



RESEARCH ARTICLE

Changes in climate and land use interact to create an ecological trap in a migratory species

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Abstract

1. Anthropogenic landscape alteration and climate change can have multiscale and interrelated effects on ecological systems. Such changes to the environment can disrupt the connection between habitat quality and the cues that species use to identify quality habitat, which can result in an ecological trap. Ecological traps are typically difficult to identify without fine-scale information on individual survival and fitness, but this information is rarely available over large temporal and spatial scales.
2. The Prairie Pothole Region (PPR) of the United States and Canada has undergone extensive changes in the latter half of the 20th century due to advancements in agricultural technologies, water management practices and climate change. Historically, the PPR has been a highly productive area for breeding waterfowl. While the overall trends for dabbling ducks in the PPR have exhibited increasing abundances since the late 1980s, some species, such as the northern pintail, have been declining in abundance.
3. We used a long-term dataset of pintail counts across the PPR to separate count data into a demographic process and a habitat selection process using a hierarchical model. The hierarchical model provided an alternative way of identifying ecological traps in the absence of individual survival and fitness. Our model also allowed us to account for the indirect pathways by which climate and agriculture impact pintail through their additional contribution to wetland availability, which is a primary driver of pintail demography and habitat selection.
4. Decoupling these processes allowed us to identify an ecological trap related to increasing cropland land cover, in which pintail selected for cropland over alternative nesting habitat, likely due to the similarities with productive native mixed-grass prairie. However, large proportions of cropland within a region resulted in fewer pintail the following year, likely due to nest failures from predation and agricultural practices. In addition, we identified several regions in Canada where this ecological trap is contributing significantly to mismatches between habitat selection and demographic processes.

KEYWORDS

Bayesian, demography, habitat selection, hierarchical, management, waterfowl

1 | INTRODUCTION

Anthropogenic modification of landscapes and changing climatic conditions are interrelated processes that can result in unexpected effects on ecosystem functions and individual species responses (Betts, Falloon, Goldewijk, & Ramankutty, 2007; Jetz, Wilcove, & Dobson, 2007; Northrup, Rivers, Yang, & Betts, 2019; Oliver & Morecroft, 2014). Separating the effects of anthropogenic land use and climate change is of critical importance for understanding temporal changes in species abundance and for managing the effects of those changes on species of concern. Many traditional approaches to evaluating and managing habitat rely on the manager's ability to correctly assess habitat quality (Beerens, Frederick, Noonburg, & Gawlik, 2015; Stephens, Pettolelli, Barlow, Whittingham, & Cadotte, 2015). Quality habitat consists of two components: ultimate quality, factors that influence long-term survival and reproductive success, and proximate cues, attributes that indicate an area may be productive habitat for selection and use (Johnson & Grier, 1988). An ecological trap can develop when the proximate cues do not align with the ultimate quality of the habitat. Ecological traps can form in one of two ways: selection cues are altered such that the appearance of habitat does not match its suitability or habitat that appears suitable declines in actual quality (Kristan, 2003; Robertson & Hutto, 2006). Anthropogenic changes are one pathway for the development of an ecological trap, as changes disrupt the expected relationship between habitat appearance and quality, resulting in maladaptive habitat selection (Hollander, Dyck, San Martin, & Titeux, 2011; Schlaepfer, Runge, & Sherman, 2002).

In addition, habitat appearance and quality may be a function of processes that operate at vastly different spatial scales. For example, studies have shown that the effect of climate on species distributions is most apparent at macro-scales, while local factors, such as land cover, are the dominant determinants at finer scales (Pearson, Dawson, Berry, & Harrison, 2002; Pearson, Dawson, & Liu, 2004). In addition, models built for determining fine-scale ecological dynamics can be moderately successful for prediction at coarse scales, but the same is not true for downscaling coarse predictions to make fine-scale inference (Collingham, Wadsworth, Huntley, & Hulme, 2000). Not only do the effects of environmental conditions vary across spatial scales, but ecological processes themselves can operate at different scales (Levin, 1992). For example, inference made on annual abundance at local scales may include the confounding effects of demographic processes, such as survival, with permanent emigration (Schaub & Royle, 2014). Linking local scale abundance with demographic processes may be particularly difficult for species that demonstrate incomplete site fidelity (Horton & Letcher, 2008; Marshall, Diefenbach, Wood, & Cooper, 2004). Other processes, such as the effect of density dependence, may also be ameliorated by behaviour, such as individual heterogeneity and memory-based movements, that violate the assumption that individuals are spatially well mixed (Riotte-Lambert, Benhamou, Bonenfant, & Chamaillé-Jammes, 2017). Conversely, inferring drivers of species presence

and habitat selection at coarse scales can be masked by processes operating at finer spatial scales (Azalee, Cornell, & Kunin, 2012). Therefore, management actions based on one scale of inference may have unintended consequences, or be ineffective for reaching management goals, at another scale (Mahoney et al., 2018).

Using only one aspect of the ecological process can limit inference and lead to erroneous assumptions about what habitat is good for a species, because presence or density of individuals may not be indicative of true habitat quality (Stephens et al., 2015; Van Horne, 1983). Mismatches between abundance or habitat selection and demographic parameters have been observed in a number of systems, including richness and density of waterfowl in corn and soybean fields with low reproductive success (Best, 1986), nesting waterfowl preference for habitats that confer poor nest survival (Clark & Shutler, 1999), ground-nesting farmland bird preference for territories in areas with higher predation rates (Gilroy, Anderson, Vickery, Grice, & Sutherland, 2011), density of lions in areas with low reproductive success (Mosser, Fryxell, Eberly, & Packer, 2009), habitat selection by grizzly bears in areas with high risk of bear-human conflict (Northrup, Stenhouse, & Boyce, 2012), and giant kangaroo rat presence and low survival (Bean et al., 2014). Decoupling habitat selection and demographic processes can help identify drivers of ecological traps, such as anthropogenic influences on habitat, and where they occur on the landscape. Ecological traps have typically been identified by looking for discrepancies between the effects of covariates on abundance (or habitat selection) and demographic parameters (e.g. survival, fecundity). However, demographic parameters are typically estimated using cohort- or individually marked animals (Murray & Patterson, 2006), which may only be available across a limited spatial and temporal extent.

We used an exemplar study system, a North American waterfowl dataset that has been collected continuously since 1955, to elucidate potential ecological traps for a managed species of conservation concern, the northern pintail *Anas acuta*. Previous fine-scale studies have demonstrated the potential for cropland to act as an ecological trap for pintail, whereby pintail readily nest in cropland that is visually similar to their preferred native habitat and the similarity in timing of pintail nesting and agricultural production practices (Duncan & Devries, 2018; Richkus, 2002). A hierarchical model allowed us to separate the effects of land cover and climate on both habitat selection and demographic processes (e.g. the balance of survival and reproduction) across the primary breeding range of pintail over a 53-year period. The hierarchical model we present allows for the identification of ecological drivers that differ in their effect on habitat selection and demographic processes, which can contribute to the development of an ecological trap. In addition, we can identify areas on the landscape where ecological traps have resulted in observed abundance deviating from demographically expected abundance. This method is broadly applicable to large-scale count-based studies that do not monitor individuals; by applying this method to northern pintail in a dynamic and rapidly changing landscape, we identified an ecological trap in the south-western portion of the Canadian prairies caused primarily by changes in agricultural practices.

2 | MATERIALS AND METHODS

2.1 | Study system

Certain species may be more vulnerable to ecological traps due to their habitat preferences and life-history requirements (Jetz et al., 2007; Oliver & Morecroft, 2014). Among waterfowl species, there is significant concern about the population status of the northern pintail (hereafter pintail). Pintail abundance in North America (2.3 ± 0.1 million; U.S. Fish & Wildlife Service, 2019) is currently well below the objective dictated by the North American Waterfowl Management Plan (NAWMP; North American Waterfowl Management Plan Committee, 2014), which is set at 4 million. Pintail abundance declined dramatically between 1980 and 1990, and has fluctuated below the NAWMP goal since then, despite the resurgence of all other dabbling ducks past objective goals (U.S. Fish & Wildlife Service, 2019). In addition, pintail fecundity varies spatially, but on average has declined in both the United States and Canada since the 1980s (Specht & Arnold, 2018). Of particular concern is the limited evidence supporting the ability of the population to rebound, even with generally favourable wetland habitat conditions (North American Waterfowl Management Plan Committee, 2014), highlighting the discrepancy between pintail dynamics and those of other dabbling ducks.

The Prairie Pothole Region (PPR) of Canada and the United States, along with areas of forest and tundra in Alaska and Canada, contains 85%–98% of all breeding pintails across their North American range (Miller & Duncan, 1999). Pintail are adapted to nesting in landscapes of native mixed-grass prairies within the PPR, and in meadows of low-lying graminoids within coastal tundra landscapes farther north (Clark et al., 2016). In both biomes they nest near small ephemeral and seasonal wetlands that warm up in early spring and support teeming densities of insect larvae that provide pintail with nutrients needed for egg formation (Drever, 2006; Krapu, 1974; Naugle, Johnson, Estey, & Higgins, 2001). Their early nesting phenology, one of the earliest of the dabbling duck species that breed in the PPR, make pintail particularly sensitive to changes in the number of productive, small wetlands that have occurred across the PPR (Naugle et al., 2001; Reynolds, Shaffer, Loesch, & Cox, 2006). Despite increased precipitation and the abundance of wetlands in recent decades across much of the PPR, and a parallel increase in total waterfowl abundance (U.S. Fish & Wildlife Service, 2019), pintail abundance has not recovered and appears to have become decoupled from surveyed wetland abundance (Miller & Duncan, 1999; Podrutzny, Devries, Armstrong, & Rotella, 2002). Moreover, the climate has generally become drier in the western PPR, but wetter in the eastern PPR, resulting in changes to wetland dynamics (fewer in the west, more in the east; Niemuth, Fleming, & Reynolds, 2014). Compounding climate change, a large proportion of wetlands have been drained or altered from their historical attributes (e.g. depth, vegetative characteristics; Dahl, 2014; Watmough, Li, & Beck, 2017). In certain areas of the PPR, drainage has focused on smaller wetlands, which often consolidates surface water into larger and deeper

wetlands (Anteau, 2012; Watmough et al., 2017) that dry out less frequently and have more surface–water connections to other wetlands (McCauley, Anteau, Burg, & Wiltermuth, 2015). Despite being an early-spring nester, which typically allows for reproductive plasticity to climatic conditions (Drever et al., 2012), pintails have demonstrated inflexible breeding behaviour (e.g. nest initiation date, nesting duration, renesting frequency) in response to climatically varying pond conditions when compared to other species (e.g. their nesting behaviour was not closely related to pond counts; Raquel et al., 2016). Inflexible breeding behaviour may result in greater vulnerability to unpredictable weather events and changes in climatic conditions (Gurney et al., 2011).

Given their preponderance for nesting among landscapes of grass-like low-lying cover, pintails readily nest in summer fallow, mulched stubble, standing stubble and other untilled agriculture fields (Higgins, 1977). Unlike other ducks that generally avoid nesting in stubble, pintail in the PPR range from selecting crop stubble nest sites in proportion to availability, to preferring it over remnant patches of grass and other cover (Devries, Armstrong, MacFarlane, Moats, & Thoroughgood, 2008; Devries, Clark, & Armstrong, 2018; Greenwood, Sargeant, Johnson, Cowardin, & Shaffer, 1995; Klett, Shaffer, & Johnson, 1988; Richkus, 2002). But with technological advancements, farmers can now harvest grain crops in less time and till more stubble prior to fall freezing conditions, leaving less standing stubble suitable for nesting in the following spring (Higgins, 1977). In addition, pintails often initiate nests before remaining stubble is worked in the spring (Guyn & Clark, 2000), making nests vulnerable to mechanical spring tilling and planting of remaining standing stubble that can destroy a large percentage of initial nests (Miller & Duncan, 1999; Richkus, 2002). The amount of land in the PPR that is annually tilled for spring-seeded crops has increased by approximately 34% since 1959, with an increase of 6%–63% across PPR sub-regions (Appendix A in Supporting Information). While pintails may avoid the risks of mechanical spring tillage and planting by nesting in fall-seeded crops like winter wheat, they may not be able to differentiate between this habitat and spring-seeded cropland when selecting nest sites early in spring (Devries et al., 2018). Duncan and Devries (2018) estimated that 47% of pintail nests in Canadian agricultural systems are initiated in spring-seeded cropland, and that 95% of those are destroyed by predation and mechanical tillage and planting. Pintail nests in the remnant small, isolated patches of untilled agricultural fields and grassland are heavily preyed upon by meso-predators that forage efficiently in patchy habitats (as reviewed in Clark & Nudds, 1991; Devries et al., 2008; Garrettson & Rohwer, 2001; Richkus, 2002). Compounding the negative effect of mechanical planting on first nesting attempts, renesting attempts are limited (~1; Guyn & Clark, 2000; Richkus, 2002) and do not recruit as many offspring as initial attempts because clutch size declines with nest initiation date, and brood and duckling survival decline with hatch date (Guyn & Clark, 1999).

Pintail are thus vulnerable to changes in both climate and land use, but as is common in many systems, managers and policymakers could benefit from a rigorous understanding of the relative and

combined impacts of these aspects of global change. In addition, land conversion and drainage practices are often a consequence of national wetland and agricultural policies, and can lead to very different dynamics across international boundaries (Doherty, Howerter, Devries, & Walker, 2018). Large-scale and long-term surveys of pintail nest-site selection and nest survival do not exist for providing such inference, but the world's most extensive spatio-temporal survey of vertebrate abundances overlaps greatly with the PPR breeding range of pintail.

2.2 | Data collection

The United States Fish and Wildlife Service (USFWS) and the Canadian Wildlife Service have monitored spring population sizes for North American waterfowl using the WBPHS since 1955 (Smith, 1995). The Traditional Survey Area covers central Canada, the north-central United States and Alaska, and is delineated into strata (regions) that reflect both habitat differences and political boundaries. Waterfowl are counted by aerial crews flying fixed-wing aircraft along established transect lines at low altitude (for details, see Smith, 1995). Transects are 400 m wide and divided into segments which are each 29 km in length; each segment is surveyed once per year between early and late May. Aerial observers count numbers of lone drakes or unknown sex singles, pairs and birds in mixed sex groups within a segment. The USFWS also conducts nearly simultaneous ground counts on a subset of segments, which is used to calculate a visibility correction factor (VCF; described in more detail in Section 2.5). For the purposes of our analyses, we calculated a 'breeding pintail count'

by doubling the aerial counts of lone drakes (though we acknowledge that the social grouping of males does not perfectly reflect breeding pair status; Brasher, Kaminski, & Burger Jr., 2002) and pairs (a pair is counted as one bird in the data). We did not include individuals in mixed sex groups, because we don't want habitat selection by potentially non-breeding individuals contributing to the description of local breeding habitat. In addition, wetland counts are performed by the aerial crew; surveyed wetlands include seasonal and permanent wetlands, both artificial and natural, expected to persist for at least 3 weeks beyond the survey date. We note that these pond counts may not represent the ephemeral ponds that pintail are most attracted to. We focused our analysis on the PPR, which includes strata 26–49, 75 and 76 within the Traditional Survey Area, but removed 36, 75 and 76 due to unavailable covariate data (Figure 1). We used data from 1958 to 2011, when all segments were consistently sampled and during which time land cover and climate variables were available for the necessary spatial extent (Appendix A in Supporting Information).

2.3 | Statistical models

We used a hierarchical model to capture processes operating at different spatial and temporal scales, but used the scale of data collection (the segment) as the foundation of the model. Separating multiscale processes using count data allows us to make inference across a much larger spatial and temporal scale compared to fine-scale and short-term field studies of vital rates (Richkus, 2002). In the following, we will discuss two different intensity parameters that operate at different spatial scales and ultimately give rise to the

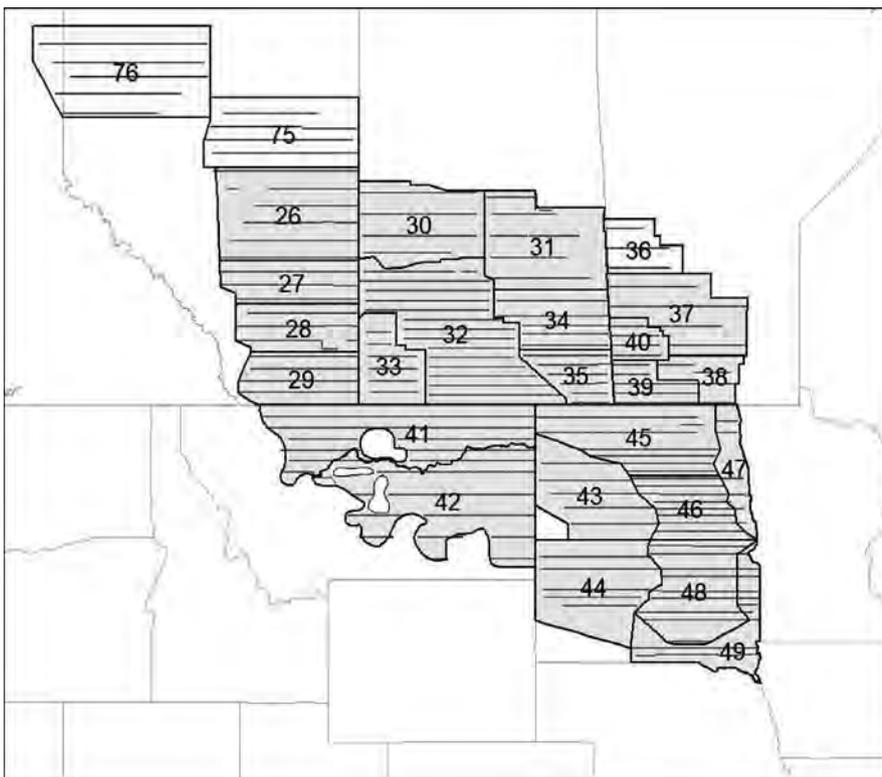


FIGURE 1 Map of the Waterfowl Breeding Population and Habitat Survey strata in the Prairie Pothole Region (PPR), which spans Canada (strata 26–40 and 75–76) and the United States. Strata 36, 75 and 76 were removed from this analysis due to missing covariate information. Within each strata are transects consisting of variable numbers of 29-km segments which are surveyed via fixed-wing aircraft

observed counts. For clarity, n_{ist} is the latent intensity of abundance on each segment ($i = 1, \dots, I_s$), in a given strata ($s = 1, \dots, S$), and year ($t = 1958, \dots, 2011$) and n_{st} is the latent strata-level intensity of abundance in a given year. Hereafter, we will refer to intensity of abundance as abundance.

The strata-level model (see Section 2.4) describes how abundance changes between the breeding season in year $t - 1$ and the number of pintail that arrive in a strata in year t , which represents unobserved demographic processes, such as survival and reproduction, that occur between the two observation periods. Using strata-level abundances, or some spatial summary of them, as being representative of the combined effects of survival and recruitment is a very common assumption when analysing the WBPHS data (e.g. Drever et al., 2012; Osnas, Zhao, Runge, & Boomer, 2016; Reynolds & Sauer, 1991; Zhao et al., 2019; Zhao, Boomer, Silverman, & Fleming, 2017; Zhao, Silverman, Fleming, & Boomer, 2016). We acknowledge that annual fidelity to a breeding stratum is not perfect, but environmental processes contributing to variation in site fidelity are accounted for using the habitat selection model (see below for more detail). The estimated strata-level abundance is then scaled down (by dividing by the number of segments within a strata) to represent an expected number of pintail per segment given no habitat selection.

The segment-level model (see Section 2.5) allowed us to evaluate what variables contribute to the fine-scale distribution of pintails within a stratum, given how many should be available based on conditions during the breeding season in year $t - 1$ and the subsequent non-breeding season on the wintering grounds (the demographic process model). The segment-level model results in deviations to the expected number of pintail on a segment (given the strata-level process) as a result of habitat selection. Aggregating segment-level abundances within a stratum can produce stratum-level abundances greater or less than that predicted by the strata-level process, which indirectly accounts for immigration and emigration out of the stratum. We modelled the distribution of pintails using a negative binomial distribution with a log link function, which is similar to the Poisson point process that is commonly used to model habitat selection (Aarts, Fieberg, & Matthiopoulos, 2012; Hooten, Johnson, McClintock, & Morales, 2017; Nielson & Sawyer, 2013). Previous work has found that initial nests in the PPR were initiated from mid-April (Duncan, 1987; Krapu, Sargeant, & Perkins, 2002) to mid-May (Guyn & Clark, 2000), and initial nesting lasted 60–66 days (Krapu et al., 2002), which would coincide with the WBPHS observation period. Therefore, we can assume that habitat selection during the WBPHS period is representative of breeding habitat selection for the types of counts (pairs) that we included in our analysis.

The observed counts on a segment are then linked to the statistical model by further adjusting the latent segment-level abundance by an observation process that includes zero-inflation, overdispersion in segment-level counts, and a VCF that the WBPHS uses to correct under-counting by aerial surveys. The models were fit using the R package `jagsUI` (Kellner, 2017) for Jags 4.3.0 (Plummer, 2003) and convergence was assessed using the Gelman–Rubin statistic ($\hat{R} < 1.1$) and visual examination of trace plots. Inference was made using five

chains of 100,000 iterations, each thinned to 20,000, with an additional 10,000 iterations for burn-in; due to storage limitations, estimates of strata- and segment-level intensities were thinned to 1,430 samples per chain.

2.4 | Demographic process

We modelled demographic processes by using a Gompertz population model to represent the log of the latent strata-level abundance, where r is the intrinsic growth rate and θ is the strata-level effect of density dependence. Previous literature is inconclusive regarding the degree of density dependence in pintail; Jamieson and Brooks (2004) found little evidence for density dependence, whereas Murray, Anderson, and Steury (2010) and Devries (2014) found evidence for density dependence. Deviations from the classical Gompertz model are incorporated through Q covariates, \mathbf{z}_{st} and their corresponding effect sizes, γ_s :

$$\log(n_{st}) \sim \mathcal{N} \left(\frac{r_s}{1 - \theta} + \theta \log \left(\sum_{i=1}^{I_s} n_{ist-1} \right) + \mathbf{z}'_{st} \boldsymbol{\gamma}_s, \sigma_s^2 \right).$$

Feldman, Anderson, Howerter, and Murray (2015) found that the effect of environmental stochasticity on population dynamics was stronger at the edge of the breeding range, compared to areas in the core of breeding range; therefore, we let σ^2 vary by strata (σ_s^2). The strata-level demographic drivers, $\boldsymbol{\gamma}_s$, are normally distributed and share a mean and variance where $\boldsymbol{\mu}_\gamma \sim \mathcal{N}(\mathbf{0}, \text{diag}(\mathbf{1000}))$ and $\sigma_\gamma^2 \sim \text{IG}(0.0001, 0.0001)$. Although the Gompertz model is typically written on the log scale, deterministically, as $\log(n) = r_{\text{int}} + \theta \log(n_{t-1})$, we note that in Dennis, Ponciano, Lele, Taper, and Staples (2006), the intercept, which we will call r_{int} to distinguish it from the intrinsic growth rate, is actually composed of a function of r_s and $1 - \theta$; therefore one must be careful not to interpret the intercept of the log-linear model as the intrinsic growth rate (but note the alternative parameterization in Dennis et al. (2006) with sequential state variables on the left and right side of the equation, e.g. Koons, Colchero, Hersey, & Gimenez, 2015).

There was also preliminary evidence that r_s and θ were not uniquely identifiable. In cases of non-identifiability, external information can be used to improve identifiability through an informative prior (Lebreton & Gimenez, 2013). We used a strong prior such that $r_{\text{real}} \sim \mathcal{N}(0.435, 0.001)$ and $\theta \sim \text{Unif}(0, 1)$, which is the range of reasonable values of density dependence for a non-chaotic system. We obtained the prior information on r_{real} from Murray et al. (2010); however, the value of the intercept changes with covariates in the model and how they have been standardized. Therefore, we transformed r_{real} to match the scale of the covariates by inverting the process one would use to back-transform the intercept of a linear regression estimated with Q standardized covariates to the 'real' scale, which gives us $r_s = r_{\text{real}} + \sum_{q=1}^Q (\bar{z}_q / \text{SD}(z_q)) \gamma_{s_q}$ for each strata. Because we are estimating r_{real} and $\boldsymbol{\gamma}_s$, this is performed as part of the Markov chain Monte Carlo (MCMC) sampling process (e.g. r_s is

derived from samples of r_{real} and γ on each iteration). The parameter for density dependence, θ , typically modifies the effect of n_{st-1} on n_{st} ; in our model it instead modifies $\sum_{i=1}^l n_{ist-1}$. This is because the 'realized' number of birds on the landscape (the sum across segments within a strata given habitat selection) may be significantly different from the expected number of birds, based on the demographic model, that basing n_{st} on n_{st-1} effectively breaks the link between the two modelling scales.

We hypothesized that pintail abundance in a given year may be a function of habitat and climatic conditions during the previous year, such as temperature and precipitation during the breeding season, the intensity of the El Niño-Southern Oscillation (ENSO) event, pond count, and the per cent crop and summer fallow acreage the prior year (Appendix B in Supporting Information). In addition, we included a latitude bias correction that accounts for pintail overflight in drought years, which may reduce the overall number of pintail available to settle in the PPR (e.g. emigration out of the survey area). We selected among three models that varied in which temporal component of the breeding season in year $t - 1$ was used as a predictor for abundance in year t : May–June (nesting and hatching success), July–August (offspring survival) and May–August (full breeding season).

2.5 | Habitat selection and observation process

We modelled the observed count of pintail pairs on each segment, d_{ist} as a zero-inflated negative binomial, where an indicator variable for each segment, z_{ist} , determines which component of the mixture model gives rise to the observed count:

$$d_{ist} \sim \begin{cases} 0 & \text{if } z_{ist} = 0 \\ \text{NB}(n_{ist}, M) & \text{if } z_{ist} = 1 \end{cases},$$

where $z_{ist} \sim \text{Bern}(p)$, $p \sim \text{Beta}(1, 1)$ and $M \sim \text{Unif}(0, 20)$. We adjusted the intensity of the negative binomial process, n_{ist} , which gives rise to non-zero counts and sampling zeros, to the appropriate spatial scale by dividing the corresponding strata level abundance, n_{st} , by the total number of segments in a given strata, l_s : $n_{ist} = \frac{n_{st}}{l_s}$. We used a log-link to model the segment-level abundance as a function of a vector of u covariates, \mathbf{x}_{ist} , and effect sizes that vary by strata, β_s , to represent deviations from the downscaled strata-level abundance, n_{st} , according to the processes hypothesized to affect annual habitat selection (i.e. spatial adjustments of abundance determined by where pintail decide to move and settle, as opposed to what should primarily be the balance of birth and death since the previous year given our model structure):

$$\log(n_{ist}) = \log\left(\frac{n_{st}}{l_s}\right) + \mathbf{x}'_{ist}\beta_s.$$

The effect sizes were modelled as $\beta_s \sim \mathcal{N}(\mu_\beta, \text{diag}(\sigma_\beta^2))$, and share an overall mean and variance via shrinkage estimation (we use the term shared mean to indicate when some distribution is shared across units, such as strata): $\mu_\beta \sim \mathcal{N}(\mathbf{0}, \text{diag}(\mathbf{1000}))$ and $\sigma_\beta^2 \sim \text{IG}(0.0001, 0.0001)$.

Throughout we parameterize the normal distribution with mean and variance, and the inverse gamma such that it is the reciprocal of a gamma distribution with shape and rate parameters.

Zero-inflated models account for excess zeros, which can arise from two processes: sampling zeros and actual zeros. Sampling zeros arise when individuals are present and unobserved or present but temporarily absent during the survey and actual zeros represent survey units that individuals do not occupy. Essentially, p is the probability of occupancy. The parameter M is the overdispersion parameter for the negative binomial distribution, such that as M goes to infinity the negative binomial approaches a Poisson distribution. Occasionally, segments were not sampled in a given year, or had yet to be incorporated into the study design. To account for this, we used multiple imputation (e.g. data augmentation; Tanner & Wong, 1987) to impute estimates for the missing observations on each iteration of the MCMC algorithm. This uses the entire hierarchical model to estimate abundances, including habitat selection and demographic processes, instead of non-parametric smoothing used by the USFWS (Moore, 1995). In addition, imputing segment-level data results in strata-level abundance estimates that represent a consistent number of segments across years, regardless of how many were actually surveyed.

Pintail habitat selection in a given year is likely a function of habitat and climatic conditions that individuals encounter when they arrive at the breeding grounds in a given year, such as spring snow duration, pond counts relative to counts on other available segments (spatial effect), pond counts relative to counts on that segment in other years (temporal effect) and the per cent crop and summer fallow acreage (Appendix B in Supporting Information). In addition, we used the VCF as a covariate in the habitat selection model; the VCF is calculated by the USFWS using a ratio of concurrent ground and air surveys during the WBPBS, in which it is assumed that counts from the air underestimate the true number of individuals (ground counts). Although the VCF is an observation-level covariate, it was included in the segment-level model because the VCF only adjusts non-zero counts and would not be relevant to the zero-inflated component of the observation process.

2.6 | Pond dynamics

Spring pond counts (i.e. seasonal and permanent wetlands), collected concurrently with waterfowl counts, were used as the most direct indicator of spring wetness. By modelling pond counts, we were able to account for the indirect influence of weather and land cover on pintail via their contribution to pond counts. We hypothesized that pre-breeding season weather covariates, such as temperature, precipitation, Standardized Precipitation-Evapotranspiration Index (SPEI) and snow cover duration, can contribute to the formation or loss of ponds on the landscape. In addition, we expected that as agricultural intensification increased, pond counts may decrease due to drainage. Modelling the pond counts allowed us to use data augmentation to estimate pond counts in years when either ponds were not counted or segments were not surveyed (Tanner & Wong, 1987). Imputing the

missing covariate values allowed us to estimate waterfowl counts even when the pond covariate was missing.

We modelled pond counts at the segment level as a Poisson process $p_{ist} \sim \text{Poisson}(g_{ist})$ where g_{ist} is a function of an intercept and weather covariates, such that $\log(g_{ist}) = \mathbf{y}'_{ist} \boldsymbol{\delta}_s$, and $\boldsymbol{\delta}_s \sim \mathcal{N}(\boldsymbol{\mu}_\delta, \text{diag}(\sigma_\delta^2))$, where $\boldsymbol{\mu}_\delta \sim \mathcal{N}(\mathbf{0}, \text{diag}(\mathbf{1000}))$ and $\sigma_\delta^2 \sim \text{IG}(0.0001, 0.0001)$. Spring pond counts were modelled as a function of late winter and spring measures of wetness, such as temperature, precipitation, SPEI and snow duration (Appendix B in Supporting Information).

Before incorporating the pond covariates into the hierarchical model for both pintail habitat selection and population dynamics (such that all parameters were estimated simultaneously), we evaluated two potential models for pond dynamics. In the first model, pond numbers were driven by environmental conditions immediately preceding the counts. However, because changes in pond counts likely occur over long time spans, we also implemented a model where the same set of covariates were derived as moving 3-year averages ($t, t-1, t-2$). We selected between these two pond models by minimizing the negative log-likelihood (again, each model had the same number of parameters). The models were fit using the same specification as previously detailed.

2.7 | Population growth rates

We calculated two forms of the average finite population growth rate: expected growth rate and realized growth rate. The expected average growth rate over time was calculated using the strata-level abundance parameters, n_{st} such that $\lambda_e = e^{\sum_t \log(n_{st}) - \log(n_{st-1})/T}$. The strata-level intensities tell us how many pintail are expected to be in a strata given the demographic processes contributing to population dynamics, which given our hierarchical model structure, should primarily be recruitment and survival. However, the habitat selection component of the model can cause the number of pintail in a strata to deviate from the expectation, due to segment-level properties that make segments within a strata attractive or unattractive to settling pintail as they move and select habitats. Therefore, we

also calculated a realized average growth rate using the sum of the segment-level abundance parameters n_{ist} within each strata, such that $\lambda_r = e^{\sum_t (\log(\sum_i n_{ist}) - \log(\sum_i n_{ist-1})) / T}$.

2.8 | Explanatory variables

The effects of explanatory variables for population dynamics and habitat selection were allowed to vary by strata, as trends in the breeding population vary spatially (Murray et al., 2010). Barker, Cumming, and Darveau (2014) found that fine-scale predictive ability for pintail distribution was based on, in order of importance, hydrologic, landscape and climatic variables (Barker et al., 2014). We therefore used hydrologic, land cover and climatic covariates to predict dynamics at multiple process levels (see Table 1 for a summary of all covariates and the scale at which they were incorporated). For segment-level covariates describing the habitat selection process, we used the raster value at the segment centroid. To obtain strata-level covariates for the demographic process, we averaged the segment-level covariates within a stratum. All covariates were standardized to be mean zero with a standard deviation of one across all strata and years, and segment-level covariates were centred again to reflect the mean within a strata and year (therefore relative to other habitat within a strata and year). Sources and calculations for climatic variables can be found in Supporting Information, Appendix A, while additional details about the mechanisms of how each predictor may contribute to pintail abundance, habitat selection and pond counts can be found in Supporting Information, Appendix B.

Given the reliance of pintail on smaller wetlands, we expect a positive relationship between the abundance of wetlands and the abundance of pintail at the local scale because of evolved senses for selecting these habitat characteristics, and a positive relationship at larger scales because of the contribution of wetlands to reproductive success. In addition, we expect that temperature and precipitation will have a primarily indirect effect on pintail demographic processes via their contributions to wetlands, including small ephemeral wetlands not included in the aerial pond counts. Finally, we anticipate that there will be evidence for an ecological trap, one

TABLE 1 Predictor variables used to model each response variable in year t ; habitat selection variables were summarized at the segment level and demographic variables were summarized at the strata level. For strata-level climatic variables, we selected among models that incorporated temperature and precipitation for one of three seasons in year $t-1$: May–June (early breeding), July–August (late breeding) and May–August (breeding). The visual correction factor (VCF) was also used as a predictor variable for segment-level counts. SPEI is the Standardized Precipitation-Evapotranspiration Index, an indicator of drought

Response (year t)	Climatic	Hydrologic	Land cover
Habitat selection (segment counts)	Nov–April snow duration t	Pond count t	% Crop acreage t % Summer fallow acreage t
Demography (strata abundance)	ENSO intensity $t-1$ Selected season temp. $t-1$ Selected season precip. $t-1$	Adjusted latitude bias correction Pond count $t-1$	% Crop acreage $t-1$ % Summer fallow acreage $t-1$
Pond counts	Dec–April temp. t Dec–April precip. t Dec–April SPEI t Nov–April snow duration t		% Cropland t

in which local population abundances (habitat selection) increase with increasing proportions of cultivated land, whereas population growth will decrease with increasing proportions of cultivated land. We expect that this effect will vary by region due to regional differences in agricultural production and practices, which in turn affect wetland drainage and nesting cover.

3 | RESULTS

The model with early seasonal (May–June) climatic covariates contributing to population dynamics had the smallest negative log likelihood; therefore, we restricted our inference to this model. Below, we truncated distributions within violin plots to represent the 95% equal-tailed credible interval for all estimated parameters.

3.1 | Demographic process

The intrinsic population growth rate reflected the constraint imposed via the prior such that $r_{\text{real}} = 0.435$ (0.373:0.497). The density dependence term was low, $\theta = 0.128$ (0.029:0.306; where one implies

density independence), indicating that density dependence was strong. Estimates of process variance (i.e. environmental stochasticity) were heterogeneous across strata and are available in Supporting Information, Appendix C.

The strength of an ENSO effect from the end of the breeding season in year $t - 1$ to just prior to the breeding season in year t had a negative effect on abundance the following year, indicating that an El Niño event during the non-breeding season generally resulted in a decrease in abundance (Figure 2). Temperature and precipitation in the early breeding season (May–June, year $t - 1$) both had positive effects on abundance the following year, and the effects were consistent across strata (Figure 2). The negative effect of the adjusted latitude bias correction supports the hypothesis that in drought years, when the centre of the breeding population shifts northward, fewer pintail are available to settle in the PPR region (Figure 2). Proportion of cropland acreage had a negative effect on change in abundance the following year, whereas the proportion of fallow acreage had a positive effect, particularly in Canada (Figure 2). The effect of proportion of fallow acreage was also variable across strata, with some strata showing, on average, stronger positive responses than the shared mean (e.g. 28 and 37), and others showing no significant response (Figure 2). The number of ponds in year $t - 1$ was not significant

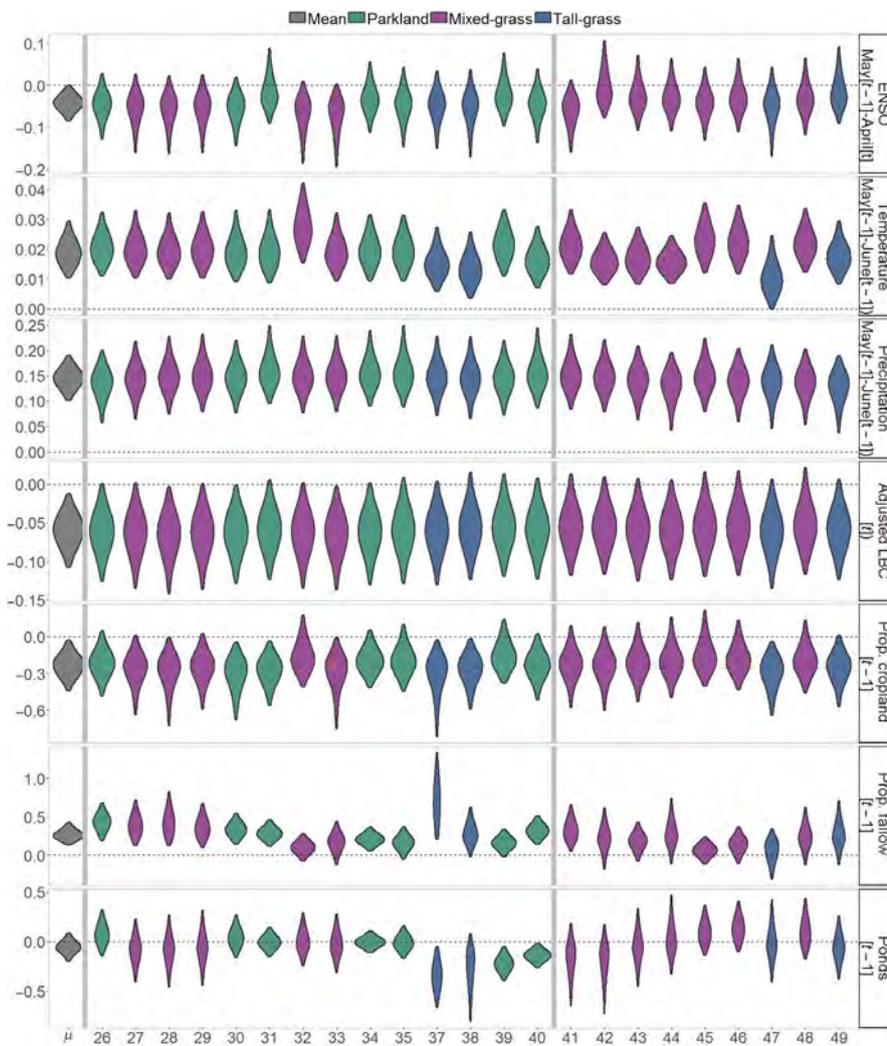


FIGURE 2 Posterior 95% distribution of coefficients (log scale) contributing to northern pintail population dynamics in the Prairie Pothole Region (PPR) from 1958 to 2011. The left panel on each plot shows the posterior distribution of the population-level mean across the PPR, while the centre (Canada) and right (United States) panels correspond to the posterior distribution of the strata-level coefficients. Strata are coloured by predominant ecoregion (aspen parkland, mixed-grass prairie or tall-grass prairie). Axes are different for each variable; however, the horizontal line in each plot provides a reference for zero

across all strata, and individual strata showed strong variability in response to ponds, with strata 37–40 even showing a negative response of change in abundance to ponds (Figure 2).

3.2 | Habitat selection and observation process

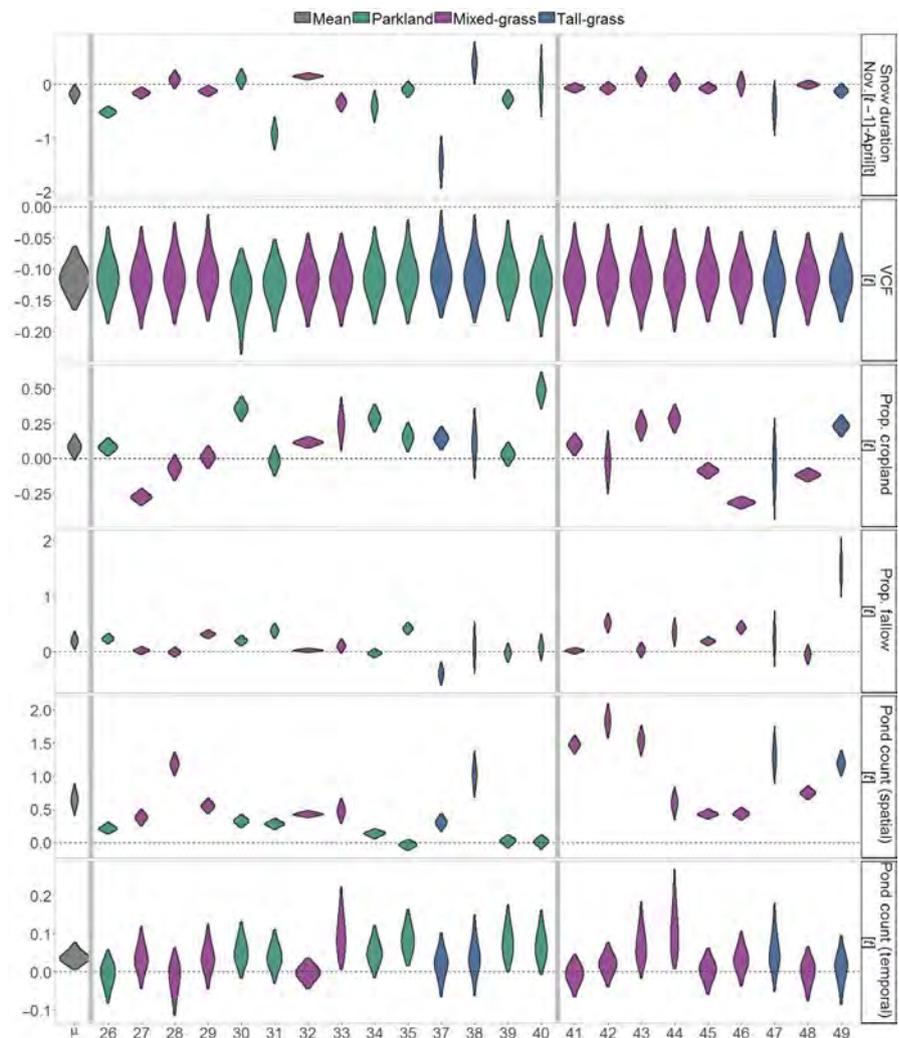
Segment-level counts within a strata were extremely overdispersed, with $M = 1.483$ (1.446:1.520). In addition, p , the probability of occupancy, was high (0.841; 0.835:0.847) indicating that many of the segments provided habitat that was conducive to pintail presence, even if pintail were absent from a segment during the survey. The VCF was negative across all strata, as expected, given that as the VCF increases, detection of pintail from the air decreases (thus decreasing the count; Figure 3). The shared mean effect of snow duration was significant (-0.178 ; -0.369 : 0.005 , with the proportion of the posterior density below 0 being 0.972); however, there were a number of strata that demonstrated a statistically significant positive (32, 38) and negative (26, 27, 31, 33, 34, 35, 37 and 39) response (Figure 3). The shared mean effect of proportion cropland and fallow both positively affected habitat selection (Figure 3). However, deviations from the positive effect of cropland were observed for

one stratum in Canada (27) and three strata in the United States (45, 46 and 48); deviations from the positive effect of fallow were also observed for one stratum in Canada (37; Figure 3). The spatial effect of pond counts, relative to the mean number of ponds in a strata in a year, positively affected habitat selection across all strata, however the strongest effects were observed in the United States (41, 42, 43 and 47; Figure 3). In Canada, the majority of spatial pond effects were lower than the posterior shared mean, whereas in the United States a number of strata-level effects were higher than the shared mean (Figure 3). The temporal effect of pond counts, relative to the mean number of ponds in a segment over time, on habitat selection was not statistically significant; however, uncertainty in the effect was large across strata (Figure 3). The trajectories of summed segment-level abundances within strata over time (realized abundance) are presented in Supporting Information, Appendix E.

3.3 | Pond dynamics

The number of ponds in a segment varied significantly by strata, with more ponds per segment in Canada compared to the United States. In particular, the lowest baseline number of ponds was

FIGURE 3 Posterior 95% distribution of coefficients (log scale) contributing to habitat selection (i.e. within-strata settling dynamics) of northern pintails in the Prairie Pothole Region from 1958 to 2011. The left panel on each plot shows the posterior distribution of the population-level mean, while the centre (Canada) and right (United States) panels correspond to the posterior distribution of the strata-level coefficients. Strata are coloured by predominant ecoregion (aspen parkland, mixed-grass prairie or tall-grass prairie). Axes are different for each variable; however, the horizontal line in each plot provides a reference for zero



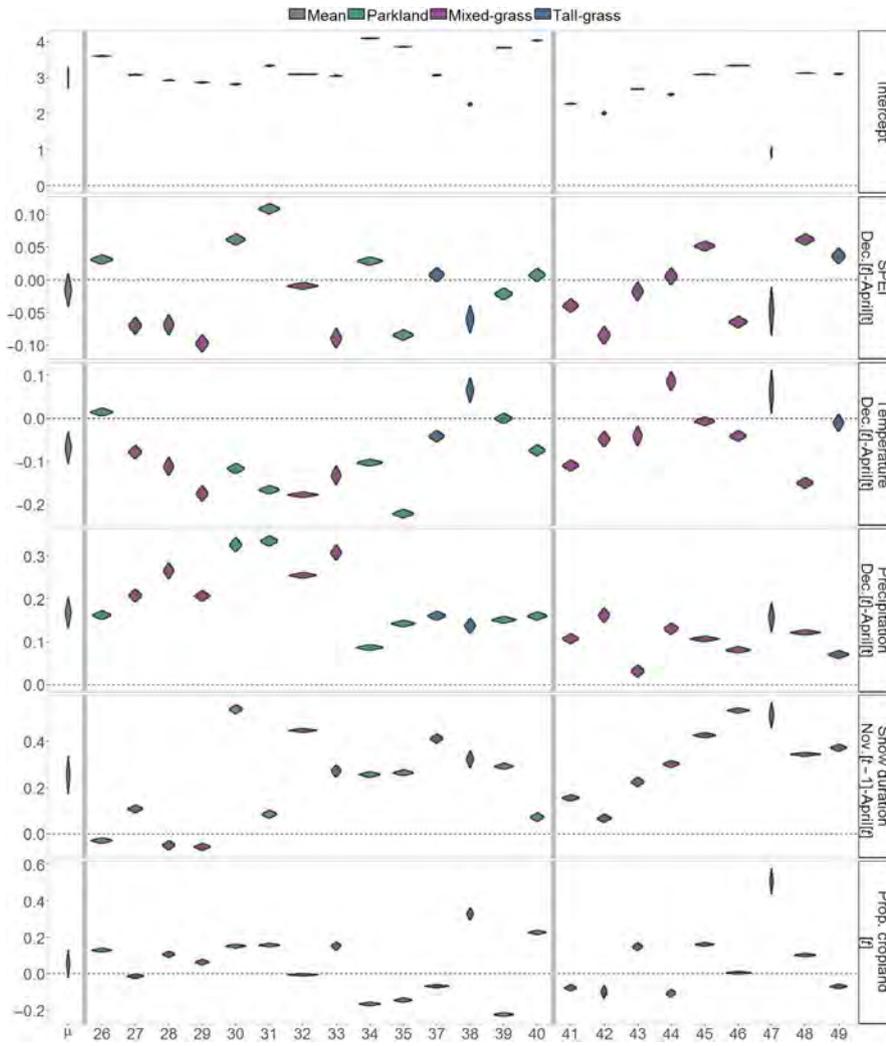


FIGURE 4 Posterior 95% distribution of coefficients (log scale) contributing to segment-level pond counts in the Prairie Pothole Region from 1958 to 2011. The left (Canada) and right (United States) panels correspond to the posterior distribution of the strata-level coefficients. Strata are coloured by predominant ecoregion (aspen parkland, mixed-grass prairie or tall-grass prairie). Axes are different for each variable; however, the horizontal line in each plot provides a reference for zero

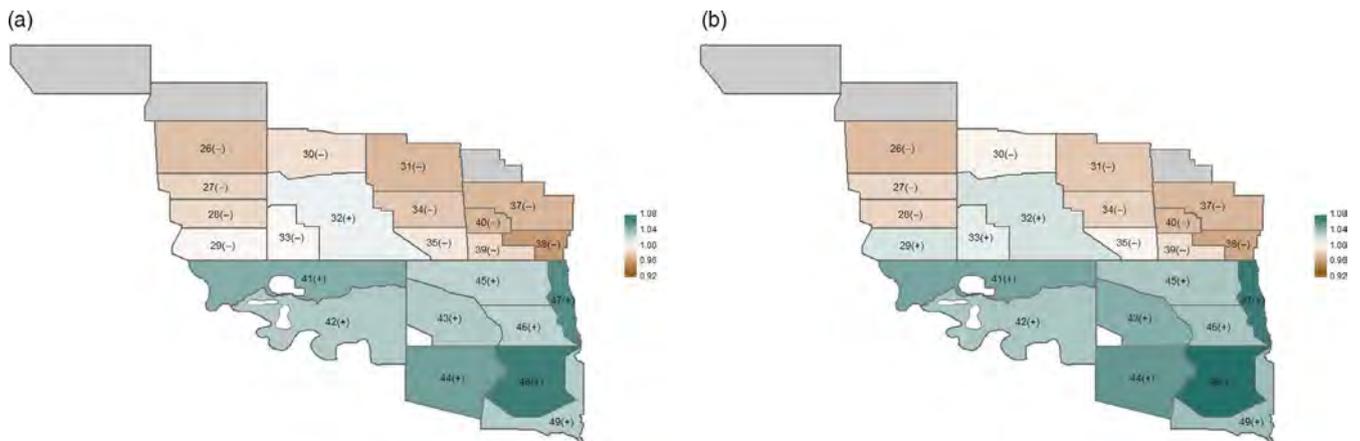


FIGURE 5 Posterior mean of the expected geometric mean growth rate (a), which is based on how many pintail are expected to be in a strata given the demographic processes contributing to population dynamics, and realized geometric mean growth rate (b), which is based on the sum of the segment-level abundance parameters affected by habitat selection, of northern pintails in the Prairie Pothole Region from 1958 to 2011. Strata are labelled with their Waterfowl Breeding Population and Habitat Survey number. A positive sign indicates the mean growth rate was greater than one, and a negative sign indicates the mean growth rate was less than one

observed in stratum 47 (Figure 4). The shared mean effect of temperature on pond counts was negative, whereas for precipitation and snow duration (e.g. potentially deeper snowpack) it was

positive (Figure 4). However, there were large amounts of variation across strata for the effect of SPEI and proportion of cropland (Figure 4). Nor was there consistency across covariates in

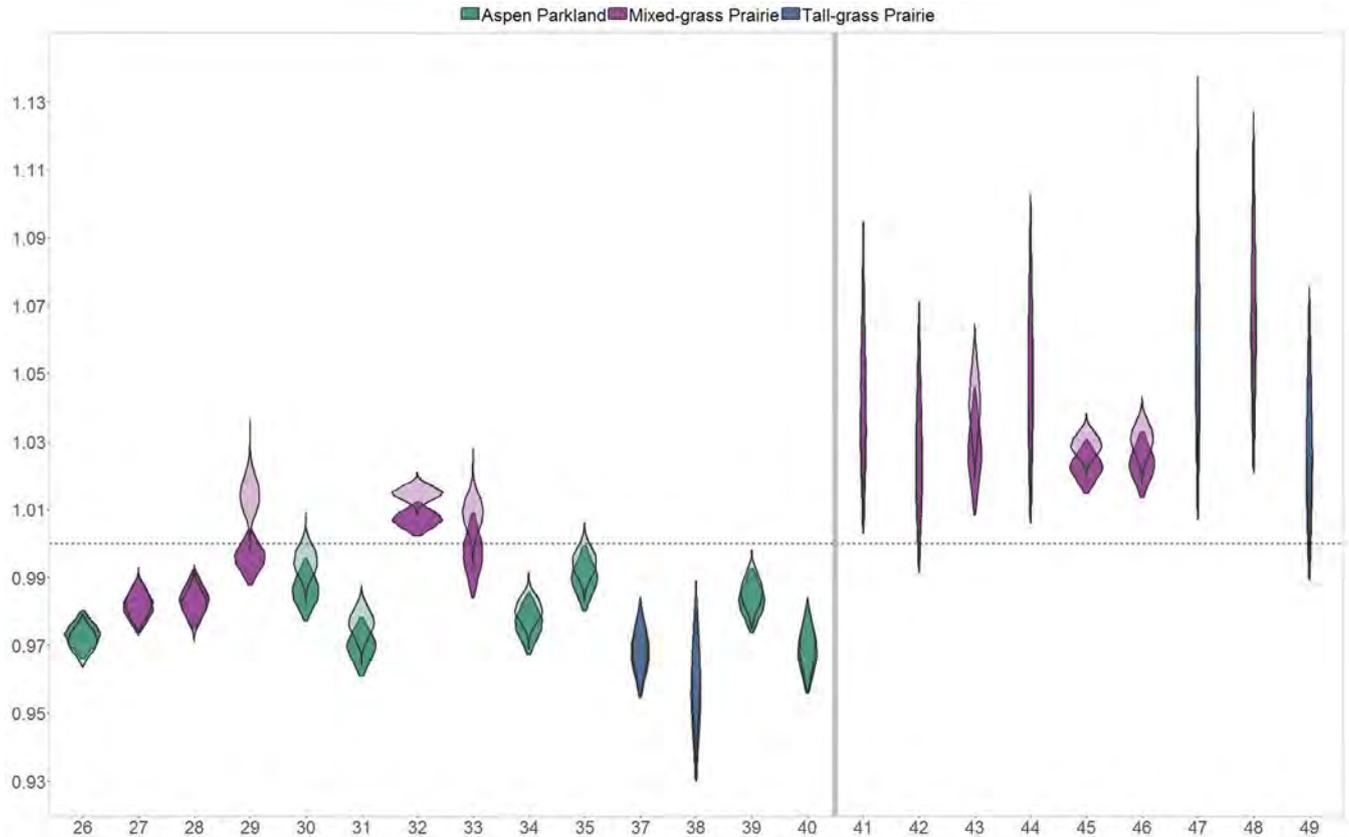


FIGURE 6 Posterior 95% distribution of expected geometric mean growth rate (darker colours; based on the expected number of pintail as a function of demographic processes) and realized geometric mean growth rate (lighter colours; based on the realized sum of the segment-level abundances at time t as a function of habitat selection) of northern pintails in the Prairie Pothole Region from 1958 to 2011. The left panel includes strata located in Canada, while the right panel shows strata located in the United States. If the realized growth rate is greater than the expected growth rate, then more ducks are settling in a strata than we would expect based on the demographic process

terms of which strata responded positively or negatively. Although there were more ponds per segment in Canada than in the United States, trends in pond counts indicate that the number of ponds has increased in all strata in the United States since 1958, whereas pond counts in only approximately half of the stratum in Canada increased over the same time period (29, 30, 32, 33, 34 and 39; Appendix A in Supporting Information). Within strata, pond counts were also more temporally variable in Canada compared to the United States (Appendix A in Supporting Information).

3.4 | Population growth rates

On average, the mean expected population growth rate over the duration of the study period was negative for strata in Canada and positive for strata in the United States (Figure 5). In addition, the lowest expected growth rates were observed in Canada (Figure 5). Realized growth rate demonstrated a similar pattern; however, there were important differences in some strata (Figures 5 and 6; Appendix D in Supporting Information). When combining inference on expected and realized growth rates, five strata in Canada showed deviations between expected and realized

growth rates, with realized growth rates greater than expected (Figure 6; Appendix D in Supporting Information). Partitioned growth rates for 1958–1976, 1976–1995 and 1995–2011 are available in Supporting Information, Appendix D. The average rates of growth over shorter time periods indicate that despite generally low pintail abundance, many of the strata demonstrated positive growth rates during the most recent time period, in contrast to the largely negative growth rates of the period from 1976 to 1995 (Appendix D in Supporting Information). In addition, temporal variability in annual growth rates was greater in Canada compared to the United States (Appendix D in Supporting Information).

4 | DISCUSSION

Our multiscale model allowed us to identify the relative influence of long-term changes in climate and land use on both the selection and demographic quality of habitat for northern pintail in the PPR. In turn, this allowed us to identify the spatial distribution of ecological traps across this critical North American landscape for waterfowl and other species. Consistent with the theory of ecological traps, our model moreover allowed us to identify the

proximate cue that is likely responsible for the mismatch between habitat selection and demographic performance in certain locations. We achieved all of this inference using abundance data that were collected systematically across aerial sampling blocks, which is of broad significance because such data are much more common across large spatio-temporal extents than individually based data that have previously been believed to have been necessary for identifying ecological traps.

A mismatch between the attractiveness of habitat and its actual demographic quality is thought to occur when the relationship between habitat choice and fitness is indirect. For example, selection of breeding habitat in which the fitness consequences occur after the selection process (Kristan, 2003), when individuals cannot evaluate the direct effect on fitness (Delibes, Ferreras, & Gaona, 2001), or when fitness consequences are stochastic (Kristan, 2003). Ecological traps are also more likely to occur where there is a high ratio of trap to high quality habitat, and in rapidly changing ecological systems that affect this ratio (Battin, 2004). All of these mechanisms could have created ecological traps for northern pintail inhabiting the PPR, which has experienced rapid change in agricultural land use in parallel with spatial differences in observed climate change (Doherty, Ryba, Stemler, Niemuth, & Meeks, 2013; Niemuth et al., 2014).

Most of the climatic and hydrological variables (e.g. pond count, precipitation and temperature) had synchronous effects on habitat selection and demography, which means that even if certain conditions led to poor demographic performance (e.g. drought), these variables could not have provided the cue responsible for attracting pintail to poor habitat. Although the proportion of fallow acreage had a positive effect at both ecological scales, crop acreage had a positive relationship with habitat selection and a negative effect on demographic processes. For pintail, nesting in stubble has no direct fitness consequences and may have had no negative consequences on offspring fitness in some historic years and fields (e.g. fallow fields; Devries et al., 2018). Unfortunately, long-term changes in agricultural practices in the PPR have shifted away from the intermittent use of fallow acreage towards vast expanses of annually cropped acreage that is still attractive to nesting pintails but deleterious to their demographic performance. The existence and severity of this ecological trap varied spatially across the PPR, but was strong enough in certain locations to affect negatively the overall long-term abundance of pintails in the region.

Measuring the severity and locations of ecological traps across a landscape is of applied importance for at least two non-exclusive reasons. First, conservation triage decisions can be based on the relative costs of taking action at identified trap habitats versus conserving the existing high quality habitat. Second, trap habitats are used disproportionately more than their availability, which makes population persistence particularly sensitive to even small changes in the proportion of trap habitat (Delibes, Gaona, & Ferreras, 2001; Donovan & Thompson, 2001). The spatial distribution of ecological traps identified by our model can be visualized as the difference between realized growth rate (based on segment-level habitat selection) and expected growth rate (based on strata-level demographic

processes). Although pintail across most of the Canadian PPR had negative growth rates, these areas were not necessarily acting as ecological traps because the number of pintail settling in the strata often matched the number expected based on demographic processes. Deviations between the growth rates were nevertheless observed in predominately mixed-grass landscapes in the south-western portion of the Canadian PPR (strata 29, 32 and 33) and North Dakota in the United States (strata 43, 45 and 46), as well as aspen parkland landscapes in Saskatchewan (strata 30 and 31). The areas that may be particularly important for pintail conservation are those in which expected growth rate is negative, with a greater or even positive realized growth rate (strata 29–33). These areas, all located in Canada, are attracting an increasingly greater number of pintail than expected given demographic processes, thereby acting as strong ecological traps that metaphorically act like pintail black holes. In portions of North Dakota (strata 43, 45 and 46), however, individuals are settling at higher rates than expected in areas where demographic processes yield positive long-term growth rates, effectively serving as pintail supernovas that help offset the vast areas of the Canadian PPR where pintail abundance is declining. In these and adjoining parts of the United States PPR, conservation easements and U.S. Farm Bill programs (e.g. the Conservation Reserve Program [CRP]) on private land accounted for 93% of grassland and 66% of wetland protections between 2001 and 2010 (Doherty et al., 2013). The well-known benefits of expansive CRP on waterfowl nest survival, and how it counteracts crop cover on the landscape, are the likely explanation for the strong demarcation between poor pintail population growth rates in Canada versus generally recent positive trends in the United States (Reynolds, Shaffer, Renner, Newton, & Batt, 2001; Figure 6; Appendix D in Supporting Information).

Previous work on fine-scale nest site selection and success in south-central Saskatchewan supports our broad-scale evidence for an ecological trap, as pintail propensity to nest in crop stubble compared to other dabbling duck species (as reviewed in Baldassarre, 2014) made them susceptible to nest destruction from predators and cultivation (Richkus, 2002). The generally positive effect of ponds on demographic processes is likely related to increased fecundity, as documented in Specht and Arnold (2018). The negative effect of ponds on demographic processes in strata 37–40 (a deviation from a positive response among other strata) is likely because the eastern PPR has become wetter over time (Niemuth et al., 2014). Long-term wet conditions can indirectly result in higher nest predation rates (a primary contributor of pintail nest failure; Richkus, 2002) through a bottom-up trophic response in which higher net primary production increases small mammal abundance, which can eventually support increased numerical abundance of predators and overall predation on waterfowl nests (Walker et al., 2013). This indirect predation effect is likely compounded by the reduced availability of native grass cover in these strata compared to strata in the United States.

Recent studies by Specht and Arnold (2018) and Zhao et al. (2019) have also attempted to quantify spatial variation in the underlying demographic vital rates that determine pintail

population dynamics. Zhao et al. (2019) found that reproductive success varied temporally (as we did, Appendix D in Supporting Information), and observed that beginning in 1970 most of the Canada PPR populations were declining in reproductive success. Over this same period, reproductive success in the U.S. PPR was increasing, consistent with our results of higher geometric mean growth rates in the U.S. PPR. Specht and Arnold (2018) generally found similar spatial patterns in reproductive success as our measures of expected growth rate (low reproductive success in the north, particularly the northeast, and higher reproductive success in the United States). Of notable difference, however, Specht and Arnold (2018) found that areas in the south-western Canada PPR strata were particularly productive (strata 28 and 29), whereas we found that part of that region was attracting more individuals than we would expect demographically (the realized growth rate in stratum 29 indicates an increasing abundance utilizing the stratum but demographically they should be stable at best). Interactions between strata-level responses and environmental changes may explain this discrepancy between the two studies. For example, greater declines in proportion of fallow acreage, a predictor not used in Specht and Arnold (2018), in stratum 29 compared to 28 would result in reduced expected abundances in stratum 29 (Appendix A in Supporting Information), whereas using cropland in proportion to its (increasing) availability in stratum 29 (as opposed to slight avoidance as in stratum 28) would result in increasing realized abundance in stratum 29 (Figure 3). Additionally, when considering differences in results, both Zhao et al. (2019) and Specht and Arnold (2018) based their estimates of reproductive success on the proportion of juvenile females to adult females from late summer banding stations. We suggest that careful attention be given to the use of such data because adult female movement after breeding (e.g. moult migration) could artificially inflate or deflate estimates of reproductive success.

We observed that agricultural effects were more influential across scales than the climatic effects (using the absolute value of the sum of the effect sizes standardized by the number of relevant variables). However, pond counts are themselves a product of land management and environmental conditions. When we account for the additional effect of agricultural practices and climate on pond dynamics, the cumulative effect of climate increased by more than the observed increase for agriculture (13% increase compared to 5%), but still remained less than the net effect of agriculture. Rapid annual changes in the proportion of crop acreage and the quickly adopted technological advancements associated with mechanical spring tillage could result in a rapid increase in the proportion of visually appealing habitat for pintails, ideal conditions for an ecological trap to have developed over time. In the PPR, native mixed-grass prairie has largely already been converted to cropland, and habitat alteration is arising through changes to existing crop cover types (Doherty et al., 2013). For example, conservation tillage (i.e. minimum tillage, zero tillage) has become increasingly popular because it reduces pre-planting preparation costs and erosion, and also helps

retain soil moisture (as reviewed in Best, 1986; Busari, Kukul, Kaur, Bhatt, & Dulazi, 2015; Uri, Atwood, & Sanabria, 1999). The practice of conservation tillage leaves at least 30% crop residue on the soil surface between harvest and planting the following year. This practice provides standing stubble and low-lying cover similar in structure to native mixed- and short-grass prairie before greenup towards which nest habitat selection was presumably adapted. However, agricultural operations, which can destroy nests, eventually occur on this seemingly attractive habitat during planting or pre-planting tillage. The benefit of conservation tillage (e.g. reduced frequency of field operations, nesting cover) can have negative impacts on species with long nesting cycles, a low tendency to re-nest and nesting periods that overlap agricultural operations, all of which describe pintail life-history characteristics (Best, 1986; Clark et al., 2016).

Agricultural intensification and global climate change are ongoing challenges with regard to conservation objectives. Agriculture is one of the primary anthropogenic threats to species persistence, particularly in areas of increasing human population growth (Tilman et al., 2017) and is the leading cause of environmental degradation (as reviewed in Clark & Tilman, 2017). Under future climate scenarios, areas of biodiversity significance in the Midwestern United States are projected to be under high crop demand (Martinuzzi et al., 2013) due to the increasing need for food production and biofuels (Doherty et al., 2013). Declines in farmland-associated avian species are not limited to the PPR, as declines in European farmland birds have been greater in countries with more intensive agricultural production (Daskalova, Phillimore, Bell, Maggs, & Perkins, 2019; Donald, Green, & Heath, 2001; Donald, Sanderson, Burfield, & Bommel, 2006). As increasing world-wide crop yield becomes a greater priority, and it becomes more profitable to farm more acres with larger machinery, farms will focus on converting small wetlands and grass margins to cropland (Higgins, Naugle, & Forman, 2002). It has also become less risky to farm areas that were previously considered marginal habitat (e.g. drought-prone soils, which will likely increase in areas of the PPR under future climate scenarios) due to availability of alternative crops (e.g. soybeans), genetic modification (Higgins et al., 2002) and federal farm programs (Doherty et al., 2013). In addition, the effects of climate and agriculture are actually compounded by pintail reliance on ponds for breeding, and effects can even be masked by ignoring the contribution of climate to pond counts. For example, snow cover duration did not have a detectable effect on habitat selection, but had a positive effect on ponds, which in turn contributes positively to habitat selection. This hierarchical chain of events is important to consider and naturally accommodated by our model structure, which can be thought of as a hierarchical structural equation model (Grace, 2006). However, we are likely underestimating the effect of ponds on pintail because the spring pond counts do not capture the small, ephemeral ponds that pintail prefer and that are particularly sensitive to the effects of agricultural drainage.

Linking fine-scale count data indicative of habitat selection to large-scale demographic processes is a step towards decoupling multiscale conditional processes when individual-level data are unavailable across large spatial and temporal expanses. As

we have demonstrated, solely using count data as an indicator of habitat quality can lead to erroneous conclusions about habitat quality for certain species (Van Horne, 1983), particularly those in which the fitness consequences are indirect and there has been rapid changes in the ratio of trap habitat to quality habitat (e.g. Bohner & Diez, 2019). Our model uses temporal variation in abundance data as a proxy for information on collective demographic processes that give rise to those counts (similar to *N*-mixture models, which further attempt to separate counts into contributions from survival and reproduction). Our model is currently unable to identify which demographic process is the primary contributor to the formation of an ecological trap. Inference about habitat selection and demography could be improved by incorporating individual-level movement behaviour at multiple spatial scales within and among years, whereas mark–recapture and nest-survival data could inform survival and reproductive success. However, current sample sizes for telemetered individuals tend to be small, and individual-level vital-rate information is spatially and temporally restricted due to financial and logistical constraints. In the absence of individual-level information, our model framework can guide the focus of future vital-rate and movement studies. In addition, it can be used to identify areas in which land can be managed to close the gap between expected and realized growth rates, and increase habitat quality to match its preferential use for a wide variety of species.

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AUTHORS' CONTRIBUTIONS

D.N.K. and F.E.B. conceived the ideas; F.E.B. designed the modelling framework with ecological insights from D.N.K. and J.H.D.; F.E.B. analysed the data; F.E.B. led the writing of the manuscript with input from D.N.K. and J.H.D. on waterfowl ecology and management. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The Waterfowl Breeding Population and Habitat Survey data can be obtained from the Division of Migratory Bird Management ([https://](https://migbirdapps.fws.gov/mbdc/databases/db_selection.html)

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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