Forecasting waterfowl population dynamics under climate change — Does the spatial variation of density dependence and environmental effects matter?

Qing Zhao a,b,⁎, Emily Silverman b, Kathy Fleming b, G. Scott Boomer b

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Reliable ecological forecasts are essential for conservation decision-making to respond to climate change. It is challenging to forecast the spatial structure of wildlife population dynamics because density dependence and environmental effects vary spatially. We developed models that incorporated density dependence and climatic (precipitation and temperature) effects to explain pond (wetland) dynamics and models that incorporated density dependence and pond effect to explain Mallard (Anas platyrhynchos) population dynamics. We trained the models using data from 1974 to 1998 and tested their hindcast performance with data from 1999 to 2010 to examine the scale at which the spatial variation of density dependence and climatic/pond effects should be incorporated to forecast pond and Mallard population dynamics. The pond model that did not allow density dependence and climatic effects to vary spatially (ΔMSE = 0.007–0.018) and the Mallard model that incorporated the spatial variation of density dependence and pond effect at the scale of Bird Conservation Regions (ΔMSE = 0.011–0.012) had the best hindcast performance. Using these models we forecasted the largest decrease (34.7%–43.0%) of Mallard density in the northern Prairie Pothole Region under two climate change scenarios, suggesting that the local Mallard population in this area might be particularly vulnerable to potential future warming. Our results provide insight into the factors that drive the spatial structure of waterfowl population dynamics. Because the spatial variation of density dependence and environmental effects is commonly found in wildlife populations, our framework of modeling and evaluation has wide application for conservation planning in response to climate change.

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1. Introduction

Climate change has already caused, and is likely to continue causing, shifts in the distributions, abundance, and dynamics of wildlife populations across a broad range of landscapes and habitats (Parmesan, 2006; Rosenzweig et al., 2008; Thomas et al., 2004; Walther, 2010). These large-scale ecological shifts have altered the effectiveness of current conservation efforts (Hannah et al., 2007; Virkkala et al., 2013). For instance, it has been suggested that fewer than half of the Important Bird Areas in Africa will retain their current conservation value under future climate conditions (Hole et al., 2011). Reliable ecological forecasts of system shifts associated with climate change are therefore needed to support long-term conservation decision-making (Clark et al., 2001).

North American waterfowl populations have been monitored and managed since the 1950s (Smith, 1995; U.S. Fish and Wildlife Service, 2012), but the current monitoring and management framework is challenged to account for large-scale system shifts driven by climate change (Nichols et al., 2011). The Prairie Pothole Region (PPR) is the most important area for waterfowl production in North America (Batt et al., 1989). Climate change in the PPR has not been spatially uniform (Millett et al., 2009). Consequently, wetland availability has decreased in the northern PPR and increased in the south-eastern PPR during the last several decades (Niemuth et al., 2014). Warming is predicted to continue in the PPR in the next century, which may cause further southeast-ward shifts of wetland availability (Johnson et al., 2005; Johnson et al., 2010; Niemuth et al., 2010). Because wetland availability is a key factor that drives waterfowl population dynamics (Batt, 1992; Dzus and Clark, 1998; Johnson and Grier, 1988), studies have recommended shifting conservation efforts from the western and central portion of the PPR to the eastern PPR (Johnson et al., 2010).

However, it is challenging to forecast the spatial structure of waterfowl population dynamics under climate change, due to the fact that waterfowl population dynamics are driven by both density dependence process (Murray et al., 2010; Vickery and Nudds, 1984; Vlijmgrein et al., 2005) and wetland availability (Batt, 1992; Bethke and Nudds, 1995; Johnson and Grier, 1988; Reynolds et al., 2006), and density dependence and wetland effects vary spatially (Bethke and Nudds, 1995; Sæther et al., 2008). While the spatial variation of density dependence...
and wetland effects has been incorporated in forecast models (Bethke and Nudds, 1995), it remains unclear if such models provide better forecasts than models that do not allow density dependence and wetland effects to vary spatially (Sorenson et al., 1998). Similarly, studies have used models that incorporate density dependence and climatic effects to explain wetland dynamics (Larson, 1995; Niemuth et al., 2014), but did not explicitly consider if incorporating the spatial variation of density dependence and climatic effects improved forecasts of wetland dynamics. Although an increase in model complexity generally improves model fit, more complex models may lead to poorer forecasts due to a reduction in generality.

In this study our goal was to forecast waterfowl population dynamics in response to future climate change. To achieve this goal, first we developed models that incorporated density dependence and climatic (precipitation and temperature) effects to explain pond (i.e. measurement of wetland availability) dynamics and models that incorporated density dependence and pond effect to explain Mallard (Anas platyrhynchos) population dynamics. Second, we trained the pond and Mallard models using data of Mallard density, pond density, precipitation, and temperature from 1974 to 1998 and tested the hindcast performance of the pond and Mallard models with data from 1999 to 2010 to examine the scale at which the spatial variation of density dependence and climatic/pond effects should be incorporated to forecast pond and Mallard population dynamics. Third, we fitted the pond and Mallard models that had the best hindcast performance and used the posterior parameter estimates to forecast Mallard population responses to potential future climate change scenarios.

2. Material and methods

2.1. Study area and population/habitat survey

The U.S. Fish and Wildlife Service (USFWS), Canadian Wildlife Service (CWS), and their partners monitor waterfowl abundance and wetland habitat conditions annually in May during the Waterfowl Breeding Population and Habitat Survey (Smith, 1995). This aerial survey extends from the U.S. prairies north through the boreal-taiga habitat and into Alaska. Two-person crews, consisting of a pilot-biologist and an observer, identify all waterfowl to species within a 200 m strip on each side of the aircraft and count the number of individuals encountered. In the PPR and surrounding areas, the observer also counts the number of natural and artificial ponds within the 200 m transect width as a measurement of wetland availability. Potential observation errors of the aerial counts are corrected by ground surveys of waterfowl and ponds, which are conducted concurrently at a subsample of the aerial surveys (Smith, 1995). Our analyses were based on the corrected survey data from the area where both waterfowl and ponds are counted (Fig. 1).

The study area covers three Bird Conservation Regions (BCRs), including the PPR, Badland and Prairie, and the southern portion of Boreal Taiga Plain. BCRs were defined in a holistic and comprehensive manner using hierarchical classifications based on a variety of ecological and biological factors including location, climate, vegetation, hydrology, and terrain (Commission for Environmental Cooperation, 1997). We used BCRs in this study to represent habitat variation at a coarse spatial scale.

The study area also encompasses six administrative regions (i.e. Canadian provinces and U.S. states): Alberta, Saskatchewan, and Manitoba in Canada, and Montana, North Dakota, and South Dakota in the U.S. Anthropogenic activities such as industrial development, agriculture, and other land use are expected to differ among these administrative regions (Bethke and Nudds, 1995; Reynolds et al., 2006; Reynolds et al., 2001). We overlaid the BCRs and administrative regions and considered each unique BCR and administrative region as a modeling unit (Fig. 1).

2.2. Climate data

We obtained temperature and precipitation data from climate data archives of the University of Delaware (Matsuura and Willmott, 2013a, 2013b). The temperature and precipitation data were interpolated...
from, and cross-validated with, weather station records, and are available by month at a spatial resolution of 0.5 × 0.5° latitude/longitude. We calculated total winter (January to April) precipitation and mean spring (March to April) temperature. Because ponds in the U.S. have been counted since 1974, and the climate data are available from 1900 to 2010, our analyses were based on data from 1974 to 2010. Time series of log Mallard density, log pond density, winter precipitation, and spring temperature for each model unit are shown in Appendix A.

2.3. Model development

In this study we considered three hypotheses regarding the factors that may affect the spatial variation of density dependence and climatic/pond effects. The first hypothesis (H1) assumes that density dependence and climatic/pond effects do not vary spatially. The second hypothesis (H2) assumes that different natural habitat conditions represented by Bird Conservation Regions (BCRs) affect density dependence and climatic/pond effects. Thus density dependence and climatic/pond effects vary at the spatial scale of BCRs. The third hypothesis (H3) assumes that, in addition to the effect of natural habitat conditions, anthropogenic activities further influence such spatial variation at sub-BCR scale.

H1: Density dependence and climatic/pond effects do not vary spatially.

\[ \alpha_{\text{pond}, t} = \alpha_{\text{pond}} \times \left(1 - \beta_{\text{pond}} \times \text{pond}_{i,t-1} \right) \times \beta_{\text{prec}} \times \text{prec}_{i,t} + \beta_{\text{temp}} \times \text{temp}_{i,t} \]

H2: Natural habitat conditions affect the spatial variation of density dependence and climatic/pond effects at BCR scale.

\[ \alpha_{\text{pond}, t} = \alpha_{\text{pond}} \times \left(1 - \beta_{\text{pond}} \times \text{pond}_{i,t-1} \right) \times \beta_{\text{prec}} \times \text{prec}_{i,t} + \beta_{\text{temp}} \times \text{temp}_{i,t} \]

H3: Natural habitat conditions affect the spatial variation of density dependence and climatic/pond effects at BCR scale. Anthropogenic activities further influence such spatial variation at sub-BCR scale.

\[ \alpha_{\text{pond}, t} = \alpha_{\text{pond}} \times \left(1 - \beta_{\text{pond}} \times \text{pond}_{i,t-1} \right) \times \beta_{\text{prec}} \times \text{prec}_{i,t} + \beta_{\text{temp}} \times \text{temp}_{i,t} \]
effects that were specific for each BCR \( j \). Note that the subscript \( j \) in M2 indicated that modeling units (indexed by \( i \)) were nested in BCRs (indexed by \( j \)). Thus M2 was a varying-slope model, with the varying slopes representing interactions between the predictors and an indicator variable of BCRs (Gelman and Hill, 2007). Density dependence and climatic effects were treated as fixed effects, which represented the spatial variation of density dependence and climatic effects related to different natural habitat conditions across BCRs.

The third pond model (M3) incorporated the spatial variation of density dependence and climatic effects at the spatial scale of sub-BCRs:

\[
\log(\text{pond}_{it}) = \alpha_{\text{pond}} + \left(1 - \beta_{\text{pond}}^{\text{prec}}\right) \times \log(\text{pond}_{i,t-1}) + \beta_{\text{pond}}^{\text{temp}} \times \text{temp}_{i,t} + \beta_{\text{pond}}^{\text{prec}} \times \text{prec}_{i,t} \]

where \( \beta_{\text{pond}}^{\text{prec}} \) represented density dependence that was specific for each modeling unit \( i \), and \( \beta_{\text{prec},i}^{\text{temp}},\beta_{\text{prec},i}^{\text{prec}} \) represented climatic effects that were specific for each modeling unit \( i \). Thus M3 was a varying-slope model, with the varying slopes representing interactions between the predictors and an indicator variable of modeling units. Density dependence and climatic effects were treated as random effects such that \( \beta_{\text{pond}}^{\text{temp}},\beta_{\text{pond}}^{\text{prec}} \sim \text{Normal}(0, 0.5^2) \), and \( \beta_{\text{prec},i}^{\text{temp}},\beta_{\text{prec},i}^{\text{prec}} \sim \text{Normal}(0, 0.5^2) \). In this model, \( \beta_{\text{pond}}^{\text{prec}} \) was a varying-slope that was related to the spatial variation of density dependence and climatic effects related to different natural habitat conditions across BCRs, and \( \beta_{\text{pond}}^{\text{temp}} \) was a varying-slope that was related to climatic effects and density dependence.

We modeled Mallard density in a year as a function of the Mallard density in the previous year and the pond density observed in the same year. The first Mallard model (M1) did not allow density dependence and pond effect to vary spatially:

\[
\log(\text{duck}_{it}) = \alpha + \left(1 - \beta_{\text{pond}}\right) \times \log(\text{duck}_{i,t-1}) + \beta_{\text{pond}} \times \log(\text{pond}_{i,t}) + \epsilon_{i,t}
\]

where Mallard density \( \text{duck}_{i,t} \) was calculated as \( N_{i,t}^{\text{duck}}/A_{i,t} \), in which \( N_{i,t}^{\text{duck}} \) was the sum of the corrected counts of Mallard in modeling.
unit $i$ and year $t$, and $A_{i,t}$ was the total area surveyed in that unit and year. The intercept $\alpha$ represented the intrinsic multiplicative rate of population increase that was unique for the study area. $\beta_{ddp}$ represented density dependence that did not vary spatially, and $\beta_{pond}$ represented pond effect that did not vary spatially. In this model, a larger/smaller positive $\beta_{ddp}$ value represented stronger/weaker density dependence. Also, the log of carrying capacity was a parameter of modeling units. Density dependence and pond effect variation of density dependence and pond effect at the spatial scale of sub-BCRs:

$$\log(duck_{i,t}) = \alpha + (1 - \beta_{ddp,j}) \times \log(duck_{i,t-1}) + \beta_{pond,j} \times \log(pond_{i,t}) + \epsilon_{i,t}$$

where $\beta_{ddp,j}$ represented density dependence that was specific for each BCR $j$, and $\beta_{pond,j}$ represented pond effect that was specific for each BCR $j$. $M2$ was a varying-slope model, with the varying slopes representing interactions between the predictors and an indicator variable of BCRs. Density dependence and pond effect were treated as fixed effects, which represented the spatial variation of density dependence and pond effect related to different natural habitat conditions across BCRs.

The third model (M3) incorporated the spatial variation of density dependence and pond effect at the spatial scale of sub-BCRs:

$$\log(duck_{i,t}) = \alpha + (1 - \beta_{ddp,i}) \times \log(duck_{i,t-1}) + \beta_{pond,i} \times \log(pond_{i,t}) + \epsilon_{i,t}$$

where $\beta_{ddp,i}$ represented density dependence that was specific for each modeling unit $i$, and $\beta_{pond,i}$ represented pond effect that was specific for each modeling unit $i$. M3 was a varying-slope model, with the varying slopes representing interactions between the predictors and an indicator variable of modeling units. Density dependence and pond effect were treated as random effects such that $\beta_{ddp,i} \sim \text{Normal}(\mu_{ddp,i}, \sigma^2_{ddp,i})$ and $\beta_{pond,i} \sim \text{Normal}(\mu_{pond,i}, \sigma^2_{pond,i})$, in which $\mu$'s represented the spatial variation of density dependence and pond effect related to different natural habitat conditions across BCRs, and $\sigma^2$'s governed the spatial variation of density dependence and pond effect influenced by anthropogenic activities at the sub-BCR scale.

We analyzed the models using a hierarchical Bayesian framework. We used non-informative prior distributions $\text{Normal}(0, 10,000)$ for $\alpha$ (M1–3), $\beta$'s (M1 and M2), and $\gamma$'s (M3), and Gamma (0.0001, 0.0001) for the precision parameters $\sigma^2$'s (M1–3) and $\sigma^2$'s (M3; Table 1). We used Markov Chain Monte Carlo methods via Gibbs sampling with the software WinBUGS 1.4.3 (Lunn et al., 2000) to obtain the posterior distributions of the parameters. We used three chains, each of which contained 100,000 iterations including 50,000 burn-in and were thinned by 10. Thus the posterior distribution of each parameter contained 15,000 values, which were saved for the simulation process (see below). We checked convergence using the Brooks–Gelman–Rubin potential scale reduction factor where $R$ ≤1.05 was considered to indicate convergence (Brooks and Gelman, 1998).

2.4. Model evaluation

We used cross-validation to evaluate model fit and hindcast performance of the models. We divided the entire time series into a training set and a testing set: the training set included 25 years of data from 1974 to 1998 and the testing set consisted of data from the last 12 years (1999 to 2010). We evaluated the pond models and Mallard models separately to identify a pond model that represented the factors driving the spatial structure of pond dynamics and a Mallard model that represented the factors driving the spatial structure of Mallard population dynamics.

First we fit the pond models with the training set and calculated errors as the difference between the fitted and observed pond densities. We also fit the Mallard models with the training set and calculated errors as the difference between the fitted and observed Mallard densities. We calculated mean squared error (MSE) as a measure of model fit, and decomposed MSE into the variance of error and the squared bias to understand the bias-variance tradeoff.

We then used the posterior parameter estimates of the pond models and observed precipitation and temperature data to simulate pond dynamics of the testing period. We also used the posterior parameter estimates of the Mallard models and observed pond density to simulate Mallard population dynamics of the testing period. In each simulation we used the posterior values or parameters from the same chain and iteration of MCMC sampling. The values of process errors for each modeling unit were taken from the same chain and iteration of MCMC sampling as the parameters, but were randomly drawn from one of the years of the training period in each step of the simulation. The simulations were conducted in an accumulative manner, i.e. the simulation of pond/Mallard density in a year was based on the pond/Mallard density simulated for the previous year. The simulations were repeated 15,000 times, and the simulated density was calculated as the mean of the simulations for each modeling unit $i$ and year $t$. We calculated errors as the difference between the simulated and observed pond/Mallard densities. We calculated MSE as a measure of hindcast performance, and decomposed MSE into the variance of error and the squared bias. We considered the pond/Mallard models with the lowest MSE to have the best hindcast performance, and thus represent the factors driving the spatial structure of pond/Mallard population dynamics.

We performed two additional validation exercises to examine if the model evaluation was influenced by the choice of training/testing period. First, we used the first 20 years (1974 to 1993) as the training set and the rest of the years as the testing set. Second, we used the first 30 years (1974 to 2003) as the training set and the rest of the years as the testing set. The above-mentioned evaluations of model fit and hindcast performance were repeated with these data sets.

2.5. Forecast pond and Mallard population dynamics under climate change

We forecasted the spatial structure of Mallard population dynamics under two different climate change scenarios (Johnson et al., 2010; Pachauri and Reisinger, 2007). The first scenario predicts a 4 °C increase in temperature and a 10% increase in precipitation by 2100. In the second scenario, it is predicted that by 2100 temperature will increase by 4 °C, while precipitation will remain at historic levels. We assumed that the changes in precipitation and temperature would be linear, and thus, for example, the increase in temperature per year was calculated as 4 °C divided by the number of years from 2010 to 2100. We also assumed that the fluctuation of precipitation and temperature would stay at the same level as in history.

We fitted the pond model that had the best hindcast performance using the full data set, and used the posterior parameter estimates of the pond model and calculated values of precipitation and temperature under the above-mentioned climate change scenarios to forecast pond dynamics from 2010 to 2100. We also fitted the Mallard model that had the best hindcast performance using the full data set, and used the posterior parameter estimates of the Mallard model and the forecasted pond densities to forecast Mallard population dynamics from
2010 to 2100. The forecasts were conducted using the same simulation approach as we did in the cross-validation. The forecasts were repeated 15,000 times, corresponding to the 15,000 iterations of MCMC sampling. The forecasted values of pond/Mallard densities for each modeling unit, year, and simulation were kept for further calculation.

We calculated the mean of \( \bar{y}_{i,t,k}^{\text{forecast}} \) for each modeling unit \( i \), year \( t \), and simulation \( k \) (denoted by \( \bar{y}_{i,t,k}^{\text{forecast}} \)) and compared it to the observed mean pond/Mallard densities for 1974 to 2010 (denoted by \( \bar{y}_{i,t}^{\text{historic}} \)). We calculated \( \bar{y}_{i,t,k}^{\text{forecast}} - \bar{y}_{i,t}^{\text{historic}} \) for each modeling unit as a measure of forecasted change. We calculated the standard deviation of \( \bar{y}_{i,t,k}^{\text{forecast}} - \bar{y}_{i,t}^{\text{historic}} \) for each modeling unit as a measure of forecast uncertainty.

All analyses were performed in R2.15.2 (R Development Core Team 2012). WinBUGS software was called from R using R2WinBUGS packages (Sturtz et al., 2005).

3. Results

3.1. Model evaluation

For pond models, the increase in model complexity led to better model fit: M3 had the smallest mean squared error (MSE = 0.161), followed by M2 (0.180) and M1 (0.195). However, pond M1 had the best hindcast performance, indicated by its smaller MSE (0.216) than M2 (0.223) and M3 (0.234). The variance of error was the main contributor to MSE. The most complicated pond model did not have the smallest bias in either model fit or hindcast (Table 2a).

For Mallard models, the increase in model complexity led to better model fit: M3 had the smallest MSE (0.080), followed by M2 (0.086) and M1 (0.101). However, Mallard M2 had the best hindcast performance, indicated by its smaller MSE (0.139) than M1 (0.151) and M3 (0.150). The variance of error was the main contributor to MSE. The most complicated Mallard model did not have the smallest bias in either model fit or hindcast (Table 2b).

The evaluations of model fit and hindcast performance held for both pond and Mallard models when using the first 20 or 30 years as the training set and the rest of the years as the testing set (Appendix B).

3.2. Parameter estimates

Pond model M1, which had the best hindcast performance, was fitted using the full data set to obtain posterior parameter estimates. Pond density was positively correlated to the lag-1 term (0.44 ± 0.04). Precipitation had a positive effect (0.12 ± 0.02), and temperature had a negative effect (−0.18 ± 0.03) on pond dynamics. The interactive effect of precipitation and temperature on pond dynamics was positive (0.05 ± 0.02; Table 3a), indicating that temperature had a stronger negative effect on pond dynamics in areas with low precipitation than in areas with high precipitation (Fig. 2).

Mallard model M2, which had the best hindcast performance, was fitted using the full data set to obtain posterior parameter estimates. Mallard density was positively correlated to the lag-1 term, and the effect was highest in the Badland and Prairie (posterior mean ± S.D.: 0.59 ± 0.06), followed by the PPR (0.40 ± 0.04), and lowest in the southern Boreal Taiga Plain (0.17 ± 0.04). The positive pond effect on Mallard population dynamics was highest in the Badland and Prairie (0.56 ± 0.06), followed by the PPR (0.36 ± 0.04), and lowest in the southern Boreal Taiga Plain (0.09 ± 0.04; Table 3b). The ratio of pond effect to density dependence was similar for the Badland and Prairie (0.94) and the PPR (0.92), but was lower for the Boreal Taiga Plain (0.56).

3.3. Forecasts

Pond density was forecasted to decrease in all the modeling units under both climate change scenarios (scenario 1: temperature + 4 °C & precipitation + 10%, scenario 2: temperature + 4 °C). The largest decrease was forecasted in the Boreal Taiga Plains (scenario 1: −41.7% to −49.5%; scenario 2: −46.6% to −53.4%), followed by the northern PPR (scenario 1: −29.7% to −46.7%; scenario 2: −36.4% to −50.7%), and the smallest decrease was forecasted in the southern PPR and Badland and Prairies (scenario 1: −11.1% to −39.2%; scenario 2: −26.0% to −45.0%). PPR-South Dakota had the highest forecast uncertainty (scenario 1: 34.8%; scenario 2: 28.6%) among all modeling units under both scenarios (Fig. 3a).

Mallard density was forecasted to decrease in all the modeling units under both scenarios. The largest decrease was forecasted in the northern PPR (scenario 1: −34.7% to −39.3%; scenario 2: −40.0% to −43.0%), followed by the Boreal Taiga Plain, Badland and Prairie, and PPR-Montana (scenario 1: −6.6% to −28.0%; scenario 2: −19.3% to −31.9%), and the smallest decrease was forecasted in PPR-North Dakota and PPR-South Dakota (scenario 1: −2.2% to −2.6%; scenario 2: −10.8% to −16.6%). PPR-North Dakota and PPR-South Dakota had the highest forecast uncertainty (scenario 1: 38.7%–40.3%; scenario 2: 33.6%–35.2%) among all modeling units under both scenarios (Fig. 3b).

4. Discussion

4.1. Spatial variation of density dependence and pond effect

Our study provides further evidence that climatic factors including winter precipitation and spring temperature influence pond dynamics (Niemuth et al., 2014) and pond density affects Mallard population dynamics (Batt, 1992; Dzus and Clark, 1998; Johnson and Grier, 1988). The Mallard model that incorporates the spatial variation of density dependence and pond effect at the scale of Bird Conservation Regions (BCRs) has the best hindcast performance, suggesting that such spatial variation is likely to be affected by the differences in natural habitat conditions among BCRs.

We found that pond effect on Mallard population dynamics was strongest in the Badland and Prairie and weakest in the Boreal Taiga Plain. Similarly, studies that cover a similar area found that wetland effects tended to be stronger in the Canadian PPR than in the southern Boreal Taiga Plain (Bethke and Nudds, 1995), or found a negative correlation between pond effect on Mallard abundance and latitude (Sæther et al., 2008). Our model also suggested that density dependence was strongest in the Badland and Prairie and weakest in the Boreal Taiga Plain, indicating that populations that are highly influenced by pond conditions are also strongly regulated by density dependence. The spatial variation of density dependence and pond effect seems to reflect the adaptation of local populations to natural habitat variation at BCR scale. Because BCRs are defined based on a variety of geographical and ecological factors, the particular factors that affect such spatial variation remain unclear and warrant further investigation.

Spatial variation in density dependence and environmental effects is commonly found in wildlife populations (Bjornstad et al., 1995; Cattadori and Hudson, 1999; Forchhammer et al., 1998; Grettan et al., 2009; Kojola and Helle, 2010; Sæther et al., 2003; Stenseth et al., 1999; Williams et al., 2003), and such spatial variation may provide important information for forecasting the spatial structure of population dynamics under environmental alteration such as climate change. Our study provides supportive evidence that incorporating the spatial variation of density dependence and pond effect can improve the hindcast performance of population dynamic models. However, our results also show that incorporating the spatial variation of density dependence and pond effect at sub-BCR scale, instead of BCR scale, does not further improve hindcast performance, indicating that the increase of model complexity does not necessarily lead to better forecasts. Indeed, the...
most complicated model (i.e. M3) did not have the smallest hindcast bias, indicating that the poor hindcast performance of this model is not only a result of high variance of error, but also a consequence of the decrease in hindcast accuracy. Thus our study demonstrates that it is necessary to examine the spatial scale at which the spatial variation of density dependence and environmental effects should be incorporated to forecast the spatial structure of wildlife population dynamics.

Studies have shown that anthropogenic activities such as land use can influence wetland habitat and waterfowl population dynamics (Bethke and Nudds, 1995; Drever, 2006; Miller, 2000). Our pond/Mallard models that allow the spatial variation of density dependence and climatic/pond effects across administrative regions have the best model fit, suggesting that land use may have altered density dependence and climatic/pond effects at the sub-BCR scale. However, these models do not have the best hindcast performance, suggesting that the impacts of land use may have changed during the study period (Bethke and Nudds, 1995; Reynolds et al., 2006; Reynolds et al., 2001).

4.2. Pond and waterfowl population dynamics under climate change

The forecasted decrease of pond density shows an evident spatial gradient, with the largest forecasted decrease in the north and the smallest in the south. This reflects the spatial gradient of precipitation and temperature in the study area, as the southern portion of the study area tends to be warmer and wetter than the northern portion (Millett et al., 2009). This is also because of the positive interaction between precipitation and temperature on pond dynamics. Because of this interaction, the increase in temperature has a stronger negative effect on pond dynamics in the northern portion of the study area with relatively low precipitation, compared to the southern portion of the study area with relatively high precipitation.

The forecasted decrease of Mallard density shows a different spatial pattern than the forecasted decrease of pond density, despite the fact that pond density is a key driver of Mallard population dynamics. This is due to the spatial variation of density dependence and pond effect. Although the Boreal Taiga Plain is forecasted to have the largest decrease of pond density, the forecasted decrease of Mallard density in this area is relatively small, because pond density has relatively small effect on Mallard density in this area, indicated by the small ratio of pond effect to density dependence. By contrast, the northern portion of the PPR is forecasted to have the largest decrease of Mallard density under potential future warming, not only because the forecasted decrease of pond density is large, but also because the same amount of change in pond density leads to a large change in Mallard density in this area, indicated by the large ratio of pond effect to density dependence. The Badland and Prairie and the southern portion of the PPR is forecasted to have a relatively small decrease of Mallard density, due to the relatively small forecasted decrease of pond density in these areas. Our results show that the spatial structure of waterfowl population dynamics in response to climate change is driven by the spatial variation of density dependence and pond effect.

The forecast results under two different climate change scenarios suggest that the local Mallard population in the northern PPR may be particularly vulnerable to potential future warming. By contrast, the local Mallard population in the south–eastern PPR seems to be resilient to potential future warming. However, the relatively high forecast uncertainty in the southeastern PPR suggests that further investigation of the factors that drive waterfowl population dynamics is needed for this area. For example, studies have suggested that the Conservation Reserve Program in the U.S. may benefit waterfowl populations by increasing the area of grassland (Reynolds et al., 2001). Thus the apparent resilience of waterfowl population to climate change in the south-eastern PPR may be due to the improvement of habitat conditions.

4.3. Conclusion

Reliable ecological forecasts of potential system shifts associated with climate change play a key role in conservation decision-making. Our study provides a practical, comprehensive framework of modeling and evaluation for studies and conservation projects that aim to forecast the spatial structure of wildlife population dynamics in response to environmental alteration such as climate change. Once potential spatial shifts of wildlife distributions, abundance, and population dynamics are forecasted, monitoring efforts can be reallocated and used to redefine target populations, possibly leading to the adaptation of population and habitat management strategies. In particular, our study highlights the importance of identifying the appropriate scale for incorporating the spatial variation of density dependence and environmental effects in forecast models. Because the spatial variation of density dependence and environmental effects is commonly found in many wildlife populations, our framework of modeling and evaluation can have wide applications for a variety of systems.

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