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The non-linear, interactive effects of population density and climate drive the geographical patterns of waterfowl survival

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ABSTRACT

On-going climate change has major impacts on ecological processes and patterns. Understanding the impacts of climate on the geographical patterns of survival can provide insights to how population dynamics respond to climate change and provide important information for the development of appropriate conservation strategies at regional scales. It is challenging to understand the impacts of climate on survival, however, due to the fact that the non-linear relationship between survival and climate can be modified by density-dependent processes. In this study we extended the Brownie model to partition hunting and non-hunting mortalities and linked non-hunting survival to covariates. We applied this model to four decades (1972–2014) of waterfowl band-recovery, breeding population survey, and precipitation and temperature data covering multiple ecological regions to examine the non-linear, interactive effects of population density and climate on waterfowl non-hunting survival at a regional scale. Our results showed that the non-linear effect of temperature on waterfowl non-hunting survival was modified by breeding population density. The concave relationship between non-hunting survival and temperature suggested that the effects of warming on waterfowl survival might be multifaceted. Furthermore, the relationship between non-hunting survival and temperature was stronger when population density was higher, suggesting that high-density populations may be less buffered against warming than low-density populations. Our study revealed distinct relationships between waterfowl non-hunting survival and climate across and within ecological regions, highlighting the importance of considering different conservation strategies according to region-specific population and climate conditions. Our findings and associated novel modelling approach have wide implications in conservation practice.

1. Introduction

On-going climate change has major impacts on ecological processes and patterns ranging from individual- to ecosystem-level (Grimm et al., 2013; Parmesan, 2006; Thomas et al., 2004; Walther, 2010), influencing population dynamics, extinction rates, and distributions of organisms (Keith et al., 2008; Moritz et al., 2008; Sæther et al., 2000; Sillett et al., 2000; Thomas et al., 2006). Models that explicitly examine the impacts of climate on the geographical patterns of demographic processes can provide insights to how populations respond to climate change across space and over time, and thus hold significance in ecological research and conservation practice (Gamelon et al., 2017; Sæther et al., 2004; Schippers et al., 2011). The impacts of climate on survival, one of the most important demographic parameters, have been examined in numerous taxa including plants (Reich and Oleksyn, 2008), insects (Paradis et al., 2008), fish (Ciannelli et al., 2007), amphibians (Griffiths et al., 2010), reptiles (Tomillo et al., 2012), birds (Robinson et al., 2007), and mammals (Molnár et al., 2010), yet the non-linear, interactive effects of population density and climate factors on survival have rarely been examined.

A major challenge to understanding the effects of climate on survival lies in the fact that the relationship between survival and climate can be non-linear. A study in Scots pine (*Pinus sylvestris*) found that an increase in temperature had a positive effect on survival in the cold northern part of their study area, but had a negative effect on survival in the warm south (Reich and Oleksyn, 2008). Such a non-linear relationship represents complex effects of temperature on survival: while warmth may benefit survival in cold areas, high temperature may cause drought and thus reduce the chance of survival in warm areas. Studies in white stork (*Ciconia ciconia*) found that an increase in precipitation only had a positive effect on survival when precipitation was insufficient, but had no effect on survival when precipitation was

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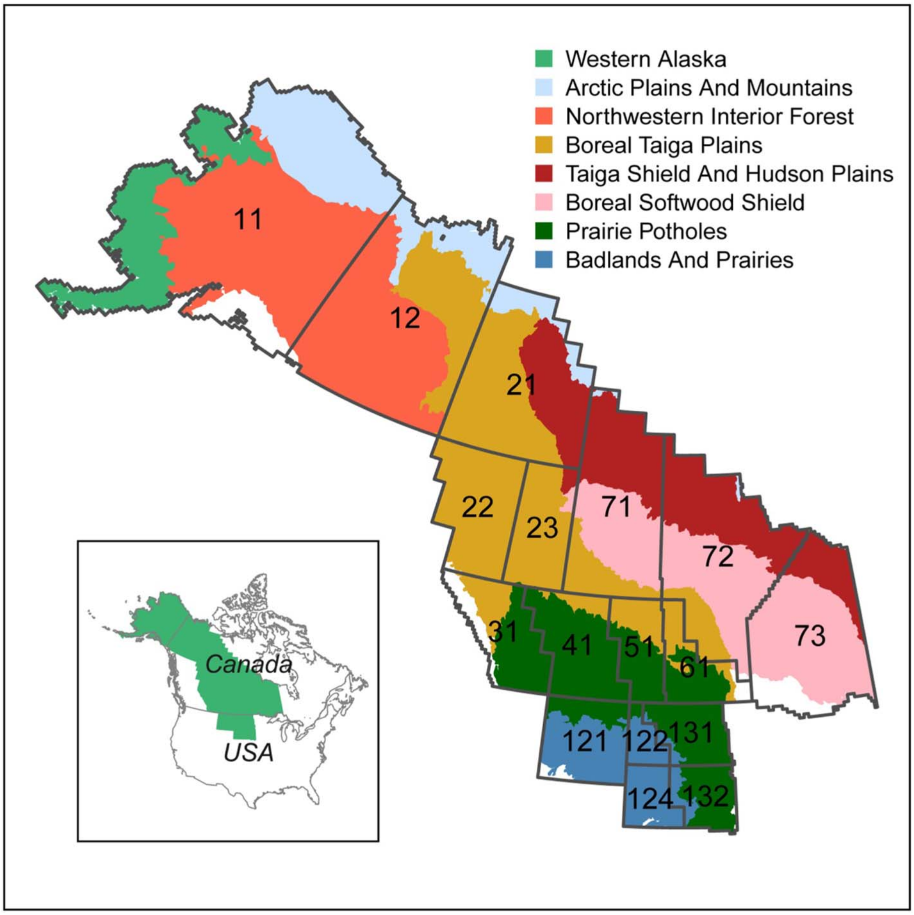

Fig. 1. The position of the study area in the North America (inner panel) and the relative position of reference areas (numbered) and ecological regions. Ecological regions are distinguished by colours shown in the legend. (For interpretation of the references to colour in this figure legend, the reader is referred to the online version of this chapter.)

abundant (Grosbois et al., 2008; Nevoux et al., 2008). While precipitation is normally considered beneficial to survival of water birds by increasing wetland habitat availability, it may also have a negative effect on their survival by reducing other important habitats, such as refugia, when high precipitation causes flood.

Alongside environmental stochasticity, density-dependent processes can also cause fluctuations in demography and population size, imposing another major challenge to understanding the effects of climate on survival. While the effects of density-dependent processes and environmental stochasticity are traditionally considered to be independent of each other, recent studies found that climate interacted with density-dependent processes to affect demography and population dynamics (Barbraud and Weimerskirch, 2003; Gamelon et al., 2017; Laws and Belovsky, 2010; Stenseth et al., 2004). Such interactions represent the fact that climate may influence resources that are essential for survival, and the competition over such resources is modified by population density (Gamelon et al., 2017). Incorporating the non-linear, interactive effects of population density and climate in model structures is important for studies that aim to identify and understand the regional and temporal variability in the relationship between survival and climate, providing information for the development of appropriate conservation strategies according to specific conditions at a regional scale.

The population size and demography of North American waterfowl populations have been monitored since the 1950's over a large spatial extent (Smith, 1995; U.S. Fish and Wildlife Service, 2012), providing a unique opportunity to understand the complex relationships among population density, climate, and survival at regional scales. The annual survival of these waterfowl populations is considered to be influenced by wetland habitat availability (Nichols et al., 1982), which is in turn affected by climate change (Larson, 1995; Sofaer et al., 2016; Zhao et al., 2016). On the other hand, these waterfowl populations are also subjected to annual recreational harvest, which is affected by management decisions. Therefore, it is important to partition hunting and non-hunting mortality and examine the effects of population density and climate on non-hunting survival. Understanding the factors that drive waterfowl non-hunting survival is not only important for testing ecological hypotheses, but also key to the conservation management of waterfowl populations (Nichols et al., 2011). However, to our knowledge, no attempt has been made to examine the non-linear, interactive effects of population density and climate on the non-hunting survival of North American waterfowl populations, limiting our ability to manage these populations and their habitats under climate change.

In this study we aimed to understand the non-linear, interactive effects of density-dependent processes and climate on the spatio-temporal variation of waterfowl non-hunting survival. We extended the Brownie model (Brownie et al., 1985; Williams et al., 2002) to partition hunting and non-hunting mortality of waterfowl populations and linked non-hunting survival to covariates. We then applied the model to four decades (1972–2014) of Mallard (*Anas platyrhynchos*) band-recovery, breeding population survey, and climate data, which covers a large spatial extent from North American prairies through boreal habitats to Alaska. We examined the non-linear, interactive effects of breeding population density, temperature, and precipitation on Mallard non-hunting survival. We also identified distinct relationships between Mallard non-hunting survival and climate across and within ecological regions. We then sought to understand the implications of our results for the conservation of waterfowl as well as other wildlife populations