors, competitive interactions can be masked (Ripa and Ives 2007, Rocha et al. 2011). Accounting for shared environmental correlation among species is thus necessary to avoid spurious conclusions about interactions (Ripa and Ives 2007). Failing to incorporate important environmental drivers into models can also yield misleading information about how many species are interacting in a community (Abbott et al. 2009). While estimating the covariance among species in a community is important for learning about how species interact, it is also critical to consider how environmental factors might be influencing, or even dominate, these interactions (Ripa and Ives 2007).

Environmental variables influence species interactions in various ways. Changes in climate can impact habitat or food availability for several different species simultaneously causing either competition when resources are limiting or concordance when they are not (Hunter and Price 1992, Hansen et al. 2013). Additionally, shifts in climate can cause cascading changes in habitat structure, resulting in decreased reproductive success across a community (Auer and Martin 2013). Environmental changes have the potential to exert a greater influence on species composition than species interactions (Adler and HilleRisLambers 2008, Almaraz et al. 2012), and can change the structure of community dynamics (e.g., Péron and Koons 2013).

Climate change can also cause shifts in species interactions, causing restructuring of the community through changes in trophic interactions such as predation (Gilman et al. 2010, Harley 2011). Additionally, predation can cause apparent competition between two prey species when an increase in one prey species causes a numerical response of predator abundance, thus resulting in higher predation pressure on the other species (Holt and Lawton 1994, Chaneton and Bonsall 2000, Iles et al. 2013). While climatic effects can cause changes in community dynamics, it can often be difficult to determine if predation effects are stronger drivers than climate, or horizontal competitive effects (Hunter and Price 1992). In order to best determine the drivers of community dynamics, there is a need for a method that allows the explicit incorporation of top-down and bottom-up effects on community dynamics while simultaneously accounting for additional sources of temporal covariation among species (e.g., environmental concordance or compensation) in observational data to avoid biased inference.

Relative to the rich study of population dynamics, only a few studies have addressed questions related to the community dynamics of waterfowl (e.g., Bethke 1993, Almaraz et al. 2012, Péron and Koons 2012). To my knowledge, no study to date has simultaneously quantified the extent of bottom-up and top-down effects on waterfowl community dynamics while also investigating interactions among species (but see Péron and Koons (2012) for a two species case). The waterfowl community of the Northwest Territories (NWT) of

Canada is an ideal system for quantifying community dynamics because environmental variables (Brook and Clark 2005, Drever et al. 2012) and the influence of density dependence (Viljugrein et al. 2005, Sæther et al. 2008) have already been shown to affect the population dynamics of co-occurring species present in the region. Additionally, the interactions of related species in other regions is predicted to shift under various climate change scenarios (Péron and Koons 2013), indicating the importance of environmental variables in waterfowl dynamics. Bethke and Nudds (1993) concluded that duck species richness increases with increasing environmental variability, and that duck population dynamics are more related to habitat and resource heterogeneity than competition. While climatic effects can directly change the community dynamics of similar species that share resources, it can often be difficult to determine if such effects are stronger drivers than trophic interactions such as predation, which can also be altered through changes in climate conditions (Walker et al. 2013). With climate change predicted to increase the frequency of extreme demographic events (Drake 2005), it is possible that the dynamics and composition of the waterfowl community in the NWT and elsewhere will change. Understanding how potential drivers have influenced waterfowl community dynamics in the past could thus help predict how climate change might affect community dynamics in the future (Péron and Koons 2013).

In this chapter, I use long-term, broad-scale datasets of predator demographics, climate (which influences resource supply, and potentially alternative prey for predators as well), and waterfowl abundance within a hierarchical modeling framework. The goal of this chapter is to quantify the relative importance of top-down, bottom-up, and intra- and interspecific interactions in the pochard duck community of the NWT. Based on previous research (Drever et al. 2012) and the importance of climate in other waterfowl populations (Almaraz et al. 2012), I hypothesize that decreased snowpack will negatively affect the pochard community through a decrease in small mammals that are the primary prey for many predators (indirect top-down effects), or through a decrease in aquatic habitat availability and associated nest-site and food resources (direct bottom-up effects). Apparent competition may also be acting in this system through predators responding positively to

increases in primary prey (microtines) and subsequently causing an increase in predation pressure on waterfowl (Brook and Clark 2005). Additionally, I hypothesize that indices of focal predator abundance (fox [*Vulpes vulpes* and *Vulpes lagopus*]) negatively affect pochard abundances (direct top-down effect), but that the impact of snow extent will be stronger because of its potential to simultaneously influence bottom-up and top-down drivers of waterfowl dynamics. As some waterfowl species in this community have shown strong density dependence (Viljugrein et al. 2005, ?), and other waterfowl communities seem to be more driven by environmental effects than interspecific interactions (Almaraz et al. 2012), I predict that climate and predation, along with intraspecific density dependence, will have stronger impacts on community dynamics than interspecific interactions among waterfowl species.

## 4.2 Methods

### 4.2.1 Survey Methods

Every May and June since 1955, the U.S. Fish and Wildlife Service and Canadian Wildlife Service have conducted the North American Waterfowl Breeding Population and Habitat Survey (BPOP), which provides a rich source of demographic data on more than 10 focal duck species (Smith 1995). The BPOP includes over 3.3 million square kilometers in the north-central United States, much of western Canada, and Alaska, purposefully covering a large portion of each species' breeding range (Zimpfer et al. 2013). Strip-segments are flown at 145-170 km per hour at an altitude of 30-50 m and multiple 28.8 km segments are flown in each survey stratum. Ground crews then survey subsections of the total survey area, and from the comparison of the two counts, the total abundance for a stratum is estimated (Smith 1995).

The focus for this project was to determine the primary drivers of waterfowl community dynamics in the NWT of Canada (NWT; strata 13-18, covering  $\sim 713,000 \text{ km}^2$ ), a key area for waterfowl breeding where reliable indices of predator abundance are also available (Chapter 3). An initial assessment of the data indicated that breeding pairs for three species

of diving ducks were sufficiently present in the NWT to include in the analysis: canvasback (*Aythya valisineria*), ringed-neck duck (*Aythya collaris*), and combined lesser and greater scaup species (*Aythya affinis* and *Aythya marila*; which are indistinguishable from the air). My basal unit of data was then the sum of the population estimates in the 6 NWT strata,  $y_{i,t}$ , observed for species  $i$ , in year  $t$ .

#### 4.2.2 Environmental Drivers of Community Dynamics

I incorporated environmental covariates into the process model to determine the relative effects of climate (snow cover extent), and predation pressure (an index developed based on furbearer harvest data) on waterfowl community dynamics in the NWT. Density-independent covariates such as these can moderate the rate of population growth from low density ( $r_i$  specified in the Gompertz model below, Colchero et al. 2009, Rotella et al. 2009).

Snow cover extent is an important driver of some species' population dynamics in the NWT (Chapter 3, Drever et al. 2012); perhaps because the spring melt of winter snowpack may have a greater effect on wetland dynamics than other forms of precipitation. Snow cover extent data were obtained online (Robinson and Frei 2000), and the average snow cover extent for the NWT was calculated for a "waterfowl year," from June of year  $t-1$  to May of year  $t$ .

Alternatively, changes in snowpack could affect rodent communities in the boreal forest, as decreased snowpack dampens the population cycles and eliminates population 'booms' often exhibited by these species (Kausrud et al. 2008, Ims et al. 2008). Thus, a decrease in snow cover extent could cause apparent competition between small mammals and waterfowl via shared predators. If meso-predators are forced to switch from their primary food source, such as small mammals, due to limited availability (Ims et al. 2008), they may be more likely to pursue waterfowl nests, incubating females, and ducklings when available. For example, Brook and Clark (2005) found a positive correlation between microtine abundance and lesser scaup productivity, suggesting prey-switching by predators to duck nests and ducklings in years of low microtine abundance.



To address the effects of predation on the abundance of breeding waterfowl, covariates for a relative predator index in the NWT were used. I evaluated the response of waterfowl pair numbers to indices for total fox (red *Vulpes vulpes* and arctic fox, *Vulpes lagopus*), which are known to prey heavily upon waterfowl nests, ducklings (Talent et al. 1983, Pietz et al. 2003) and reproductive females (Brook and Clark 2005) in this territory and elsewhere (Afton 1984, Sargeant et al. 1984, Koons and Rotella 2003, Zschille et al. 2014). Furthermore, the relative abundance of total foxes in the NWT was previously shown to have a greater impact on the most abundant breeding ducks (scaup) in the region than other predators (e.g., mink; Chapter 3). From 1970 to 1999, the number of furbearer pelts harvested was not reported separately for the current Northwest and Nunavut territories (previously one large territory). In order to estimate the proportion of fox pelts harvested in the boundaries of the current NWT alone (that overlaps with the waterfowl TSA), I calculated the average proportion of pelts harvested from each territory using data available from 2000-2006. The proportion of fox pelts harvested from the NWT during 2000-2006 was then applied to past data to obtain estimates of the fox pelts harvested in the NWT from 1970-1999.

To develop covariates for the hierarchical model, but before examining effects on waterfowl, furbearer data from Statistics Canada was first used as the response variable in linear regression models with the following predictive variables: price per pelt adjusted for inflation and the lag-1 adjusted price per pelt. Models based on quadratic parameterizations of the predictor variables were also used. Relative to other furbearer species, the harvest of fox fluctuates the least relative to price, further removing socio-economic factors unrelated to predator abundance in the area. Models with univariate and additive effects of these variables were developed, and the best model was selected using Akaike's Information Criterion adjusted for sample size ( $AIC_c$ ; Akaike 1973). The standardized residuals from the best model for each predator species were then used as a covariate in the hierarchical model.

### 4.2.3 Hierarchical Model Description

I used a Gompertz form of density dependence to describe the influences of inter- and intraspecific interactions among species in the NWT waterfowl community, as this form of density dependence describes waterfowl population dynamics (Sæther et al. 2008, Almaraz et al. 2012) and other species interactions (Mutshinda et al. 2011). The NWT BPOP estimates of abundance,  $y_{i,t}$ , for waterfowl species  $i$  at time  $t$  were modeled as

$$(11) \quad \log(y_{i,t}) = z_{i,t} + \eta_{i,t}$$

where  $z_{i,t}$  is the log abundance at time  $t$  ( $t = 1, \dots, T$ ) for species  $i$  ( $i = 1, \dots, n_s$ ) and  $\eta_{i,t}$  denotes modeled sampling errors for species  $i$ .

Using my observation model (Eq. 11), I described the waterfowl community dynamics as

$$(12) \quad z_{i,t} = z_{i,t-1} + r_i \left( 1 + \sum_{j=1}^I \alpha_{j,i} z_{j,t-1} / k_i \right) + \beta_{i,snow} X_{snow} + \beta_{i,fox} X_{fox} + \epsilon_{i,t}$$

where  $r_i$  is the intrinsic growth rate from low density for species  $i$ ,  $k_i$  is the carrying capacity,  $\beta_{i,snow}$  and  $\beta_{i,fox}$  are the coefficients for the effect of snow cover extent and total fox (red and arctic fox) on species  $i$ , and  $\epsilon_t \sim \text{MNV}(\mathbf{0}, \mathbf{\Sigma}_t)$  is the random effect for the combined effects of demographic stochasticity and environmental factors (i.e., latent variables not included in eqn. 2) for observation periods  $t = 1, \dots, T$  (i.e., years 1967-2010). Interspecific interactions between species  $j$  and  $i$  are described through the  $\alpha_{j,i}$ , with  $\alpha_{j,i}/k_i$  expressing the per capita effect of species  $j$  on  $i$  for all the species in the community (Almaraz et al. 2012). Intraspecific density dependence is then estimated when  $i = j$  via the size of the population relative to its carrying capacity on the log scale.

The covariance matrix  $\mathbf{\Sigma}_t$  can be further decomposed into environmental and demographic components such that

$$(13) \quad \boldsymbol{\Sigma}_t = \mathbf{C} + \mathbf{D}_t$$

where  $\mathbf{C}$  represents the effects of latent environmental factors not incorporated into Eq. 2 and  $\mathbf{D}_t = \text{diag}(\delta_i^2/\exp\{z_{i,t-1}\})$  where  $\delta_i^2/z_{i,t-1}$  denotes the latent population level demographic stochasticity affecting the dynamics of species  $i$  from time  $t-1$  to  $t$ . Additionally, the off-diagonals of  $\mathbf{C}$  describe covariation between species  $i$  and  $j$  in response to environmental factors not captured by the fixed effects in the model, while the diagonals of  $\mathbf{C}$  describe intraspecific responses to latent environmental stochasticity. The environmental components of the model can be further decomposed to include the two observable environmental variables, snow cover extent and total fox abundance, to determine the relative contributions of these variables to the overall effects of environmental variation on each species. In this instance then,  $E_i$ , the total environmental variance affecting species  $i$  is  $E_i = \beta_{snow,i} + \beta_{fox,i} + C_{i,i}$ .

I used stochastic search variable selection to test whether the interspecific effect,  $\alpha_{j,i}$ , of duck species  $j$  on  $i$  should be included in the model, for which the indicator variable  $\gamma_{i,j} \sim \text{Bern}(p_{i,j})$ , and  $\alpha_{j,i}$  was included in the model when  $\gamma_{i,j} = 1$  and not included when  $\gamma_{i,j} = 0$ . I specified the conditional prior on  $\alpha_{j,i}$  as a mixture of two Gaussians,  $\alpha_{j,i}|\gamma_{i,j} \sim (1 - \gamma_{i,j}) \times N(0, c_1) + \gamma_{i,j} \times N(0, c_2)$  with the constant  $c_1 = 0.01$  and  $c_2 = 1$ . The other priors were specified as  $\eta_{i,t} \sim U(0, 10)$ ,  $r_i \sim N(0.3, 5)$ ,  $k_{canvasback} \sim N(7, 140)I(0, \infty)$ ,  $k_{ring} \sim N(10, 140)I(0, \infty)$ ,  $k_{scaup} \sim N(15, 140)I(0, \infty)$  where  $I$  is an indicator function that truncates the distribution,  $\boldsymbol{\beta} \sim N(0, 100)$ ,  $\mathbf{C} \sim \text{Inverse Wishart}(\mathbf{I}, n_s)$ , where  $\mathbf{I}$  is an  $n_s \times n_s$  identity matrix, and  $\delta_i \sim U(0, 10)$ . Note that prior parameterizations were specified for dynamics on the log scale. I then implemented the MCMC runs for the above models using the R (v. 3.0.1, R Core Team 2013) package R2WinBUGS (Sturtz et al. 2005) to call WinBUGS (Spiegelhalter et al. 2003) with the following settings: number of chains = 3; number of iterations = 300,000; and burn-in period = 100,000.

### 4.3 Results

The model with the lowest  $AIC_c$  from the furbearer regression models was a model with a linear effect for the price of pelts in the previous year for total fox (see Appendix 2 for model comparisons), as well as a factor for the implementation of CITES. Residuals from these models were z-standardized and used as covariates in the process model (Eq. 12).

The mean of the posterior distribution of canvasbacks in the NWT did not change significantly between 1968 and 2010 (Fig. 4.1), but the dynamics did fluctuate greatly. Of note, canvasbacks decreased during the first 10 years of the study, increased to their original abundance after 20 years, but there has been no notable trend in NWT canvasback abundance since the 1980s. Abundance of ring-necked ducks in the NWT, on the other hand, increased throughout the study period, beginning with approximately 50,000 individuals in 1967 and reaching a high of 237,000 by 2010. By the late 1990s, the abundance of ring-necked ducks had reached recorded highs at the time, but their abundance decreased during the early 2000s, followed by another increase from 2002 onward. Estimates of scaup abundance in the NWT decreased from the 1980s until the late 2000s. Estimated abundance did increase between 2008 and 2010 but abundance remains far below levels in the 1970s that are used to set NAWMP population objectives (Fig. 4.1). Scaup were nevertheless more abundant than canvasback or ring-necked ducks throughout the study period in the NWT.

There were no significant effects of interspecific interactions, i.e., all estimated 95% Bayesian credible intervals (CI) for the  $\alpha_{j,i}$  that model the effect of species  $j$  on  $i$  included 0 (Table 4.1). Furthermore, the latent environmental covariation between species  $i$  and  $j$  was not significant for any two species (Table 4.2). While the mean covariation was estimated to be negative between each pair of species (possible community compensation), the 95% CIs for all of these covariances included 0.

The intraspecific interaction of density dependence did not explain much variation in the dynamics of scaup or ring-necked ducks, but did contribute more greatly to variation in canvasback population dynamics (Fig. 4.4). In addition, canvasbacks had the highest

intrinsic growth rate (2.1), followed by ring-necked ducks (1.1) and scaup (0.3), though the 95% CIs overlapped 0 for both ring-necked ducks and scaup (Fig. 4.2). It is moreover important to note that species-specific rates of population growth can be moderated by environmental covariates and stochasticity (see below). The carrying capacity was highest for scaup (13.3), followed by ring-necked ducks (9.0), and canvasbacks (4.1) on the  $\log(y_{i,t} \times 1000)$  scale. Estimates of scaled carrying capacities were nevertheless imprecise for all species (Fig. 4.2).

For each species, the estimated biological effects of total fox abundance on population dynamics was close to null and the estimated 95% CIs widely overlapped 0. Lack of biological and statistical effects were also found for the snow cover extent covariate. There was some indication of a negative effect of snow cover (-0.17) on canvasback population dynamics, but this estimate was also imprecise (95% CI again overlapped 0). While the modeled covariates had little effect on population and community dynamics, latent environmental factors explained the largest proportion of variance in the dynamics of all three species (Fig. 4.4). When decomposing the total environmental variance, snow cover extent explained slightly more variation than total fox abundance in canvasbacks, but both variables contributed roughly the same small amount to variance in ring-necked ducks and scaup (Fig. 4.5). There was no significant difference between the proportion of variance explained by extrinsic environmental and intraspecific effects (density dependence) for canvasbacks, but environmental effects explained significantly more variance than intraspecific interactions in ring-necked ducks and scaup (Fig. 4.4). As noted above, interspecific competition explained little variance ( $< 0.01$ ) in the population dynamics of each sympatric species (Fig. 4.4).

#### 4.4 Discussion

Several studies have rigorously assessed how North American waterfowl species are affected by the environment (Drever et al. 2012) and density dependence (Sæther et al. 2008, Murray et al. 2010), but none of these studies additionally accounted for how species interactions may influence population and community dynamics. By using hierarchical

modeling to account for process and sampling variance, I was able to assess the proportion of process variance related to various drivers of community and population dynamics, and ultimately quantify how synchrony, compensation, and competition may affect the pochard duck community in the NWT relative to environmental covariates related to measurable bottom-up and top-down variables that may affect duck population dynamics. My results indicate that species interactions have little impact on the variability of pochard population dynamics relative to environmental variability and intraspecific competition. Interspecific competition contributes relatively little to the proportion of variance in wintering European waterfowl species as well, which are more so affected by local climatic changes (Almaraz et al. 2012).

The lack of interspecific competition and synchrony (positive environmental covariation that is not attributable to direct interactions) among the ducks in this study could be due to differences in evolved bill morphology, as canvasbacks, lesser and greater scaup, and ring-necked ducks all have distinct bill morphologies (Lagerquist and Ankney 1989). Thus, despite considerable overlap in prey at certain times of the year (Perry et al. 2007), artifacts of past competition among species may have led to distinct feeding niches and relatively little competition among pochard species in the NWT today. Pochards also have unique nest-site selection strategies, which may also limit interspecific competition (Krasowski and Nudds 1986). In addition to not having strong interspecific competition, the diving ducks in the NWT also did not exhibit synchrony, indicating that each species might be uniquely affected by environmental factors.

In addition to the lack of direct interspecific community interactions, my results indicated no significant relationship of snow and total fox abundance with the NWT pochards once other processes were accounted for. Perhaps snow cover extent and total fox abundance are not the primary drivers of population and community dynamics in the NWT. Other studies (Drever et al. 2012) have concluded otherwise about snow cover extent for a subset of the species included here, though Drever et al. (2012) focused on the chronology of when snow cover extent dropped below a certain threshold in the spring and how that affected

waterfowl population dynamics. Additionally, the model from this chapter did not include covariates for lag effects of snow, other climatic variables (i.e., Palmer Drought Severity Index), or interactions between climate and predation, which might partially be the cause for the discrepancy between results from this chapter and Chapter 3. In particular, scaup may be unique in this community model and not influenced by the same factors that affect the rest of the diving ducks in the region. Scaup had the greatest correlation between predicted abundance and observed estimates, indicating not only a good model fit, but also that the model described their population dynamics better than other species. My results do nevertheless indicate that the decline in the scaup population is likely not related to competition between scaup and other diving ducks in the NWT.

While the two environmental covariates included in the model did not have significant effects on population dynamics, the latent environmental effects did explain a large proportion of population variation for all species. Scaup and ring-necked ducks were most responsive to environmental effects, though snow cover extent and total fox abundance only explained a relatively small ( $< 20\%$ ) proportion of the environmental variation. Lag year effects of climatic variables, and perhaps local environmental factors (Almaraz et al. 2012), might be contributing more to this latent variation. For example, scaup are affected by the lag effect of Palmer Drought Severity Index from July to August, which interacts with predator abundance, and may also affect other pochards in the NWT. Quadratic effects of these covariates might also affect pochards in the NWT, but will require additional study to fully explore the potential effects of measurable environmental covariates on the NWT pochard community dynamics.

Intraspecific interactions, or density dependence, contributed relatively little to the variation in scaup and ring-necked duck population dynamics, but did explain nearly 40% of the variation in canvasback population dynamics, even though canvasbacks had the smallest population abundance on average. Canvasbacks had a smaller carrying capacity, and may thus experience stronger intraspecific competition for limited quality territories, food, or both. Additionally, canvasbacks exhibit density dependence across the entire study area

(Murray et al. 2010) and in the prairie areas of Canada and the US (Viljugrein et al. 2005). Scaup and ring-necked duck did not seem to be greatly influenced by density dependence, but I previously found that scaup do nevertheless exhibit weak density dependence over the whole study area (Chapter 3, see also Murray et al. 2010), which may be attributable to their large carrying capacity.

My analysis built upon on previous comparative waterfowl population dynamics studies (Sæther et al. 2008, Murray et al. 2010) by incorporating environmental covariates as well as latent structures of density dependence and interspecific interactions. For the pochards in the NWT, it does not seem that the community dynamics as a whole are largely driven by interspecific interactions or respond in similar ways to environmental factors. In contemporary time, pochard community dynamics in the NWT may be largely neutral in relation to the factors considered in my model, and could be persisting in equilibrium with resource levels (Nudds 1983). If anything, there was a slight indication of compensatory dynamics that was not statistically precise, but may deserve further study. My work highlights the importance of latent environmental effects that need to be further explored, and to some extent density dependence, in the NWT pochard community.

Future research should consider possible environmental effects on pochards in the NWT that were not considered in my model, as environmental stochasticity accounted for a large proportion of variability in every species, but a better understanding of what latent environmental factors are driving pochard populations would aid in management actions. Additionally, it does not seem that trapping indices of combined red and arctic fox abundance in the NWT are having much impact on pochard community dynamics. Waterfowl species interactions do not seem to greatly affect population dynamics either, so changes in management actions directed at one species will likely not affect other pochard species in the NWT. At the same time, management actions aimed at enhancing populations of all waterfowl species might be difficult as there were not strong signals of synchrony. Density dependence will likely limit population growth of each species independently, and decreased abundance of one species (e.g., scaup) may simply be compensated for by an increase in



abundance of the species with the closest niche characteristics (e.g., ring-necked duck).

TABLE 4.1. Relative influence of waterfowl species  $j$  (rows) on species  $i$  (columns;  $\alpha_{j,i}$ ) with Bayesian 95% credible intervals in brackets. ‘Ring’ stands for ring-necked duck.

	Canvasback	Ring	Scaup
Canvasback	-	-0.03[-0.42,0.22]	0.09[-0.16,0.76]
Ring	0.03[-0.56,1.11]	-	0.20[-0.22,1.47]
Scaup	0.06[-0.66,1.14]	0.06[-0.66,1.25]	-

TABLE 4.2. Latent environmental covariance between species  $j$  and  $i$  ( $\mathbf{C}$ ) with Bayesian 95% credible intervals in brackets. ‘Ring’ stands for ring-necked duck.

	Canvasback	Ring	Scaup
Canvasback	-	-0.60[-4.52,3.11]	-0.97[-5.40,3.07]
Ring	-	-	-0.15[-4.46,3.70]
Scaup	-	-	-

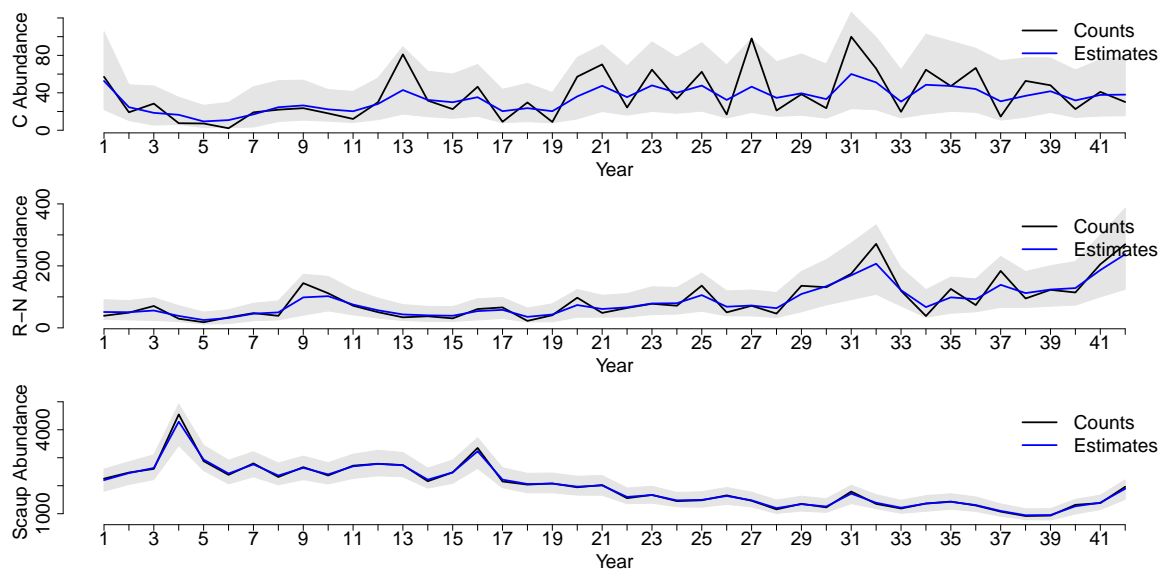


FIG. 4.1. Posterior predicted and observed abundance (in 1000s) for (top) canvasbacks, (center) ring-necked ducks, and (bottom) scaup in the NWT for 1968-2010 with 95% Bayesian credible intervals.

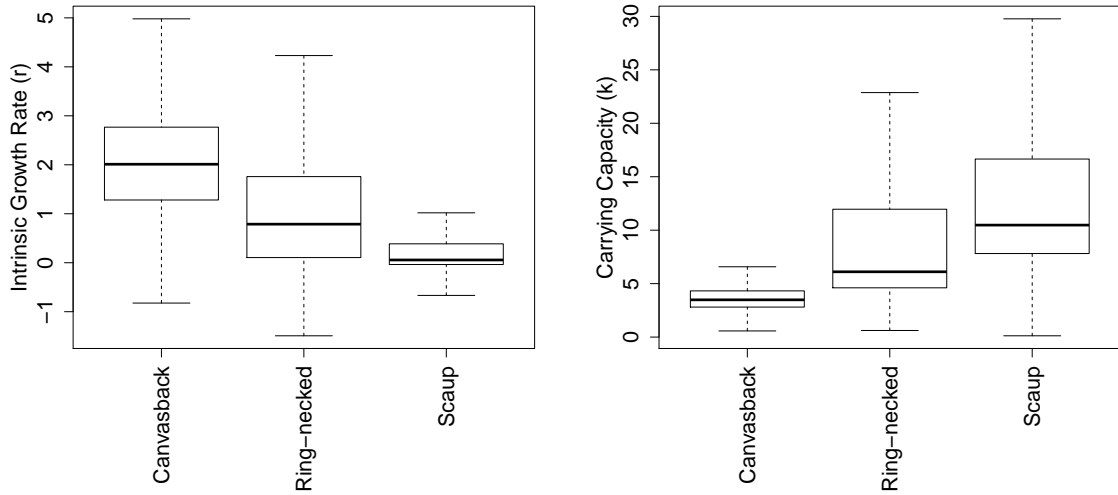


FIG. 4.2. Boxplots of posterior distributions for intrinsic population growth rates ( $r_i$ ; left) and carrying capacities ( $k_i$ ; right) for waterfowl species  $i$

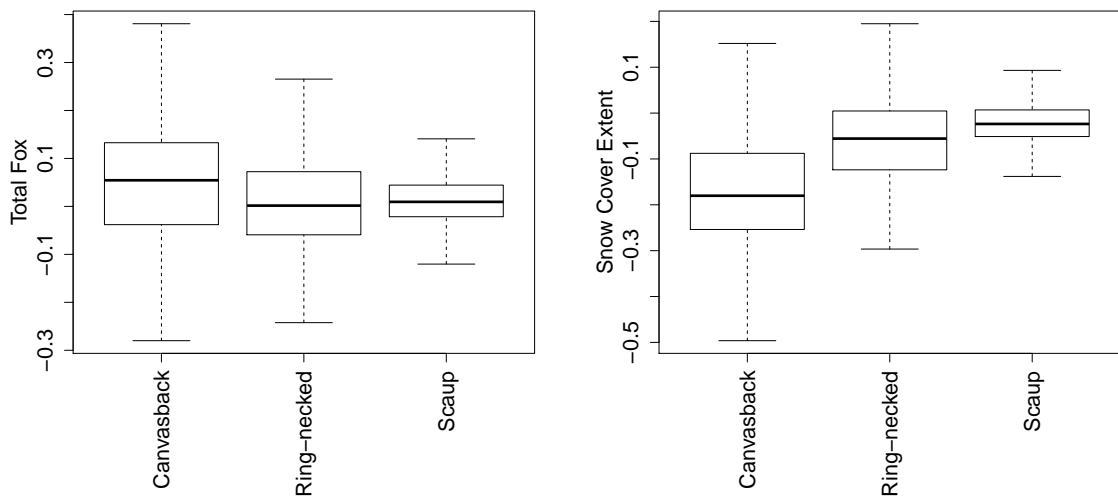


FIG. 4.3. Boxplots of posterior distributions for  $\beta$  estimates for the effects of total fox abundance ( $\beta_{i,fox}$ ) and snow cover extent ( $\beta_{i,fox}$ ) on the population dynamics of species  $i$  in the Northwest Territories of Canada.

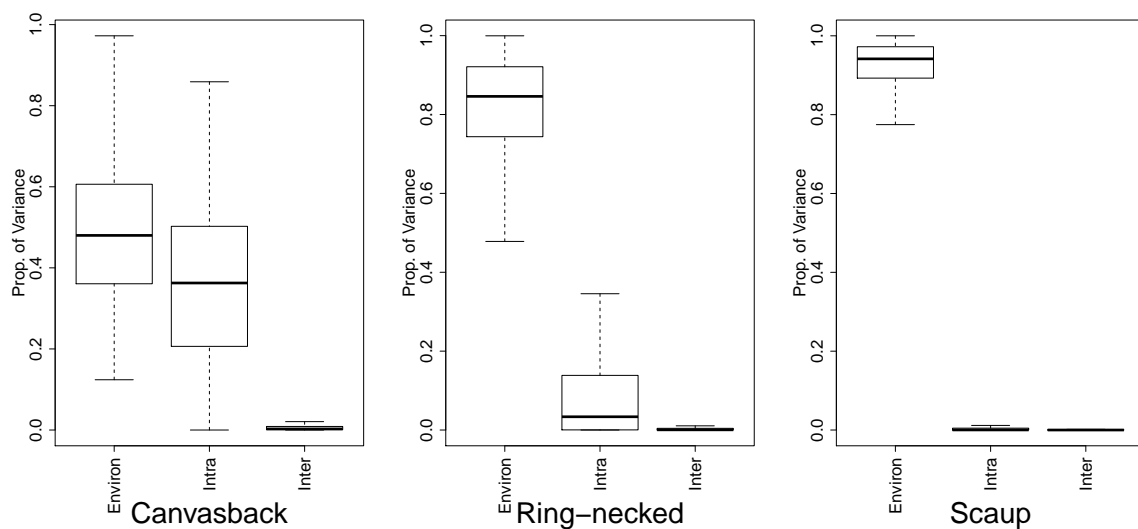


FIG. 4.4. Boxplots of posterior distributions indicating relative influence of variation in the population dynamics of waterfowl species  $i$  explained by environmental ('environ'), intra- ('intra'), and interspecific ('inter') interactions. Environmental factors are total fox abundance, snow cover extent, as well as latent environmental stochasticity.

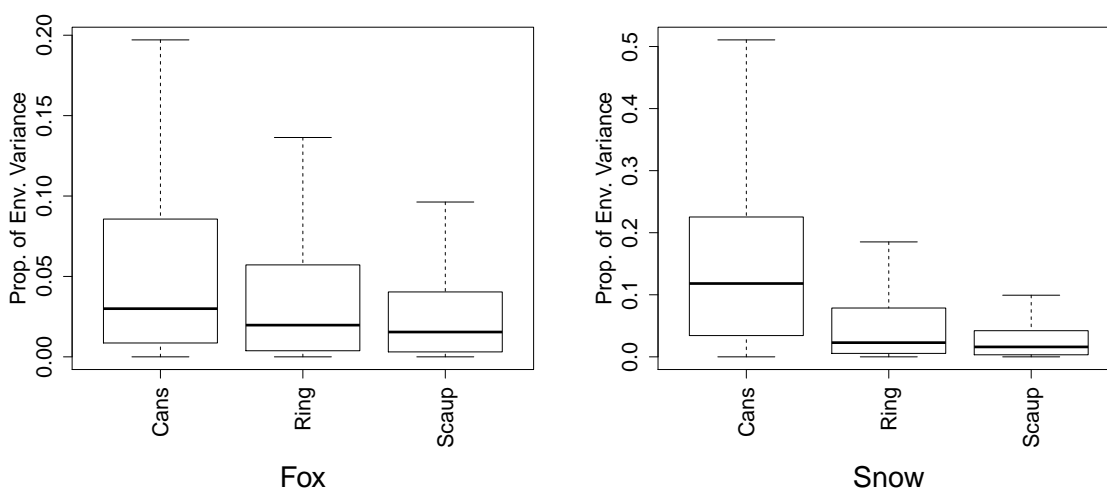


FIG. 4.5. Posterior distributions of the proportion of environmental variance explained for each species  $i$  by total fox abundance and snow cover extent

## CHAPTER 5

### CONCLUSIONS

The results from my dissertation highlight the importance of climate and, in some cases, density dependence in driving the population and community dynamics of waterfowl in the Northwest Territories (NWT). These drivers are likely impacting scaup nest success or survival of young or breeding females because results from Chapter 2 indicate that scaup are still attempting to breed regularly. As in other studies (Drever et al. 2012), snow cover extent was important in describing population changes in scaup in the single-species model. Perhaps reduction in snow cover has impacted food availability during the breeding season, resulting in either a mismatch of available food (e.g., *Amphipods spp.* spawning at a different time) or a reduction in total food for ducklings. Altered carrying capacity and density dependence may also be exacerbating competition for either nest sites or food availability among young. Results from Chapter 4 seem to imply that scaup may have different drivers than the rest of the community.

Assuming that density dependence is operating in the system to some extent, this implies that some population-level compensation will result from waterfowl harvest (Lebreton 2005). As the management of North American waterfowl populations is largely implemented through harvest regulations, compensatory mechanisms for population growth deserve further study (e.g., via mortality, reproduction, or both).

In addition to implications for harvest regulations, this research also indicates ways in which managers might alter habitat to increase the abundance of breeding waterfowl. While it would prove difficult to replicate years of high snow cover extent, managers might need to consider managing for resilience across the landscape, or protecting the wetlands of highest quality for scaup and other waterfowl species.

Future work could build on this research in several ways. Broadly, analyses of long-term datasets would benefit from the inclusion of random effects that account for autocorrelation, as random effects can account for variation in parameter estimates, reducing the possibility of erroneous statistical inference (Kramer and Donninger 1987). Additionally, studies need

to continue to include fixed effects for relevant ecological processes, as they provide better insights into the drivers of the population or community, while also reducing uncertainty. Improvements could also be made to long-term monitoring efforts by including adaptive monitoring designs, as these designs reduce both error in parameter estimates and costs, subsequently providing more funds for additional sampling in sites of great biological importance but associated with statistical uncertainty about the underlying dynamics (Hooten et al. 2009).

Future work on the BPOP dataset would benefit from integrated modeling approaches (e.g., Péron and Koons 2012), as these models allow for the incorporation of other datasets (e.g., banding data) to simultaneously estimate all vital rates of the population. Additionally, simulation studies could be developed to assess the accuracy of the BPOP survey (Nuno et al. 2013). Simulations would be especially useful for assessing how scaup migration has potentially shifted over the last decade, as some research implies it may have (Austin et al. 2002). A simulation study could include comparisons between a model based on a shift in scaup migration timing and a model without any shift in scaup migration and use goodness-of-fit testing to see which best aligned with the data.

Lastly, future research on scaup would benefit from more on-the-ground research focused in areas of the NWT to determine how the drivers found in Chapter 3 might be affecting scaup vital rates and resulting population dynamics. Alternately, research focused on the prairie parkland region where scaup breeding pairs are increasing (Ross et al. 2012) would be useful for determining if these same factors are causing population increases, or if different drivers are acting in this region. Work on other stages of the scaup migration cycle, such as survival estimates from wintering and migratory grounds, could also be helpful in assessing how all of these factors are impacting scaup across seasons.

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APPENDICES

TABLE 6.1. Estimates of  $\beta$  parameters (with associated standard errors and confidence intervals) from the top occupancy model.

Parameter	$\beta$	SE	LCI	UCI
$\psi_1$ : Intercept	20.226	3.919	12.545	27.907
$\psi_1$ : year	-0.471	0.091	-0.65	-0.293
$\psi_1$ : Crew Areas 1&2	-8.792	21.306	-50.551	32.968
$\psi_1$ : Crew Area 3	-6.371	5.935	-18.004	5.261
$\psi_1$ : Crew Area 4	-14.069	4.31	-22.516	-5.622
$\psi_1$ : Crew Area 5	-18.267	3.935	-25.979	-10.555
$\psi_1$ : Crew Area 6	-18.345	3.93	-26.047	-10.643
$\psi_1$ : Crew Area 7	-22.031	3.977	-29.827	-14.236
$\psi_1$ : Crew Area 8	-19.75	3.943	-27.478	-12.023
$\psi_1$ : Year Crew Areas 1&2	0.465	0.529	-0.571	1.501
$\psi_1$ : Year Crew Area 3	0.256	0.128	0.005	0.508
$\psi_1$ : Year Crew Area 4	0.463	0.101	0.265	0.661
$\psi_1$ : Year Crew Area 5	0.573	0.098	0.38	0.765
$\psi_1$ : Year Crew Area 6	0.512	0.093	0.33	0.695
$\psi_1$ : Year Crew Area 7	0.669	0.107	0.46	0.879
$\psi_1$ : Year Crew Area 8	0.546	0.094	0.362	0.731
$\psi_2$ : Intercept	3.076	0.616	1.868	4.284
$\psi_2$ : Year	-0.038	0.021	-0.079	0.003
$\psi_2$ : Crew Areas 1&2	5.341	1.504	2.392	8.289
$\psi_2$ : Crew Area 3	-1	0.703	-2.378	0.378
$\psi_2$ : Crew Area 4	2.518	1.216	0.134	4.901
$\psi_2$ : Crew Area 5	0.415	0.796	-1.144	1.975
$\psi_2$ : Crew Area 6	0.1	0.809	-1.487	1.687
$\psi_2$ : Crew Area 7	-1.531	0.712	-2.927	-0.135

TABLE 6.1. (Continued)

Parameter	$\beta$	SE	LCI	UCI
$\psi_2$ : Crew Area 8	-2.986	0.67	-4.299	-1.674
$\psi_2$ : Year $\times$ Crew Areas 1&2	-0.032	0.038	-0.107	0.042
$\psi_2$ : Year $\times$ Crew Area 3	0.125	0.033	0.06	0.19
$\psi_2$ : Year $\times$ Crew Area 4	0.009	0.032	-0.054	0.071
$\psi_2$ : Year $\times$ Crew Area 5	0.013	0.024	-0.035	0.061
$\psi_2$ : Year $\times$ Crew Area 6	0.018	0.024	-0.03	0.066
$\psi_2$ : Year $\times$ Crew Area 7	0.019	0.023	-0.026	0.063
$\psi_2$ : Year $\times$ Crew Area 8	0.074	0.022	0.03	0.118
$p_1$ : Intercept	-3.226	0.102	-3.426	-3.026
$p_1$ : Before 1974	0.537	0.172	0.2	0.873
$p_2$ : Intercept	0.228	0.024	0.181	0.274
$p_2$ : Decade 1	0.14	0.03	0.08	0.199
$p_2$ : Decade 2	-0.049	0.029	-0.106	0.008
$p_2$ : Decade 3	0.072	0.029	0.016	0.128
$p_2$ : Decade 4	-0.182	0.028	-0.237	-0.127
$p_2$ : Decade 5	-0.097	0.028	-0.152	-0.042
$\delta$ : Intercept	0.965	0.074	0.821	1.11
$\delta$ : Crew Area 1	2.072	0.088	1.9	2.244
$\delta$ : Crew Area 2	1.644	0.084	1.48	1.808
$\delta$ : Crew Area 3	0.692	0.081	0.534	0.851
$\delta$ : Crew Area 4	1.818	0.089	1.645	1.992
$\delta$ : Crew Area 5	1.186	0.087	1.016	1.356
$\delta$ : Crew Area 6	1.14	0.089	0.965	1.315
$\delta$ : Crew Area 7	0.835	0.097	0.644	1.026
$\delta$ : Crew Area 8	0.708	0.089	0.534	0.883



TABLE 6.1. (Continued)

Parameter	$\beta$	SE	LCI	UCI
-----------	---------	----	-----	-----

TABLE 6.2. Estimates of  $\delta$  from the top occupancy model.

Crew Area	$\delta$
1	0.954
2	0.931
3	0.840
4	0.942
5	0.896
6	0.891
7	0.858
8	0.842
9	0.724

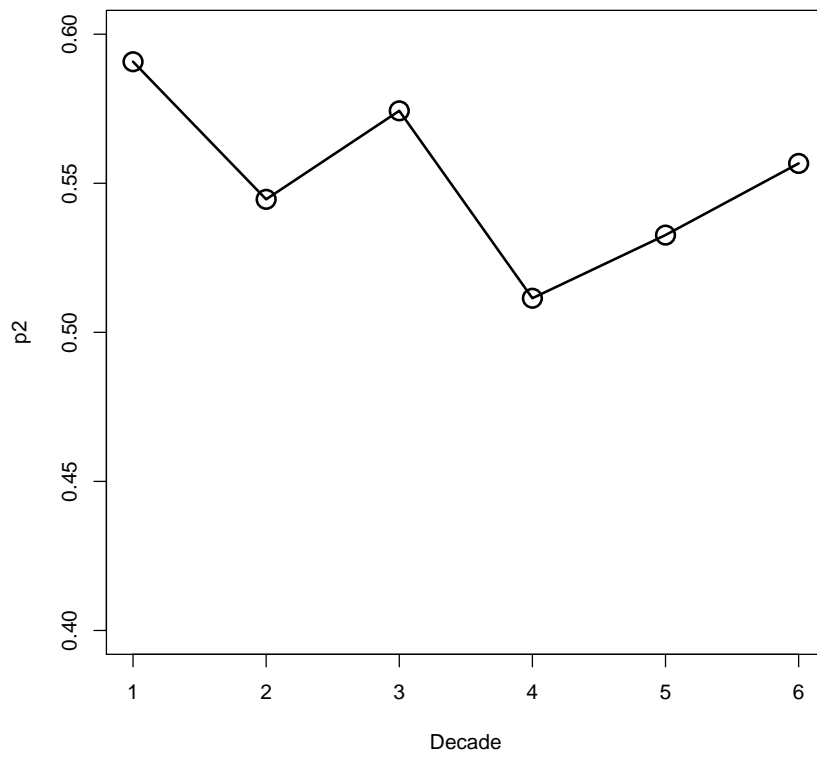


FIG. 6.1. Estimates of  $p_2$  from the top occupancy model.

R code for INLA and related analysis in Chapter 3  
 Analysis conducted using R version 3.0

The process model for the code described below is:

$$(14) \quad z_{j,t} = \alpha z_{j,t-1} + \beta_{0,j} + \mathbf{x}_{j,t}' \boldsymbol{\beta} + \epsilon_{j,t}$$

where  $x_{j,t}$  is a covariate for snow cover extent.

```
## Data manipulation for state-space model

ss.data <- read.csv("ss_model_inla.csv",header=TRUE)
n=length(unique(ss.data$stratum)) #number of study sites
k=length(unique(ss.data$year)) #number of years
y=matrix(as.vector(ss.data$y),nrow=6,ncol=43) #matrix of counts
nd <- n*k
Y <- matrix(NA, nd*2-n, 2)
Y[1:nd, 1] <- as.vector(t(y))
Y[1:(nd-n) + nd, 2] <- 0

id1 <- (1:nd)[-((1:n)*k)]
id2 <- (1:nd)[-c(1,((1:(n-1))*k)+1)]
ix1 <- c(1:nd, id2) ## indices for x1_t
ix1b <- c(rep(NA,nd), id1) # indices for x1_{t-1}
wx1b <- c(rep(1,nd), rep(-1,nd-n)) ## weights for x1_{t-1}
iw22 <- c(rep(NA,nd),id2) ## indices for w_t
#st.1-st.6 are strata-specific growth rates
st.1=c(rep(NA,nd),rep(1,(k-1)),
rep(0,(nd-6-(k-1))))
```

```

st.2=c(rep(NA,nd),rep(0,(k-1)),rep(1,(k-1)),
rep(0,(nd-6-((k-1)*2))))
st.3=c(rep(NA,nd),rep(0,((k-1)*2)),rep(1,(k-1)),
rep(0,(nd-6-((k-1)*3))))
st.4=c(rep(NA,nd),rep(0,((k-1)*3)),rep(1,(k-1)),
rep(0,(nd-6-((k-1)*4))))
st.5=c(rep(NA,nd),rep(0,((k-1)*4)),rep(1,(k-1)),
rep(0,(nd-6-((k-1)*5))))
st.6=c(rep(NA,nd),rep(0,((k-1)*5)),rep(1,(k-1)),
rep(0,(nd-6-((k-1)*6))))
snow.idx <- matrix(ss.data$stand.snow[7:258],6,42)
snow <- c(rep(NA,nd),c(snow.idx[1,],snow.idx[2,],
snow.idx[3,], snow.idx[4,],snow.idx[5,],
snow.idx[6,]))
dat.snow=list(Y=Y, ix1=ix1,ix1b=ix1b,wx1b=wx1b,iw22=iw22,
snow=snow,st.1=st.1,st.2=st.2,st.3=st.3,st.4=st.4,
st.5=st.5,st.6=st.6)

```

I then specify the model for the state-space model and call the `inla()` function

```

library(INLA)

formula.snow <- Y ~ f(iw22,model="iid") +
f(ix1, model="iid",initial=-10, fixed=TRUE) +
f(ix1b, wx1b, copy="ix1",fixed=FALSE) + st.1 +
st.2 + st.3 + st.4 + st.5 + st.6 + snow -1

r.snow <- inla(formula.snow, data = dat.snow,

```

```
family = c("nbinomial","gaussian"),
control.family = list(list(link="log"),
list(initial=10, fixed=T)),
control.predictor=list(compute=TRUE),
control.compute=list(dic=TRUE,cpo=TRUE))

summary(r.snow)
```

TABLE 6.3. Comparison of models (using the  $-\text{mean}(\log(\text{CPO}))$ ) with various climatic covariates affecting scaup pair abundance in the Northwest Territories from 1967-2010. Models include covariates for snow cover extent (Snow), Arctic Oscillation (AO), Pacific Decadal Oscillation (PDO), number of ponds in the prairie parkland region (Pond), and El Niño Southern Oscillation (ENSO) for both a year ranging from June of year  $t-1$  to May of year  $t$ , as well as the lag-1 year ( $\text{lag}-1$ ). Palmer Drought Severity Index (PDSI) was also included for various seasons in the year  $t-1$  leading up to year  $t$ . All models include an unstructured random effect and latent density dependence, and ‘Null’ indicates a model with no climate covariates.

Model	$-\text{mean}(\log(\text{CPO}))$
Snow + Snow <sub>lag-2</sub>	5.0066
PDSI <sub>July-Aug,lag-1</sub>	5.0082
Snow	5.0093
Snow + Snow <sub>lag-1</sub> + Snow <sub>lag-2</sub>	5.0119
PDSI <sub>May-Aug,lag-1</sub>	5.0107
Snow + Snow <sub>lag-1</sub>	5.0126
PDSI <sub>May-July,lag-1</sub>	5.0173
PDO <sub>lag-1</sub>	5.0174
Pond	5.0191
PDO	5.0203
PDSI <sub>May-July</sub>	5.0215
PDSI <sub>May-Aug</sub>	5.0239
ENSO	5.0243
Null	5.0247
Snow <sub>lag-1</sub>	5.0250
Snow <sub>lag-1</sub> + Snow <sub>lag-2</sub>	5.0284
Snow <sub>lag-2</sub>	5.0342
AO	5.0319
AO <sub>lag-1</sub>	5.0337
PDSI <sub>July-Aug</sub> + PDSI <sub>July-Aug,lag-1</sub>	5.1262
PDSI <sub>May-Aug</sub> + PDSI <sub>May-Aug,lag-1</sub>	5.1301
PDSI <sub>July-Aug</sub>	5.1309
PDO + PDO <sub>lag-1</sub>	5.1333
PDSI <sub>May-July</sub> + PDSI <sub>May-July,lag-1</sub>	5.133
AO + AO <sub>lag-1</sub>	5.3159

TABLE 6.4. Comparison of models (using the  $-\text{mean}(\log(\text{CPO}))$ ) with various climatic covariates affecting scaup pair abundance in the Northwest Territories from 1958-2010. Models include covariates for Arctic Oscillation (AO), Pacific Decadal Oscillation (PDO), number of ponds in the prairie parkland region (Pond), and El Niño Southern Oscillation (ENSO) for both a year ranging from June of year  $t-1$  to May of year  $t$ , as well as the lag-1 year ( $\text{lag}-1$ ). Palmer Drought Severity Index (PDSI) was also included for various seasons in the year  $t-1$  leading up to year  $t$ . All models include an unstructured random effect latent density dependence, and ‘Null’ indicates a model with no climate covariates.

Model	$-\text{mean}(\log(\text{CPO}))$
$\text{PDSI}_{\text{July}-\text{Aug}} + \text{PDSI}_{\text{July}-\text{Aug},\text{lag}-1}$	5.0424
$\text{PDSI}_{\text{May}-\text{Aug},\text{lag}-1}$	5.0431
$\text{PDSI}_{\text{July}-\text{Aug},\text{lag}-1}$	5.0432
Pond	5.0447
$\text{PDSI}_{\text{May}-\text{July},\text{lag}-1}$	5.0450
$\text{PDSI}_{\text{May}-\text{July}}$	5.0459
$\text{PDSI}_{\text{May}-\text{Aug}} + \text{PDSI}_{\text{May}-\text{Aug},\text{lag}-1}$	5.0462
Null	5.0463
$\text{PDSI}_{\text{May}-\text{Aug}}$	5.0464
ENSO	5.0475
$\text{PDSI}_{\text{July}-\text{Aug}}$	5.0478
PDO	5.0481
$\text{PDSI}_{\text{May}-\text{July}} + \text{PDSI}_{\text{May}-\text{July},\text{lag}-1}$	5.0497
$\text{PDO}_{\text{lag}-1}$	5.0500
AO	5.0505
$\text{PDO} + \text{PDO}_{\text{lag}-1}$	5.0510
$\text{AO} + \text{AO}_{\text{lag}-1}$	5.2991
$\text{AO}_{\text{lag}-1}$	5.3180

TABLE 6.5. Comparison of models from the red fox predator analysis of scaup pair abundance in the Northwest Territories from 1957-2011. Covariates are abbreviated as ‘price’ for the inflation adjusted price of pelts in that year and ‘lag price’ for the inflation adjusted price of pelts in the previous year. ‘Null’ indicates a model with only an intercept, while ‘df’ indicates the degrees of freedom for the model.

Model	df	$\text{AIC}_c$	$\Delta\text{AIC}_c$
lag price	3	805.72	0
price	3	815.65	9.93
price + price <sup>2</sup>	4	817.26	11.54
lag price + lag price <sup>2</sup>	3	817.81	12.09
null	2	856.67	50.95

TABLE 6.6. Comparison of models from the total fox (red and arctic fox) predator analysis of scaup pair abundance in the Northwest Territories from 1957-2011. Covariates are abbreviated as ‘price’ for the inflation adjusted price of pelts in that year and ‘lag price’ for the inflation adjusted price of pelts in the previous year. ‘Null’ indicates a model with no covariates, while ‘df’ indicates the degrees of freedom for the model.

Model	df	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
lag price	3	1125.24	0
lag price + lag price <sup>2</sup>	3	1127.04	2.12
price	3	1143.92	18.67
price + price <sup>2</sup>	3	1145.41	20.50
null	2	1172.08	46.60

TABLE 6.7. Comparison of models for the socio-economic effects on mink trapping harvest in the Northwest Territories from 1957-2011. Covariates are abbreviated as ‘price’ for the inflation adjusted price of pelts in that year and ‘lag price’ for the inflation adjusted price of pelts in the previous year. ‘Null’ indicates a model with only an intercept, while ‘df’ indicates the degrees of freedom for the model.

Model	df	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
price + price <sup>2</sup>	4	993.47	0
lag price + lag price <sup>2</sup>	4	997.54	4.07
price	3	998.86	5.39
lag price	3	1005.09	11.62
null	2	1036.6	43.14

TABLE 6.8. Comparison of models (using the  $-\text{mean}(\log(\text{CPO}))$ ) with various predator covariates affecting scaup population dynamics in the Northwest Territories from 1958-2012. Models include covariates for pelt harvest of mink, red fox, and total fox (red and arctic fox combined) from year  $t-1$ , as well as quadratic terms corrected for pelt price for each. All models include an unstructured random effect and latent density dependence, and ‘Null’ indicates no predator covariates.

Model	$-\text{mean}(\log(\text{CPO}))$
Total fox + (total fox) <sup>2</sup>	5.0529
Null	5.0532
Red fox	5.0545
Total fox	5.0546
Mink	5.0558
Red fox + (red fox) <sup>2</sup>	5.0571
Mink + (mink) <sup>2</sup>	5.0580



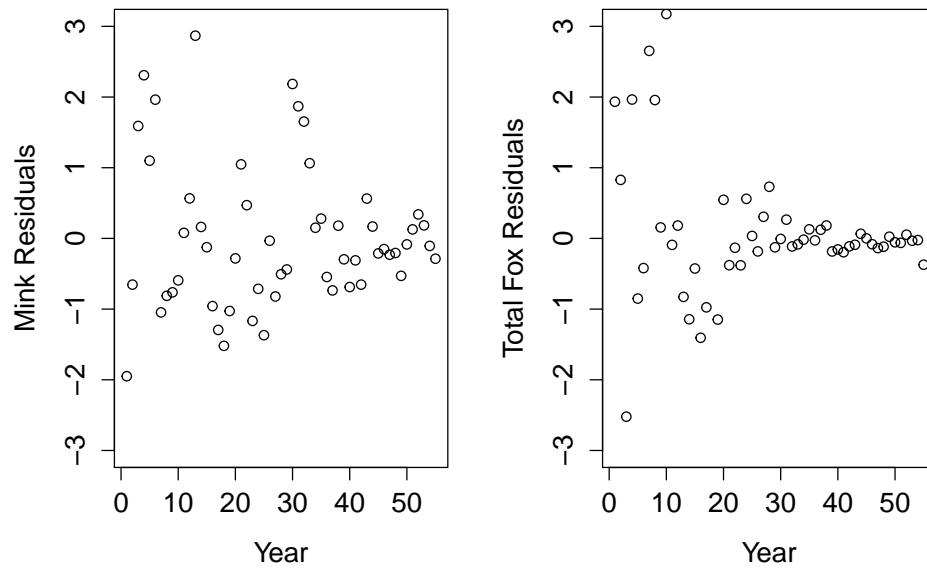


FIG. 6.2. Residuals from the top models for predator abundance through time from 1958-2012.

## CURRICULUM VITAE

Beth E. Ross

**EDUCATION***2014* Utah State University

Ph.D. Wildlife Biology

Dissertation Title: Assessing Changes in the Continental Lesser Scaup Population.

Advisor: David Koons

*2012* Utah State University

M.S. Statistics

Thesis Title: Assessing Changes in the Abundance of the Continental Population of Scaup Using a Hierarchical Spatio-Temporal Model.

Advisor: Mevin Hooten

*2007* Colorado State University

M.S. Zoology

Thesis title: The effect of habitat shape on movement of Ords kangaroo rat.

Advisor: Bruce Wunder

*2004* Kansas State University

B.S., Wildlife Biology

Thesis title: Effects of prairie vole runways on tallgrass prairie.

Advisors: Donald Kaufman, Aaron Reed

**PROFESSIONAL EXPERIENCE***2013-Present* Postdoctoral Research Associate, Kansas Cooperative Fish and Wildlife  
Research Unit*2008-13* Graduate Research Assistant, USU Department of Wildland Resources*2006* Graduate Research Assistant, Shortgrass Steppe LTER*2004* Research Assistant, Wyoming Natural Diversity Database

2003 Summer research student, National Science Foundation Research Experiences for Undergraduates, Konza Prairie Biological Station

## Publications

Ross, B.E., M. Hooten, and D.N. Koons. 2012. An accessible method for implementing hierarchical models with spatio-temporal abundance data. *PLoS ONE* 7(11). *Featured on F1000 Prime*  
<http://f1000.com/prime/718122712>

Hooten, M.B, B.E. Ross, and C.K. Wikle. 2012. Optimal spatio-temporal monitoring designs for characterizing population trends. Gitzen, R.A., J.J. Millspaugh, A.B. Cooper, and D.S. Licht (eds.). In: *Design and Analysis of Long-Term Ecological Monitoring Studies*. pp. 443-459.

Ross, B.E., A.W. Reed, R.L. Rehmeier, G.A. Kaufman, and D.W. Kaufman. 2007. Effects of prairie vole runways on tallgrass prairie. *Transactions of the Kansas Academy of Science* 110:100106.

Lauenroth, W.K., A.A. Wade, M.A. Williamson, B.E. Ross, S. Kumar, and D.P. Cariveau. 2006. Uncertainty in calculations of net primary production in grasslands. *Ecosystems* 9:842851.

## In Preparation

Ross, B.E. and D.N. Koons. Using occupancy models to examine changes in pairing propensities and population dynamics across space and time: illustration with an imperiled scaup population.

Ross, B.E., M. Hooten, J.M. DeVink, and D.N. Koons. The importance of climate, predation, and density dependence in population regulation of a waterfowl species.

Ross, B.E., M. Hooten, and D.N. Koons. A novel technique for accounting for species relatedness in community studies.

Ross, B.E. and B. Wunder. The effect of habitat shape on movement of Ords kangaroo rat in shortgrass prairie.

## Grants

*Total of \$93,811*

2013 Travel grant, Wildlife Society Biometrics Working Group. \$690

- 2013 Travel grant from Center for Women and Gender studies, USU. \$500
- 2009, 10 Travel grant from Graduate Student Senate, USU. \$300
- 2008 Delta Waterfowl Foundation, 2008-2011. D.N. Koons and B.E. Ross.  
Continental population dynamics of lesser scaup. \$20,000/year
- 2006 Travel grant from Department of Biology, CSU. \$400
- 2005 Colorado Wildlife Conservation Grant, CO Division of Wildlife. B.E. Ross.  
Habitat use, survivorship, and mortality causes of Ords kangaroo rats  
(*Dipodomys ordii*) in disturbed and fragmented habitats. \$11,821
- 2005 Travel grant from Department of Biology, CSU. \$500

### **Awards & Honors**

- 2009 Dr. John A. Kadlec Memorial Scholarship, USU
- 2004 Undergraduate Student Research Award, American Society of  
Mammalogists
- 2000-04 Youth Foundation Scholarship Recipient
- 2000 Kansas State University Foundation Scholar

### **Teaching**

Utah State University, Department of Wildland Resources

- Teaching Assistant, Animal Population Ecology (graduate course) · Fall 2009, 2010

Colorado State University, Department of Fish, Wildlife, and Conservation Biology

- Teaching Assistant, Wildlife Data Collection and Analysis (undergraduate course) · Spring 2007

Colorado State University, Department of Biology

- Lab Instructor, Mammalogy (undergraduate) · Fall 2004, 2005, 2006
- Lab Instructor, Biology of Organisms (undergraduate) · Spring 2005, 2006

Kansas State University, Division of Biology

- Undergraduate teaching practicum, Mammalogy (undergraduate) · Fall 2002, 2003

### **Invited Seminars**

- 2013* Quantifying changes in waterfowl population and community dynamics. Seminars in Ecology and Evolutionary Biology, KSU
- 2012* Understanding the Decline of Lesser Scaup. Wisconsin Waterfowl Hunters Conference
- 2011* Occupancy Modeling for Presence-Absence Data. USU Graduate Course: WILD 6400, Animal Population Ecology
- 2011* Techniques to Sample Vertebrates. USU Undergraduate Course: WILD 4750, Monitoring and Assessment in Natural Resource and Environmental Management
- 2011* Becoming a Graduate Student. USU Student Chapter of The Wildlife Society
- 2010* Techniques to Sample Vertebrates. USU Undergraduate Course: WILD 4750, Monitoring and Assessment in Natural Resource and Environmental Management
- 2010* Becoming a Graduate Student. USU Student Chapter of The Wildlife Society

### **Conference Presentations**

- Ross, B.E., M.B. Hooten, J.M. DeVink, and D.N. Koons. January 2013. How biotic and abiotic factors affect spatio-temporal population dynamics of scaup. Ecology and Conservation of North American Waterfowl. Memphis, Tennessee.
- Ross, B.E., M.B. Hooten, and D.N. Koons. October 2010. Analysis of spatio-temporal dynamics in scaup. The Wildlife Society. Snowbird, Utah.
- Ross, B.E., M.B. Hooten, and D.N. Koons. August 2009. Analysis of spatio-temporal dynamics in abundance of Lesser Scaup. 5th North American Duck Symposium. Toronto, Canada.
- Koons, D.N., and B.E. Ross. August 2009. Changes in habitat occupancy and pairing probabilities of the declining continental population of scaup. 5th North American Duck Symposium. Toronto, Canada.

Ross, B.E., M.B. Hooten, C.K. Wike, and D.N. Koons. April 2009. Analysis of spatio-temporal dynamics in abundance of scaup. U.S. Chapter, International Association of Landscape Ecologists. Snowbird, Utah.

Ross, B.E. and D.N. Koons. March 2009. Changes in habitat occupancy and breeding probabilities of a declining continental population of scaup in relation to spatial and environmental factors. Pan-European Duck Symposium, Arles, France.

Ross, B.E. June 2004. The effects of prairie vole (*Microtus ochrogaster*) runways on tallgrass prairie. American Society of Mammalogists, Humboldt State University, Arcata, California.

Ross, B.E., A.W. Reed, R.L. Rehmeier, G.A. Kaufman, and D.W. Kaufman. Sept. 2003. The effects of prairie vole (*Microtus ochrogaster*) runways on tallgrass prairie. Central Plains Society of Mammalogists, Bull Shoals Field Station, Missouri.

Ross, B.E. July 2003. The effects of prairie vole (*Microtus ochrogaster*) runways on tallgrass prairie. REU symposium, Division of Biology, Kansas State University.

### **Poster Presentations**

Ross, B.E., M.B. Hooten, J.M. DeVink, and D.N. Koons. October 2013. The importance of climate, predation, and density dependence in population regulation of a waterfowl species. The Wildlife Society. Milwaukee, Wisconsin.

Ross, B.E., M.B. Hooten, J.M. DeVink, and D.N. Koons. April 2013. The importance of climate, predation, and density dependence in population regulation of a waterfowl species. Workshop on Spatial Statistics, Colorado State University.

Ross, B.E. and B.A. Wunder. April 2007. The effects of habitat shape on movement of Ords kangaroo rat (*Dipodomys ordii*). Front Range Student Ecology Symposium, Colorado State University.

Ross, B.E. and B.A. Wunder. September 2006. The effects of habitat shape on movement of Ords kangaroo rat (*Dipodomys ordii*). LTER All Scientists Meeting, Estes Park, Colorado.

Ross, B.E. and B.A. Wunder. June 2006. The effects of habitat shape on movement of Ords kangaroo rat (*Dipodomys ordii*). American Society of Mammalogists, University of Massachusetts, Amherst, Massachusetts.

Ross, B.E. and B.A. Wunder. June 2005. Habitat use and survivorship of Ords kangaroo rats (*Dipodomys ordii*) in disturbed habitats. American Society of Mammalogists, Southwest Missouri State University,

Springfield, Missouri.

Ross, B.E., A.W. Reed, R.L. Rehmeier, G.A. Kaufman, D.W. Kaufman. May 2004. The effects of prairie vole (*Microtus ochrogaster*) runways on tallgrass prairie. Undergraduate Research Forum, Division of Biology, Kansas State University.

Ross, B.E. April 2004. The effects of prairie vole (*Microtus ochrogaster*) runways on tallgrass prairie. Southwestern Association of Naturalist, San Antonio, Texas.

Ross, B.E., A.W. Reed, R.L. Rehmeier, G.A. Kaufman, D.W. Kaufman. March 2004. The effects of prairie vole (*Microtus ochrogaster*) runways on tallgrass prairie. 16th Annual Konza Prairie LTER Workshop, Kansas State University.

### **Workshops Attended**

Delta Waterfowl sponsored review of Scaup Harvest Model, 2008

Modeling Patterns and Dynamics of Species Occurrence Workshop, 2007. Instructor: Darryl MacKenzie, Proteus Wildlife Research Consultants

Short-Course on Bayesian Statistics Workshop, 2007. Instructor: Alexandra Schmidt, Associate Professor of Statistical Methods at Federal University of Rio de Janeiro, Brazil.

### **Mentoring**

Heather Franklin, Undergraduate research project. CSU, 2006

### **Professional Membership**

Ecological Society of America

The Wildlife Society

### **Professional Review Services**

Studies in Avian Biology

Journal of Animal Ecology (2)

Journal of Wildlife Management (2)

Ecological Applications

Journal of Fish and Wildlife Management

PLoS ONE