



Accounting for the temporal variation of spatial effect improves inference and projection of population dynamics models



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ABSTRACT

Population dynamics models incorporating density dependence and habitat heterogeneity are useful tools to explain and project the spatiotemporal variation of wildlife abundance. Despite their wide application in ecology and conservation biology, the inference and projection of these models may be problematic when residual spatial autocorrelation (SAC) is found. We aimed to improve the inference and projection of population dynamics models by accounting for residual SAC. We considered three Gompertz models that incorporated density dependence and the effect of wetland habitat to explain and project the abundance of Mallard (*Anas platyrhynchos*). We compared a conventional model that did not account for residual SAC (ENV) with two novel models accounting for residual SAC, one incorporating a spatial effect (a spatially autocorrelated process error) that did not vary over time (STA) and the other incorporating a spatial effect that varied over time (DYN). We evaluated model inference using data from 1974 to 1998 and projection using data from 1999 to 2010. We then forecasted Mallard abundance from 2011 to 2100 under different levels of wetland habitat loss. The DYN model eliminated residual SAC and had better model fit than the ENV and STA models ($\Delta D = 2498.3$ and 1988.8, respectively). The projection coverage rate of the DYN model was the closest to the nominal value among the three models. The DYN model forecasted smaller areas with decrease in Mallard abundance under future wetland habitat loss than the ENV and STA models. The novel and conventional population dynamics models we considered in this study, combined with the practical model evaluation approach, can provide reliable inference and projection of wildlife abundance, and thus have wide application in ecological studies and conservation practices that aim to understand and project the spatiotemporal variation of wildlife abundance under environmental changes. In particular, when conservation decision-making is based on model projections, the DYN may be used to minimize the risk of reducing conservation effort in areas that still have high conservation value, due to its favorable projection performance.

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1. Introduction

Ecologists and conservation biologists have long sought to quantify and understand the variation of wildlife abundance. Population dynamics models (e.g. Gompertz models) can be used to explain the spatiotemporal variation of abundance in relation to environmental variables and project abundance under novel environmental conditions because they explicitly consider dynamic process while accounting for environmental heterogeneity (Fahrig, 2007). However, the inference and projection of population dynamics models may be problematic when spatial autocorrelation (SAC) is found in the residuals. SAC is commonly found in ecological data (Legendre, 1993; Koenig, 1999) because extrinsic environmental drivers are

spatially autocorrelated (Lichstein et al., 2002) or due to intrinsic population processes (Wintle and Bardsos 2006; Ficetola et al., 2012). SAC can be fully accounted for only if all the extrinsic and intrinsic drivers are included in the model structure (Cliff and Ord, 1981). Examples of models that fully explain all spatial variability have rarely been achieved, however, due to our limited ability to identify or measure all the key extrinsic and intrinsic drivers. Therefore, in most cases, there is SAC in the model residuals, which violates a basic assumption of most statistical approaches. It has been shown that failure to account for residual SAC leads to biased estimates of type I error and poor model fit (Legendre, 1993; Dormann, 2007; Beale et al., 2010).

The effects of accounting for residual SAC have been well studied in species distribution models, a type of models that aim to understand and project the geographical distributions of species based on presence/absence or presence-only data (Guisan and Zimmermann, 2000; Elith and Leathwick, 2009). Numerous studies

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have shown that accounting for residual SAC in species distribution models improves parameter estimates and model fit (Keitt et al., 2002; Lichstein et al., 2002; Segurado et al., 2006; Dormann 2007; De Marco et al., 2008; Mauricio Bini et al., 2009; Beale et al., 2010; Broms et al., 2014), but see (Hodges and Reich, 2010). Studies have also shown that accounting for residual SAC in species distribution models improves their ability to project current (Augustin et al., 1996; Latimer et al., 2006; Finley et al., 2009) or future species distributions (Swanson et al., 2013). By contrast, the effects of accounting for SAC in population dynamics models remain poorly understood. In particular, despite the fact that the environmental factors and population processes causing SAC are likely to change over time, little is known about the consequence for model inference and projection of accounting for the temporal variation of spatial effect (i.e. a process error that is spatially autocorrelated) in population dynamics models (Bled et al., 2011; Ross et al., 2012; Bled et al., 2013).

In this study we compared the inference and projection of one conventional and two novel Gompertz models with a case study of Mallard (*Anas platyrhynchos*) breeding populations in relation to wetland habitat availability. North American waterfowl breeding populations have been monitored for adaptive harvest management since the 1950's, but the current monitoring and management framework is challenged to account for directional shifts in wetland habitat dynamics associated with climate change (Nichols et al., 2011; Sofaer et al., 2016; Zhao et al., 2016). In a previous study we considered a conventional model that incorporated density dependence and habitat heterogeneity, but did not account for residual SAC, to explain and project the spatiotemporal variation of Mallard abundance in relation to wetland habitat availability (Zhao et al., 2016). However, in addition to wetland habitat, waterfowl abundance can also be driven by other environmental factors such as the distributions of predators (Ross et al., 2015) and population processes such as migration (Johnson and Grier, 1988), which cannot be explicitly incorporated in population dynamics models without additional data. Thus the conventional model may suffer from the problem of residual SAC. In this study we developed two novel models to account for residual SAC, one incorporating a spatial effect that did not vary over time, and the other incorporating a spatial effect that varied over time. Our research focus was to improve the explanation and projection of Mallard abundance in relation to wetland habitat availability while accounting for residual SAC representing other latent drivers.

We considered three models to explain the spatiotemporal variation of Mallard abundance, which corresponded to three hypotheses. The first model only incorporated density dependence and the effect of wetland habitat, but not a spatial effect (hereafter ENV model). This model represented the hypothesis that wetland availability was the only environmental factor that drove Mallard abundance. The second model incorporated density dependence, the effect of wetland habitat, and a spatial effect that did not vary over time (hereafter STA model). This model represented the hypothesis that, in addition to wetland availability, there were other latent factors that drove Mallard abundance, and these factors did not vary over time. The third model incorporated density dependence, the effect of wetland habitat, and a spatial effect that varied over time (hereafter DYN model). This model represented the hypothesis that, in addition to wetland availability, there were other latent factors that drove Mallard abundance, and these factors varied over time.

First, we fit the models with a twenty-five year (1974–1998) data set of Mallard density (i.e. abundance per unit area) and pond density (a measure of wetland habitat availability) and compared the inference of the models. Second, we used the posterior parameter samples obtained from model training and observed pond density to predict Mallard density for the period of 1999–2010,

and compared the predicted Mallard density against the observed Mallard density for the same period to evaluate the projection performance of the models. Third, to illustrate the differences among the models in forecasting Mallard population vulnerability to wetland habitat loss, we fit the models with the full (1974–2010) data set and used the posterior parameter samples to forecast Mallard density for the period of 2011–2100 under different levels of loss in pond density. Based on these results, we sought to understand the implications of modeling approaches ignoring or accounting for residual SAC in conservation decision-making.

2. Materials and methods

2.1. Study area and data collection

North American waterfowl breeding populations have been monitored annually by the U.S. Fish and Wildlife Service, Canadian Wildlife Service, and their partners during the Waterfowl Breeding Population and Habitat Survey (Smith, 1995; U.S. Fish and Wildlife Service, 2012). The survey extends from the U.S. prairies north through boreal-taiga habitat and into Alaska. Waterfowl species are identified from an aircraft and individual birds within a 200 m strip on each side of the aircraft are counted.

We used the data from the Prairie Pothole Region and surrounding areas because the number of both waterfowl species and ponds (a measure of wetland availability) are counted in this area (Fig. 1). For this area, the survey is conducted in May to be consistent with Mallard's breeding season. Because the aerial counts may suffer from visibility bias, accurate ground counts of waterfowl and ponds are obtained at a subsample of the aerial surveys. An observer- and year-specific ratio of ground counts to aerial counts from the area with both aerial and ground counts is calculated and multiplied to all the aerial counts observed by the same observer in the same year. Such corrected counts are then used to calculate local population abundance, which is considered to be free from systematic observation errors (Pollock and Kendall, 1987). More details regarding survey design and the reliability of survey results can be found in (Martin et al., 1979; Smith 1995). Our analyses are based on the corrected count data of Mallard and ponds. Waterfowl and pond abundance are summarized to grids that are 2° at latitude and longitude, resulting in 174 grid cells (Fig. 1).

The study area covers three ecoregions, including the Badland and Prairie, Prairie Pothole, and the southern portion of Boreal Taiga Plain (Fig. 1). Ecoregions were delineated using hierarchical classifications based on a variety of ecological and biological factors including location, climate, vegetation, hydrology, and terrain (Commission for Environmental Cooperation, 1997). Because factors that are used to define ecoregions are likely to affect the relationship between wetland habitat and waterfowl population dynamics, we use ecoregions in this study to represent different habitat conditions at the landscape spatial scale (Zhao et al., 2016).

2.2. Model development

We used the Gompertz model (Ives et al., 2003) to explain Mallard population dynamics. We considered local Mallard density in a year as a function of local Mallard density in the previous year and local pond density in the same year. The ENV model incorporated density dependence and the effect of pond, but not a spatial effect:

$$\log(\text{duck}_{i,t}) = \alpha + (1 - \beta_{\text{dip}}^{\text{dip}}) \times \log(\text{duck}_{i,t-1}) + \beta_{\text{pond}}^{\text{pond}} \times \log(\text{pond}_{i,t}) + \varepsilon_{i,t}$$

where $\text{duck}_{i,t}$ represented the Mallard density in grid cell i and year t , and $\text{pond}_{i,t}$ represented pond density. Mallard density $\text{duck}_{i,t}$ was calculated as $n_{i,t}^c/a_{i,t}$, in which $n_{i,t}^c$ was the sum of corrected counts (abundance) of Mallard, and $a_{i,t}$ was the total area sur-

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