

Combined effects of climate, predation, and density dependence on Greater and Lesser Scaup population dynamics

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Abstract. An understanding of species relationships is critical in the management and conservation of populations facing climate change, yet few studies address how climate alters species interactions and other population drivers. We use a long-term, broad-scale data set of relative abundance to examine the influence of climate, predators, and density dependence on the population dynamics of declining scaup (*Aythya*) species within the core of their breeding range. The state-space modeling approach we use applies to a wide range of wildlife species, especially populations monitored over broad spatiotemporal extents. Using this approach, we found that immediate snow cover extent in the preceding winter and spring had the strongest effects, with increases in mean snow cover extent having a positive effect on the local surveyed abundance of scaup. The direct effects of mesopredator abundance on scaup population dynamics were weaker, but the results still indicated a potential interactive process between climate and food web dynamics (mesopredators, alternative prey, and scaup). By considering climate variables and other potential effects on population dynamics, and using a rigorous estimation framework, we provide insight into complex ecological processes for guiding conservation and policy actions aimed at mitigating and reversing the decline of scaup.

Key words: *Aythya affinis*; *Aythya marila*; climate change; density dependence; Greater Scaup; Lesser Scaup; Northwest Territories, Canada; population dynamics; predators; trophic interactions.

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 alters 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; 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 mechanisms affecting population dynamics (Viljugrein et al. 2005).

In this paper, we use a long-term, broad-scale abundance data set of Lesser Scaup (*Aythya affinis*) and Greater Scaup (*Aythya marila*), which are combined during surveys because of their similar appearance, 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 ~8% below the long-term average, an average that declines with the trajectory of the population (Zimpfer et al. 2014). The most precipitous declines have occurred in their preferred western boreal forest habitat in Canada (Ross et al. 2012, Zimpfer et al. 2014). Although there is not a consensus on the underlying mechanisms causing

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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 drive population dynamics is lacking.

We propose, and test, several possible drivers of the scaup decline in their core breeding range. The effects of climate, for example, could directly affect waterfowl populations through a decrease in wetland abundance and quality via increased drought (Fig. 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 alter predation on scaup through changes in alternative prey (Fig. 1). If predators preferentially feed on alternative prey species (e.g., small mammals) rather than a focal species (e.g., scaup), changes in climate 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, we might expect lagged temporal effects of climate on a focal species, because it can take time for numerical and functional responses to percolate through a food web (Walker et al. 2013). It is worth noting, however, that the effect of increased predators would only be expected if there were a shortfall in primary prey, and that the lag effects on scaup might be felt two years later if delayed breeding occurs.

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 evidence that climate may be playing a role in this decline (Drever et al. 2012), our 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 how these factors influence the dynamics of this declining species, we used a state-space modeling approach that controls for observation error (de Valpine and Hastings 2002), the

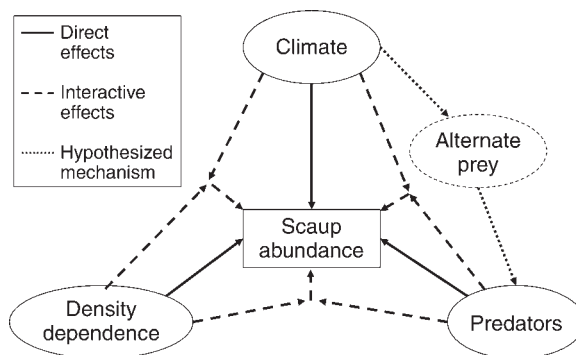


FIG. 1. Proposed direct and indirect drivers affecting scaup (*Aythya* spp.) on their breeding grounds. Dotted arrows and ovals indicate hypothesized indirect mechanisms influencing population drivers incorporated into the model, solid arrows indicate direct effects, and dashed arrows indicate interactions between effects.

latter of which can lead to erroneous conclusions about the impact of density dependence and environmental variation on population dynamics (Freckleton et al. 2006, Lebreton and Gimenez 2013). 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.

METHODS

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 km² in the north-central United States, much of western Canada, and Alaska; purposefully covering a large portion of each species' breeding range (Fig. 2; see Zimpfer et al. 2014). 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 × 0.4 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 males, flocked males (two or more), pairs, mixed-sex groups (three or more), but not lone females. Our 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. We did not use data regarding single males because the skewed sex ratio in scaup means that males are not limiting in the population (Afton and Anderson 2001), and scaup have not started breeding



FIG. 2. Traditional study area for the North American Waterfowl Breeding Population and Habitat Survey (BPOP). The area for the Northwest Territories portion of the study is shown in solid black and includes strata 13 through 18, covering ~713 000 km².

when some surveys are conducted; therefore, lone males are not necessarily indicative of breeding pairs. We 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 probably are more reflective of true furbearer demography than in other territories and states where trapping has become more recreational.

Model for population dynamics

Our 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 (N_t) is defined mathematically as

$$N_t = \lambda N_{t-1}^\theta \tag{1}$$

where λ is the population growth rate and θ represents density dependence in the system. Taking the log of both sides and incorporating a term for stochasticity (ε) yields

$$\log(N_t) = z_t = r + \theta z_{t-1} + \varepsilon_t \tag{2}$$

where $r = \log(\lambda)$, the rate of population growth from low density ($N = 1$) and θ is the effect of dependence on the log of population size at time $t - 1$ (z_{t-1}). In the Gompertz model, r takes on additional meaning because it also influences the carrying capacity. Dennis et al. (2006) provide closed-form solutions to the stationary equilibrium of a stochastic Gompertz model, conditional on estimates of r , θ , ε , and even homogenous covariates. For time-varying covariates, however, there are no closed-form solutions to the stationary equilibrium.

Moreover, equilibria are undefined when temporal variation in covariates is nonstationary (i.e., changing mean, variance, or both), but in such instances the stochastic Gompertz model is still quite useful for examining the effects of density dependence and exogenous variables on population dynamics over a defined period of time.

Our basal unit of data was the total number of recorded scaup pairs, $y_{j,t}$, summed across segments in stratum j in year t . The BPOP scaup data are overdispersed and contain a disproportionately high number of zeros at the stratum level relative to a Poisson distribution (Ver Hoef and Boveng 2007, Ross et al. 2012). Thus, we considered two potential data models for statistical estimation of population dynamics, a model where $y_{j,t} \sim \text{NegBinom}(\mu_{j,t}, \phi)$, with the parametrization of the negative binomial where $E(y_{j,t}) = \mu_{j,t}$ and $\text{var}(y_{j,t}) = \mu_{j,t} + \phi \mu_{j,t}^2$, and a zero-inflated negative binomial model where

$$y_{j,t} \sim \begin{cases} 0, & \text{with probability } \psi \\ \text{NegBinom}(\mu_{j,t}, \phi), & \text{with probability } (1 - \psi) \end{cases} \tag{3}$$

for stratum $j = 1, \dots, m$ during observation period $t = 1, \dots, T$ (e.g., years 1957–2012). The $\mu_{j,t}$ parameter is thus related to the underlying number of pairs in stratum j and year t , and ϕ is an overdispersion parameter. The overdispersion parameter accounts for extra heterogeneity in the data, and when $\phi > 10$, the negative binomial model approximates a Poisson distribution (Bolker 2007, Ver Hoef and Boveng 2007). The parameters related to the error associated with the observation model, ψ and ϕ , account for random under- and overcounting, but do not account for any systematic bias in the counts. Although there probably

are measurable variables associated with the observation process that may cause changes in the error associated with this model, our method for model implementation does not currently allow for the incorporation of such models, and custom-built models are the focus of future research efforts.

Using $\mu_{j,t}$ from the data model (Eq. 3), the process model was specified as

$$z_{j,t} = \log(\mu_{j,t}) = \beta_{0,j} + \theta z_{j,t-1} + \mathbf{x}'_{j,t} \boldsymbol{\beta} + \text{offset}_{j,t} + \varepsilon_{j,t} \quad (4)$$

where θ is the average degree of density dependence at the stratum level during the breeding season (as in Eq. 2) and the $\beta_{0,j}$ parameters are stratum-specific growth rates (analogous to r from Eq. 2). These growth rates are 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. The $\boldsymbol{\beta}$ parameters thus directly add to or subtract from the population dynamics in each stratum when covariate values differ from 0. A population exhibits density dependence when $\theta < 1$, a positive association with population density when $\theta > 1$, and density independence when $\theta = 1$ (Dennis et al. 2006). Unstructured (ε), spatial (ε_j), temporal (ε_t), or spatio-temporal ($\varepsilon_{j,t}$) stochasticity was modeled with random effects $\varepsilon \sim N(0, \sigma^2)$ (for greater detail, see Ross et al. 2012). An offset term was incorporated into the model to account for differences in the number of segments sampled in each stratum in each year. For a given year in a given stratum, $\text{offset}_{j,t}$ was the $\log + 1$ of the number of segments sampled minus the minimum number of segments ever sampled in stratum j .

To estimate the multiple processes that could have affected scaup population dynamics in the NWT during a >50 year time span, and to formalize our hypotheses about the underlying mechanisms affecting scaup population dynamics, we 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, $-(\Sigma \log(\text{CPO}_{j,t})/\text{sample size})$; Held et al. (2010). The CPO uses a form of leave-one-out cross-validation to calculate the probability of each observation ($y_{j,t}$) when the model is fit without that observation. The summary statistic of these CPO values then provides a method to rank various models based on their predictive ability (Hooten and Hobbs 2015). A lower summary statistic of CPO values simply indicates that a model is better at predicting observations relative to another; there is no theory indicating that a difference of 1 in the statistic between models is inferentially better than a difference of 0.5, for example. We then combined variables from the best models of each group (i.e., lowest CPO value) to simultaneously quantify effects of density dependence, climate, and predation.

Density-dependent effects

We chose the Gompertz form of density dependence because it performs well in population dynamics studies

of waterfowl (Sæther et al. 2008) and other species (Dennis et al. 2006, Knape and de Valpine 2012; Eq. 1), and because it is difficult to statistically identify alternative models for density dependence from one another (Dennis and Taper 1994), although the functional form of density dependence can be important for management decisions (Runge and Johnson 2002). 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). We 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, Knape and de Valpine 2012). We estimated density dependence using the entire duration of the study from 1957 to 2012 in order to gain insight into the strength of density dependence in the absence of covariates. We also used this same time period to determine which random effects to include in the process model (i.e., spatial, temporal, spatiotemporal, 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 this unique life history characteristic offers little opportunity for reneesting after failure (Afton 1984), scaup may be especially sensitive to environmental changes. To examine how climate impacts scaup population dynamics in the NWT, we 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 aquatic birds (Papineau 2001, Drever et al. 2012, Smith and Gaston 2012). Because of differences in data availability, we 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). We chose this time frame to incorporate possible 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. We 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) and

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). To help with convergence, we standardized climatic variables over all strata to a mean of 0 and variance of 1 from the period 1958–2010, except snow cover extent, which was standardized to a mean of 0 and variance of 1 from the period 1968–2010 due to a lack of data prior to 1968.

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 throughout the NWT (Papineau 2001, Morrison and Hik 2007, Smith and Gaston 2012), we also considered more fine-scale climate variables to gain deeper insight into spatiotemporal 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 scap year, we used specific time periods related to the time of breeding as the covariate. We calculated PDSI for the following three seasons: early (the months 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 scap 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 scap.

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 scap abundance (Drever et al. 2012). Here, we averaged snow cover extent, or the percentage of land covered by snow in a given grid cell, over the current scap 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 scap year would 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 scap, we also considered lag-2 effects.

We chose the climatic indices just described 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 scap life cycle, such processes could, in turn, affect the abundance of scap counted on the breeding grounds (i.e., through an availability bias; Austin et al. 2002). To account for such processes to the best of our abilities, we used the El Niño Southern Oscillation (ENSO) and the abundance of ponds in the prairies in the current scap year as covariates because each might affect the availability of habitat and food resources during scap migration northward to the NWT (Naugle et al. 2000, Stenseth et al. 2003). However, we note that changes in migratory phenology could also be affected by other variables that are difficult to measure at broad scales.

Predator effects

We also evaluated the relationship between scap population dynamics and indices of predator abundance: red fox, *Vulpes vulpes*, total fox (red and Arctic fox, *V. lagopus*), and mink, *Neovison vison*, which are known to prey heavily on scap 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, we calculated the average proportion of pelts harvested from each territory using data available from the period 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 during 1970–1999. Because 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 easily be influenced by socioeconomic factors related to fur trapping, we 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, because furbearer harvest comprises the best available data for predators in the NWT (Elton and Nicholson 1942, Yan et al. 2013). All models were fit using maximum likelihood. The best model for socioeconomic 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 scap population dynamics for 1958–2012 (Eq. 4), with the residuals in fall and winter of year $t - 2$ affecting scap abundance in year t (e.g., fox abundance in 2000 would affect recruitment of scap in 2001, the effects of which would be seen during the 2002

survey; noting that pelts harvested in late winter would be tallied in the 2000 furbearer harvest statistic).

Model implementation

We then considered additive and plausible interactive models with the variables that performed best in the preceding topical analyses. Typically, the state-space model previously described (Eqs. 3 and 4), 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, we 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). We implemented INLA using the R package (Rue et al. 2009, R Core Team 2013), and provide annotated code pertaining to our best combined model from the period 1967–2010 in the Supplement. 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).

RESULTS

Density-dependent effects

The strength of density dependence was significant ($\theta = 0.7904 \pm 0.05$; all values reported as mean \pm SD) when implemented in a model without covariates for climate or predator abundance. We thus considered density dependence in further models with climate and predator covariates 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 (ϵ) 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 ($-(\Sigma \log(\text{CPO}_{j,t})/\text{sample size})$ of 5.040 vs. a zero-inflated model, 5.043). The zero-inflation parameter (ψ) in the zero-inflated negative binomial model was 0.0030 ± 0.0028 . The relatively small value of ψ provides additional support for using the simpler negative binomial model in subsequent models.

Climate effects

When we compared climate effect models for 1967–2010 (when snow extent data were available) using the $-(\Sigma \log(\text{CPO}_{j,t})/\text{sample size})$, a model with an immediate effect of snow cover extent ranked better than models with other effects of snow extent, as well as models with

AO, PDO, and PDSI covariates, although a model with lag-1 July–August PDSI ranked second best (Appendix: Table A1). The lowest $-(\Sigma \log(\text{CPO}_{j,t})/\text{sample size})$ indicates that snow cover extent in the winter and spring immediately preceding surveyed abundance at time t was better at predicting scaup population dynamics than other covariates, although a model with a lag-2 effect was closely ranked. When eliminating snow extent from the analysis and expanding the time frame to 1958–2010, a model with a lag-1 effect of July to August PDSI ranked best (Appendix: Table A2), 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 socioeconomic 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 a quadratic effect of price of pelts in the current year for mink (Appendix: Tables A3–A5). Residuals from these models were z -standardized and used as covariates in the process model for scaup population dynamics.

In the group of models for predator index effects on scaup population dynamics, all covariates performed worse than a model with only density dependence (Appendix: Table A6); however, in order to better understand how predation may interact with climate to affect scaup population dynamics, we included total fox abundance and red fox abundance in the models with combined effects.

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, lag-1 July–August PDSI only, snow cover + lag-2 snow cover extent or snow cover extent only, respectively) were retained in the models 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 an effect of total fox abundance and the immediate and lagged effects of July–August PDSI were additionally supported by the CPO summary statistic (Tables 1 and 2). The interactive effect indicated that during times of drought (i.e., negative values of lag-1 PDSI), the abundance of scaup pairs increased when the index of total fox abundance was high. During wet conditions with lag-1 PDSI, however, the highest levels

TABLE 1. Comparison of models, ranked by the negative mean of the log of the conditional predictive ordinate (CPO) values, from the combined analysis of scaup (*Aythya* spp.) pair abundance in the Northwest Territories, Canada, 1958–2010.

Model	$-\frac{\sum \log(\text{CPO}_{j,t})}{\text{sample size}}$
Total fox × (PDSI + PDSI _{lag-1})	5.0387
PDSI _{lag-1}	5.0409
Total fox + PDSI _{lag-1}	5.0414
PDSI + PDSI _{lag-1}	5.0414
Total fox × PDSI _{lag-1}	5.0416
Total fox + PDSI + PDSI _{lag-1}	5.0416
Red fox + PDSI + PDSI _{lag-1}	5.0424
Total fox	5.0462
Red fox × (PDSI + PDSI _{lag-1})	5.0462
Null	5.0463
Red fox	5.0483

Notes: Covariates from the top models within each group are abbreviated as Total fox and Red fox for the predator group (a model with total fox or red fox, respectively) and the Palmer Drought Severity Index, PDSI and PDSI_{lag-1} for the climatic group (a model with an effect of only lag-1 July–August PDSI or a model with an effect of July–August PDSI and lag-1 July–August PDSI). 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.

of scaup abundance occurred when the index to total fox abundance was low (Fig. 3). The opposite relationship was true for PDSI with no lag effect; scaup abundance was lowest during wet conditions (high PDSI) and high total fox abundance, and was high during drought conditions and low total fox abundance (Fig. 3).

A much simpler model with only the immediate effect of snow cover extent performed best for 1967–2010 (Table 3). An increase in the time-averaged snow cover in the winter and spring immediately preceding surveys at time *t* resulted in statistical and biologically significant

increases in scaup population abundance in a given stratum at the time of survey, and vice versa (Table 4, Fig. 4). All estimates of the growth rate for each stratum from the top models ($\beta_{0,j}$, Eq. 4) were greater than 0, indicating an increasing population in each stratum at covariate levels of 0 (Tables 2 and 4, Fig. 5). When considered simultaneously with climate (e.g., snow: $\theta = 0.76 \pm 0.06$), predator effects (e.g., total fox, 1967–2010: $\theta = 0.79 \pm 0.06$), or both (e.g., snow, lag-2 snow, plus total fox: $\theta = 0.73 \pm 0.06$), density dependence was present during both time periods (Tables 2 and 4). The overdispersion parameter in the negative binomial data model was 12.13 ± 1.89 for the July–August PDSI + lag-1 July–August PDSI model and 13.15 ± 2.05 for the snow model, indicating little overdispersion in the data relative to $\mu_{j,t}$.

DISCUSSION

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

For the years when snow data were available, time-averaged snow cover extent from the winter and spring prior to the beginning of the breeding season in May of year *t* was the most important climatic variable. The importance of snow cover seems to primarily relate to the immediate effects of snow cover, which probably affect subsequent wetland conditions and scaup settling decisions, as well as breeding propensity (Afton 1984), as they arrive in the NWT, and less through trophic

TABLE 2. Parameter estimates from the top model shown in Table 1 for the combined analysis of scaup pair abundance in the Northwest Territories, 1958–2010, including mean, standard deviation, and 90% and 95% credible intervals (shown as quantiles).

Parameter	Mean	SD	0.025 quantile	0.05 quantile	0.95 quantile	0.975 quantile
$\beta_{0,13}$	0.6554	0.19	0.2868	0.3039	0.9721	0.9936
$\beta_{0,14}$	0.8862	0.20	0.3715	0.4038	1.3322	1.3686
$\beta_{0,15}$	0.6089	0.28	0.2579	0.2812	0.9139	0.9412
$\beta_{0,16}$	0.6128	0.19	0.2581	0.2772	0.9186	0.9414
$\beta_{0,17}$	0.7493	0.23	0.3209	0.3488	1.1206	1.1525
$\beta_{0,18}$	0.6693	0.21	0.2828	0.2988	1.0016	1.0226
PDSI	-0.0083	0.01	-0.0311	-0.0274	0.0109	0.0146
PDSI _{lag-1}	0.0172	0.01	-0.0060	-0.0023	0.0366	0.0404
Fox	0.0108	0.02	-0.0249	-0.0190	0.0406	0.0465
PDSI × Fox	0.0192	0.01	-0.0027	0.0009	0.0374	0.0409
PDSI _{lag-1} × Fox	-0.0196	0.01	-0.407	-0.0374	-0.0018	0.0016
θ	0.8474	0.05	0.7540	0.7689	0.9268	0.9422
Offset	-0.9790	0.02	-1.0157	-1.0102	-0.9454	-0.9386

Notes: The $\beta_{0,j}$ parameters represent the stratum-specific (*j*th) growth rates, Fox represent the beta estimates for the index of total fox abundance, PDSI represents the beta estimate for July–August PDSI, PDSI_{lag-1} represents the beta estimate for the lag-1 July–August PDSI, θ represents the strength of density dependence, and Offset represents the offset_{*j,t*} parameter related to the number of segments surveyed in each stratum and year.

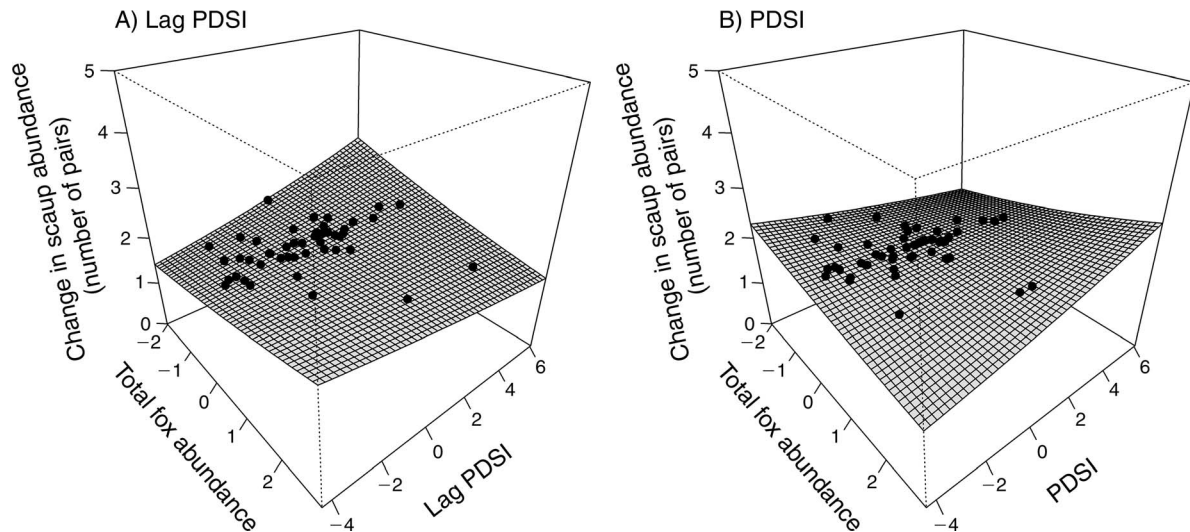


FIG. 3. The interactive effect of the Palmer Drought Severity Index (PDSI) for (A) the lag-1 July–August PDSI and (B) the July–August PDSI with the index for total fox abundance on predicted change in the abundance of scaup pairs, $N_t - N_{t-1}$ within the surveyed area of stratum 13 (relationships hold for Strata 14–18). The surface is specified for predictions across 90% of the range of lag-1 July–August PDSI, July–August PDSI, and total fox abundance. Only the $\beta_{0,13}$ parameter (the stratum-specific growth rate for stratum 13) plus the values of PDSI and total fox were used to calculate the change in abundance (i.e., density dependence and stochasticity were ignored in depicting the covariate impacts on population growth). Black circles represent observed values.

effects related to resources and alternative prey for predators. Additionally, this immediate effect of snow cover extent on surveyed abundance may simply be related to a systematic shift of migration timing by scaup, and the timing of the survey may be too early to adequately measure scaup abundance when such effects are not accounted for. Future modeling efforts could account for possible systematic observation errors like these by using covariates in the observation model (rather than the process model), which was not possible in the INLA package. Despite the possible confounding with migration timing, other studies have similarly shown a positive relationship with the “phenology of snow cover duration” (Drever et al. 2012), indicating that greater and prolonged snow cover may have positive effects on wetland resources that eventually percolate up the food web to positively affect scaup demography.

Indeed, the intensity of seasonal drought in the NWT, as measured by the PDSI, had important effects on scaup population dynamics and additionally supported our hypothesis that complex trophic interactions may play an important role. The inclusion of these covariates in the top model for 1958–2010 suggests that scaup demography responds most strongly to changes in water availability during the late breeding season, probably 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 PDSI and predators also suggests that scaup population growth is highest when water conditions are best (high PDSI) and predators are low, probably due to a release from predation pressure and improved water quality. An increase in scaup abundance with higher fox abundance during drought conditions is likely to be tied to

TABLE 3. Comparison of models, ranked by the negative mean of the log of the CPO values, from the combined analysis of scaup pair abundance in the Northwest Territories, 1967–2010.

Model	$-\frac{\sum \log(\text{CPO}_{f,t})}{\text{sample size}}$
Snow	4.9883
Snow + snow _{lag-2}	4.9889
Total fox × snow	4.9939
Total fox + snow	4.9948
Total fox + snow + snow _{lag-2}	4.9952
Total fox × (snow + snow _{lag-2})	4.9964
Red fox + snow + snow _{lag-2}	5.0017
Red fox × (snow + snow _{lag-2})	5.0107
Null	5.0238
Red fox	5.0250
Total fox	5.0327
Total fox + snow _{lag-2}	5.0409

Notes: Covariates from the top models within each group are abbreviated as Total fox and Red fox for the predator group (a model with total fox or red fox, respectively) and Snow and Snow_{lag-2} for the climatic group (model just an immediate effect of snow cover extent or 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.

TABLE 4. Parameter estimates from the top model in the combined analysis of scaup pair abundance in the Northwest Territories, 1967–2010, shown in Table 3, including mean, standard deviation, and 90% and 95% credible intervals (shown as quantiles).

Parameter	Mean	SD	0.025 quantile	0.05 quantile	0.95 quantile	0.975 quantile
$\beta_{0,13}$	0.8044	0.23	0.3823	0.4186	1.1893	1.2296
$\beta_{0,14}$	0.8622	0.33	0.2471	0.3299	1.4119	1.5011
$\beta_{0,15}$	0.8480	0.24	0.3955	0.4522	1.2522	1.3141
$\beta_{0,16}$	0.8536	0.21	0.4331	0.4724	1.2343	1.2779
$\beta_{0,17}$	0.7940	0.26	0.2584	0.3328	1.2697	1.3507
$\beta_{0,18}$	0.9617	0.23	0.5144	0.5449	1.3719	1.4108
Snow	0.1363	0.03	0.0703	0.0806	0.1934	0.2045
θ	0.7623	0.06	0.6494	0.6675	0.8569	0.8751
Offset	0.1199	0.06	0.0181	0.0339	0.2072	0.2238

Notes: The $\beta_{0,j}$ parameters represent the stratum-specific (j th) growth rates, Snow represents the beta estimates for snow in the winter and spring preceding scaup abundance surveys at time t , θ represents the strength of density dependence, and Offset represents the offset $_{j,t}$ parameter related to the number of segments surveyed in each stratum and year.

alternative prey through the lag-1 PDSI, because predators are likely to focus on primary prey species during times of decreased environmental quality. A trophic interaction between water conditions, alternative prey, predators, and scaup is also possibly supported by the interaction between PDSI (with no lag effect) and predator abundance. Scaup abundance is highest when PDSI is highest and predator abundance is high, and is lowest during drought conditions with low predator abundance. The contrast between lag-1 PDSI and PDSI could be because alternative prey species have not yet numerically responded to increased primary productivity in wetland areas. As is the case with all statistical extrapolations, our inference is conditional on the ability of the model to accurately represent the true system. Thus, as usual, we must simultaneously interpret our predictions with caution while acknowledging the value of the scientific components in the model.

Although correlative and not conclusive, our findings suggest that more detailed studies of the interactive effects among climate, predators, and alternative prey on scaup are needed. We advise some caution when interpreting our results because we were unable to control for trapping effort (e.g., through license sales) in the NWT when measuring residual indices of predator abundance. Our measures could thus be poor indices of actual predator abundance. As more detailed data become available (e.g., age-structured predator harvest), population reconstruction techniques (e.g., integrated population models) could be used to better estimate predator abundance.

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 if such changes have occurred, they are not related to the

ENSO averaged over the scaup year as we had hypothesized. 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 (1) insufficient food resources on the critical prairie pothole region staging area, or (2) 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, and potentially affecting their demographic performance as well (Anteau and Afton 2006). If this process is occurring, variation in the PPR wetland numbers does

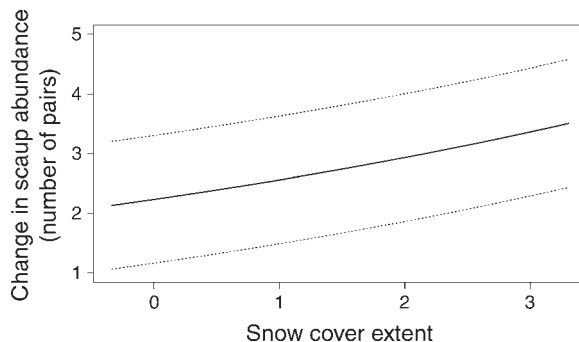


FIG. 4. The change in scaup pair abundance, $N_t - N_{t-1}$, with changes in the mean (solid line) snow cover extent between winter and spring in the season immediately prior to the BPOP waterfowl survey in year t within the surveyed area of stratum 13 in year t (relationships hold for strata 14–18), along with 95% credible intervals (dotted lines). Only the $\beta_{0,13}$ parameter plus the values of snow were used to calculate the change in abundance (i.e., density dependence and stochasticity were ignored in depicting the covariate impacts on population growth).

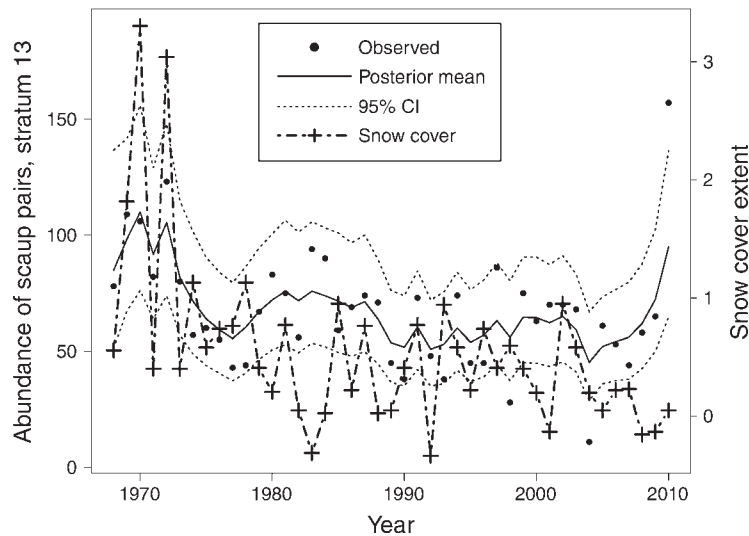


FIG. 5. Predicted number of scaup pairs (solid line with 95% credible interval in dotted lines), scaled snow cover extent in stratum 13 (dashed line with cross), and observed number of scaup pairs (black circles) within the surveyed area of stratum 13 of the Northwest Territories, given all the estimated fixed and random effects of our top model presented in Table 4.

not appear to be a good surrogate for identifying such cross-seasonal effects on scaup pairs in the boreal forest. We found no evidence for an effect of PPR pond conditions on scaup abundance farther north in the NWT. However, snow cover extent has declined over time (Fig. 5), and over the long term, scaup have loosely tracked this decrease in snow cover extent. Only in the most recent years is the pattern disparate, indicating that snow cover extent is not explaining everything. The current trend in NWT scaup abundance, however, is in the opposite direction (Fig. 5), indicating that the population may not have been declining in the last several years, despite the decrease in snow cover extent.

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 diving ducks, including scaup. Our results indicated that density dependence on the breeding grounds is an important driver of scaup pair abundance, at least in the NWT. An important aspect of our study was the reduction in bias by separately estimating sampling and process error (Freckleton et al. 2006). Previous analyses we conducted that did not properly account for this bias through state-space modeling yielded results suggesting that density dependence was not an important driver of scaup population dynamics in the NWT (results not shown), highlighting the importance of this state-space modeling approach. Although we 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. Although our results are limited to inference on the breeding grounds, density dependence could be affecting scaup

throughout their migratory cycle. Future studies will be needed to isolate seasonality of density dependence in the scaup life cycle, and how it affects population dynamics through density-dependent competition for food, 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 in which our 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 scaup to rebound following perturbations (e.g., through enhanced reproductive success), and estimates of the strength of density dependence are crucial for guiding harvest management. 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. A better understanding of how density dependence interacts with environmental processes such as predation and climate is also the focus of future research efforts, because INLA currently limits this analysis. Expanding the scale of this method to incorporate the entire BPOP survey area could also provide a better understanding of the interactive effects of harvest and density dependence on scaup population dynamics.

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 climate and pond conditions in the south, or at least are not as good at predicting population changes as snow cover extent and drought in the north. Exploration of other variables that could be affecting migratory phenology, and the potentially related effects on surveyed counts, deserve further study. Our results highlight the benefits of comparing multiple environmental and intrinsic population drivers when studying species of management and conservation concern to determine how climatic indices 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, our findings build upon the work of Drever et al. (2012) and provide insight into where future research on scaup population dynamics should be conducted.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix and the Supplement are available online: <http://dx.doi.org/10.1890/14-0582.1.sm>