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# Where does environmental stochasticity most influence population dynamics? An assessment along a regional core-periphery gradient for prairie breeding ducks

Richard E. Feldman<sup>1\*</sup>, Michael G. Anderson<sup>2</sup>, David W. Howerter<sup>2</sup> and Dennis L. Murray<sup>1</sup>

<sup>1</sup>Department of Biology, Trent University, Life & Health Science Building, Block D, 2140 East Bank Drive, Peterborough, ON K9J 7B8, Canada, <sup>2</sup>Institute for Wetland and Waterfowl Research, Ducks Unlimited Canada, PO Box 1160, Stonewall, MB R0C 2Z0, Canada

## ABSTRACT

**Aim** Geographical disparities in the effect of the environment on population dynamics have been shown to follow a core-periphery gradient when peripheral populations are less abundant and occur in marginal habitat. Whether the gradient in environmental influence occurs in the absence of a gradient in abundance is not known. We tested whether duck populations on the periphery of their main breeding region were more strongly affected by environmental stochasticity and less abundant than at the core.

**Location** The Prairie Pothole Region of central United States and Canada

**Methods** We used the North American Waterfowl Breeding Population and Habitat Survey to model the dynamics of 10 duck species at 1059 sites spanning 1961–2012. We used the North American Breeding Bird Survey to measure abundance at the same sites, averaged over the same time span. We used structural equation models to characterize relationships among a site's distance from the regional centre, a site's abundance, and the degree to which a site's ducks were affected by environmental stochasticity.

**Results** Environmental stochasticity never strongly contributed to population dynamics in the region's core. However, we did not find a linear increase in environmental stochasticity with increasing distance from the core. For seven species, we found that environmental stochasticity was stronger in sites of lower abundance. For only two species did average abundance decline from the region's core to periphery.

**Main conclusions** Variability in the magnitude of environmental stochasticity follows coarse spatial differences in wetland productivity. Yet, among peripheral sites, the contribution of the environment to population dynamics varies, possibly reflecting the importance of the local environment and dispersal.

## Keywords

**Abundance, *Anas*, *Aythya*, demographic stochasticity, density dependence, environmental stochasticity, Prairie Pothole Region, Ricker model, species ranges, wetlands.**

\*Correspondence: Richard E Feldman, Centro de Investigación Científica de Yucatán A.C., Unidad de Recursos Naturales, Calle 43 #130. Colonia Chuburná de Hidalgo, CP 97200 Mérida, Yucatán, México.  
E-mail: richard.feldman@cicy.mx

## INTRODUCTION

There is probably no more fundamental question in ecology than how populations respond numerically to environmental change. Excitingly, the answer is never simple because populations can fluctuate in abundance even in static environments due to density dependence in survival and reproductive rates (Nicholson, 1933; Murray, 1982). As a result, characterizing environmental variability as a driving factor of temporal change in population size depends on quantifying the contribution of both density dependent and density independent processes (Turchin, 1995). Recently the scope of inquiry has broadened because the dynamics of multiple populations extending over large spatial extents can be analysed (e.g. Sæther *et al.*, 2008). As a result, it is now evident that the density dependent vs. density independent dichotomy is itself dynamic; the contribution of each type of process to population growth varies among populations (Forchhammer *et al.*, 1998). The key advance to be made, then, is to determine whether there is any spatial pattern with regard to population dynamics, and whether such patterns indicate a response of species to broader environmental or spatial gradients.

One potentially general pattern is that density independent factors (i.e. environmental stochasticity, (*sensu* Fukaya *et al.*, 2014; Ohlberger *et al.*, 2014)) have a stronger effect on population growth in the periphery than the core of species ranges. Some studies have shown how peripheral populations are more variable in their abundance (Curnutt *et al.*, 1996; Mehlman, 1997; Doherty Jr *et al.*, 2003) suggesting that they are affected more by stochastic environmental fluctuations than core populations (García & Arroyo, 2001; Williams *et al.*, 2003). In turn, peripheral populations may be more responsive to the environment because they are smaller in size (Williams *et al.*, 2003). However, species for which peripheral populations are smaller than elsewhere in the range may be more the exception than the rule (Sagarin & Gaines, 2002; Samis & Eckert, 2007). Therefore, a central question is whether the influence of environmental stochasticity on population growth is higher in peripheral habitats even if they are not necessarily lower in abundance. Alternatively, the relationship between environmental stochasticity and abundance may hold regardless of how abundance is distributed across the species range.

To test these competing hypotheses, we modelled the dynamics of ten duck species in the Prairie Pothole Region (PPR) of the US and Canada. In the PPR, the optimal habitat for breeding ducks is found in the region's core, whereas soils and climate in the region's periphery lead to fewer, less persistent, and/or less productive wetlands (Werner *et al.*, 2013). Thus, if the effect of environmental stochasticity on population dynamics is stronger in marginal habitats, then we predict a positive association between distance from the centre of the PPR and the effect of the environment. On the other hand, differences in the type of range edge and the fact that other environmental factors also shift across the PPR (e.g. agricultural intensification of upland habitat [Samson *et al.*, 2004]) may obscure any core-periphery relationships. Meanwhile, overall duck abundances might still

be lower on the edge of the PPR even if they are not affected strongly by environmental stochasticity, due to dispersal and source-sink dynamics (Curnutt *et al.*, 1996; Bahn *et al.*, 2006). Further, we must caution that we are defining 'core' and 'periphery' as it pertains to habitat variability across the *region*. A lack of data precludes measuring population dynamics at the core and periphery of *species ranges*.

In summary, we characterized each of > 1000 sites for 10 duck species according to: 1) the degree to which environmental stochasticity affects population growth, 2) average abundance, and 3) distance from the centre of the PPR. We built a set of structural equation models to test how the three characteristics are related and answer the question: Are peripheral populations less abundant and more strongly affected by environmental stochasticity than core populations?

## METHODS

### Data

We used data from two surveys: the North American Waterfowl Breeding Population and Habitat Survey (BPOP) and the North American Breeding Bird Survey (BBS). With a methodology designed specifically to monitor duck numbers, we used the BPOP to build models of annual change in abundance while taking into account observer error and demographic stochasticity. Although the BBS does not have the same focus on waterfowl, we used abundances averaged over long time periods to indicate where ducks are consistently abundant or rare (see also Forcey *et al.*, 2007, 2011). Thus, we tested whether spatial differences in the influence of environmental stochasticity on population growth corresponded to areas that have supported large or small populations in the past 50 years, even if those populations are in flux (see below).

The US Fish and Wildlife Service initiated the BPOP in 1955 (Zimpfer *et al.*, 2012). In May of each year, observers fly transects from fixed-wing aircraft and count all duck species. We used the smallest survey area at which data are archived – the 28.8 km × 400 m transect segment – as the sampling unit. Further details on survey methodology can be found in Smith (1995), Sæther *et al.* (2008), and Murray *et al.* (2010).

From 1961 onward, observers also counted wetlands, which comprise natural and artificial water bodies that are expected to persist for at least three weeks beyond the survey date. Wetland numbers are known to be correlated with duck population growth (Sæther *et al.*, 2008). Hence, we included wetlands as a covariate in our models. Consequently, our measure of environmental stochasticity is independent from the deterministic influence of spatial variability in wetland numbers.

We limited our analysis to the Prairie Pothole Region (~13000 km<sup>2</sup>; 1151 transect segments) because it has the longest time series and is where breeding duck densities are at their highest in North America. From the original set of transect segments, we eliminated 92 because they had 17 or more years (> 30%) of missing wetland data. For the reduced data, there were still 2726 segment-year combinations (5.0%) missing

wetland data. We imputed the missing data using predictive means matching in the mice package (van Buuren & Groothuis-Oudshoorn, 2011) in R 3.0.2 (R Development Core Team, 2013). We used transect segment and year as predictors in the imputation. In the end, we analysed 1059 transect segments covering the years 1961–2012 (52 years).

We modelled the dynamics of the ten most common prairie duck species: the dabblers American Wigeon (*Anas americana*), Blue-winged Teal (*A. discors*), Gadwall (*A. strepera*), Green-winged Teal (*A. carolinensis*), Mallard (*A. platyrhynchos*), Northern Pintail (*A. acuta*), Northern Shoveler (*A. clypeata*); and the divers Canvasback (*Aythya valisineria*), Lesser Scaup (*A. affinis*), Redhead (*A. americana*). We used raw counts of individual ducks uncorrected for sightability differences among species or observers; we accounted for such error via the modelling process (see below). The raw counts were a summation of counts of lone drakes and individuals observed in mixed sex flocks, and twice the count of duck pairs.

We used the BBS to obtain a general picture of spatial variation of duck counts across the prairies. The BBS is a ground-based survey that censuses all birds seen or heard during 50 3-minute 400 m-radius point counts spaced 800 m apart along ~40 km roadside routes (Sauer *et al.*, 2014). The surveys are conducted on one day in late May or early June. Previously, the BBS has been used to relate duck abundances to climate and habitat factors (Forcey *et al.*, 2007, 2011). For our purposes, we averaged BBS counts for each of 3516 routes over the years 1961–2012, the years that corresponded to the BPOP data. We associated each BPOP transect segment to the closest BBS route. We also measured the Euclidean distance between each BPOP transect segment and the geographic centre of all BPOP transect segments. Thus, we had average BBS abundance and distance to the centre of the PPR for each BPOP transect segment. It is important to note, however, that all duck species we modelled have breeding ranges that extend beyond the PPR.

### Population modelling

We modelled population dynamics using a state-space Ricker model. In the state-space approach, count data such as those enumerated in the waterfowl aerial surveys are considered to be an imperfect approximation of abundance (Clark & Bjørnstad, 2004), and the first part of the model is an observation model that relates duck counts ( $Y$ ) at each point in space ( $i$ ) and time ( $t$ ) to ‘real’ but unknown abundances ( $N_{i,t}$ ). This relationship consists of stochastic and deterministic components with the stochastic component assuming that duck counts are drawn from a normal distribution with mean,  $\eta$ , and variance,  $\sigma$ :

$$Y_{i,t} \sim \text{Normal}(\eta_{i,t}, \sigma_y)$$

In the deterministic component, the mean,  $\eta$ , is linearly related (with intercept,  $a$ , and slope,  $c$ ) to the real abundance following Lillegård *et al.* (2008) and Sæther *et al.* (2008):

$$\sqrt{\eta_{i,t}} = a + c\sqrt{N_{i,t}}$$

We then used a Ricker model to relate abundance to maximum intrinsic growth rate ( $r.max_i$ ), carrying capacity ( $K_i$ ), density dependence ( $1-N_{i,t}/K_i$ ), and the environment ( $e_{i,t}$ ). To simplify the model, we assumed intrinsic growth rate and carrying capacity were fixed across time although we allowed the terms to vary across space. We chose a Ricker model because Murray *et al.* (2010) found that the best fit theta-logistic model, when fit to duck population time series data, was equivalent to the Ricker, i.e. in the majority of cases the  $\theta$  exponent was not different from 1.0.

In the stochastic component of the model, we assumed abundances were drawn from a normal distribution. The deterministic component then relates the mean of this distribution,  $\hat{N}$ , to demography and the environment via the Ricker equation:

$$N_{i,t+1} \sim \text{Normal}(\hat{N}_{i,t+1}, \sigma_N)$$

$$\hat{N}_{i,t+1} = N_{i,t} * \exp\left[r.max_i * \left(1 - \frac{N_{i,t}}{K_i}\right) + e_{i,t}\right]$$

The dependent variable in this model is more commonly expressed as population growth (Sibly & Hone, 2002), which leads to the linear equation:

$$\ln \frac{\hat{N}_{i,t+1}}{N_{i,t}} = r.max_i * \left(1 - \frac{N_{i,t}}{K_i}\right) + e_{i,t}$$

The purpose of our investigation was to quantify site-to-site variability in the contribution of the environment to annual changes in duck population growth,  $e_{i,t}$ , for a particular level of wetland availability (*Ponds*). Therefore, we added an environmental model, decomposing the contribution into stochastic and deterministic components:

$$e_{i,t} \sim \text{Normal}(\varphi_{i,t}, \sigma_e)$$

$$\varphi_{i,t} = \alpha + \beta_{Ponds} * Ponds_{i,t} + \Delta_i * Ponds_{i,t} + \mu_i + \tau_i$$

The model consists of parameter estimates for the overall effect of wetlands ( $\beta_{Ponds}$ ) (averaged across all points in space and time) as well as random deviations of this estimate for each site ( $\Delta_i$ ). The  $\mu_i$  and  $\tau_i$  represent random deviations from the average contribution of the environment (the intercept,  $\alpha$ ) for each site and year respectively. Accounting for such spatial and temporal variability is known as the Besag-York-Mollie model (Besag *et al.*, 1991) and is used frequently to model spatiotemporal variation in the incidence of disease and subsequent mortality (e.g. Lawson *et al.*, 2003).

We estimated all parameters using a Bayesian framework in the program OpenBUGS (Lunn *et al.*, 2009) because such an approach allows for hierarchical models that account for spatially and temporally autocorrelated random effects (Thomas *et al.*, 2004; Forcey *et al.*, 2007). Given that: 1) our sample unit, the transect segment, is aggregated into transects, 2) ducks are fairly mobile, and 3) environmental conditions likely are

correlated over the scale of interest, we expect strong spatial autocorrelation and thus necessarily included autocorrelation in our model. In other words, we expected the contribution of the environment at one site to depend on the contribution at adjacent sites and thus modeled this factor explicitly. In fact, the  $u$  term measures site specific environmental stochasticity and is estimated by 'borrowing' information from neighbours (Kéry & Schaub, 2011). This is done by conditioning  $u$  with an autoregressive normal prior distribution (CAR.normal; Thomas *et al.*, 2004). Likewise, year specific environmental effects ( $\tau$ ) are expected to depend on conditions in – and borrow information from – adjacent years. Such temporal autocorrelation is taken into account using the CAR.normal prior (Thomas *et al.*, 2004; Amaral-Turkman *et al.*, 2011). Our R and OpenBUGS code can be found in Appendices S1 and S2.

We estimated the posterior distribution for all unknown parameters in our model, including the variances associated with each stochastic node, using Markov Chain Monte Carlo sampling in OpenBUGS (Lunn *et al.*, 2009). We used vague priors for all the stochastic nodes, following Thomas *et al.* (2004) (Appendix S3). We ran two model chains for 35000 iterations each, discarding the first 10000 iterations as a burn-in sample. Thus, our final sample consisted of 50000 values, from which we calculated the mean and 95% credible interval. The credible interval was measured as the Highest Posterior Density (HPD) interval, i.e. the narrowest segment of all the values that contain 95% of the data, using the coda package (Plummer *et al.*, 2006) in R 3.0.2 (R Development Core Team, 2013).

### Measuring environmental stochasticity

We calculated the site-specific contribution of environmental stochasticity to population growth ( $\varphi_i$ ) by solving the equation:

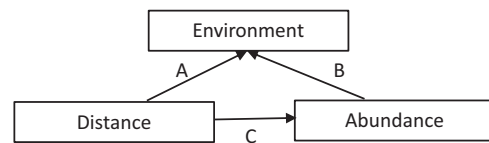
$$\varphi_{i,t} = \alpha + \beta_{Ponds} * Ponds_{i,t} + \Delta_i * Ponds_{i,t} + \mu_i + \tau_i$$

We set  $\tau = 0$  to estimate the environmental contribution for the 'average' year. We set wetland availability to the overall average across all sites and years ( $Ponds = 25.630$ ).

We plotted site-specific environmental effects on a background map provided by Global Administrative Areas (<http://www.gadm.org>) and downloaded via the raster package (Hijmans, 2015) in R 3.0.2 (R Development Core Team, 2013). For visualization purposes, we binned site-specific effects into 5% percentiles with strong effects corresponding to the 5<sup>th</sup> percentile and weak effects corresponding to the 95<sup>th</sup> percentile.

### Geographic analysis

Our aim was to test whether populations strongly affected by environmental stochasticity were located at the periphery of the PPR and in areas of low abundance. However, we included the possibility that variability in environmental stochasticity may be associated with only one or neither of these factors. Further, we included the possibility that distance to the centre of the PPR



**Figure 1** The general form of the structural equation model relating the magnitude of environmental stochasticity ('Environment') to the distance of a site to the geographic centre of the Prairie Pothole Region (PPR) ('Distance') and to the abundance of a site ('Abundance'). From the general form, we constructed eight separate models that reflect different combinations of the links, A, B, and C. Environmental stochasticity was estimated using a Ricker model of population dynamics fitted to a 52 year time series of duck counts taken from the North American Waterfowl Breeding Population and Habitat Survey. Distance to the centre of the PPR was measured in ArcGIS v.10 (ESRI, 2011). Abundance is the 52 year average of counts taken from the North American Breeding Bird Survey.

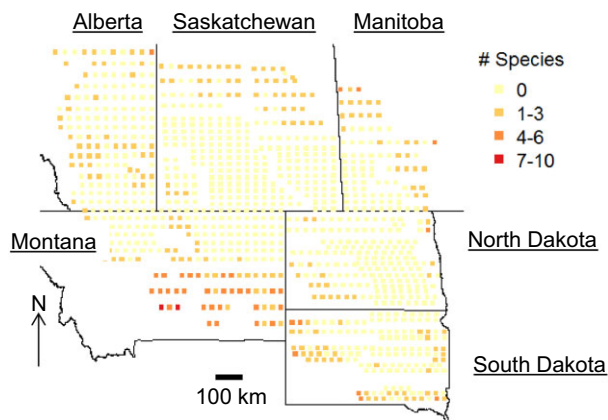
and abundance might be related even if one or neither is related to the strength of environmental stochasticity. We compared the evidence for these different relationships using structural equation modeling (SEM) in the lavaan package v. 0.5–14 (Rossee, 2012) in R 3.0.2 (R Development Core Team, 2013). We modeled eight different scenarios relating environmental stochasticity, distance from the PPR's centre, and BBS abundance (Fig. 1). For each model, we calculated a Bayesian Information Criterion (BIC). We subtracted this value from the minimum BIC in the set of eight models ( $\Delta BIC$ ). We converted  $\Delta BIC$  to a model weight:

$$Weight_i = \frac{\exp\left(-\frac{1}{2} \Delta BIC_i\right)}{\sum_{i=1}^k \exp\left(-\frac{1}{2} \Delta BIC_i\right)}$$

We averaged the model weights over 2000 draws randomly selected from the 50000 total draws. We calculated also the 95% credible interval of the distribution of model weights. We selected the final model as the one with the highest average model weight. We present the model selection results graphically (mean weight  $\pm$  95% credible interval for each model). Also, we report the parameter estimates of the relationships included in the final model.

## RESULTS

The effect of environmental stochasticity on duck population dynamics was not the same everywhere in the Prairie Pothole Region (PPR). Most striking was the dichotomy we observed between the core and periphery of the PPR: we did not find any species strongly affected by environmental stochasticity in the core (Fig. 2; Appendix S4). Instead, environmental stochasticity was strongest in peripheral sites. However, we found that each species tended to respond to the environment randomly across the periphery; no sites were consistently strong for all species



**Figure 2** The number of species in each transect segment that were strongly affected by environmental stochasticity. A strong effect is when the influence of environmental stochasticity on population dynamics comes from the top 5% of the distribution of values for each species. Background maps come from the Global Administrative Areas website (<http://www.gadm.org>) downloaded using the raster package (Hijmans, 2015) in R 3.0.2 (R Development Core Team, 2013).

(Fig. 2). The one exception was in the southwest corner of the PPR where all species had several sites strongly affected by environmental stochasticity (Appendix S4). We did not find the same core-periphery dynamic for BBS abundances; sites of high and low abundances were scattered across the region (Appendix S5).

While the influence of the environment was most extreme in the periphery, we did not find evidence that its influence declined linearly from the core to the periphery. For no species did any of the selected structural equation models include a term where the environment's influence was related to distance from the centre of the PPR (Fig. 3). Instead, for seven of the ten species, we found the most support for models that included a relationship between environmental stochasticity and abundance. As expected, the influence of environmental stochasticity weakened with increasing abundance (Table 1). Although the slope estimates were positive, the intercept term was negative implying that for small-to-average sized populations, environmental stochasticity reduces population growth from what is expected under pure density dependence (Table 1). On the other hand, the slope estimates were small and their 95% credible intervals included zero. Thus, we suggest that we only have weak support for an environmental stochasticity-abundance relationship.

For the other three species, American Wigeon, Canvasback, and Redhead, the influence of environmental stochasticity on population growth was random with respect to both space and average abundance. However, for the wigeon and Canvasback, we found that abundance declined from the core to the periphery of the PPR (Table 1). For Redhead, we found support for the null model, i.e. the effect of environmental stochasticity, abundance, and distance from the centre of the PPR were all unrelated to each other (Table 1).

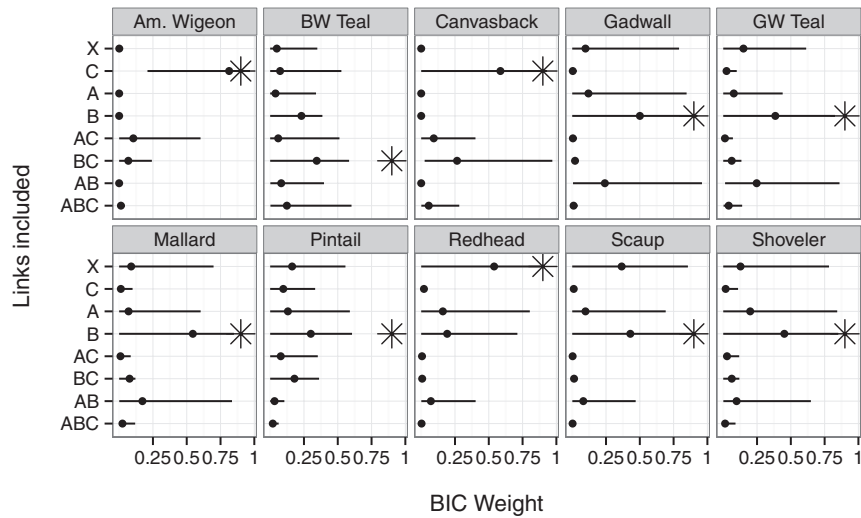
## DISCUSSION

### Importance of spatially nested environmental variability to population dynamics

Our key finding is that the effect of environmental stochasticity on population dynamics is a spatially nested phenomenon: it is highly variable at fine spatial scales but entrained by large areas of strong or weak influence that correspond to core-periphery differences in environmental productivity. For example, we never found a strong effect of environmental stochasticity for any duck species at the core of the PPR. Rather, we found that environmental stochasticity was most influential at or near the region's periphery and especially strong in the southwest corner (central Montana), which is where wetland productivity is the lowest (Werner *et al.*, 2013). Thus, the nature of environmental influence may follow the extremes of wetland productivity, with weak influence in productive wetlands and strong influence in unproductive wetlands.

Within productivity extremes, our results suggest additional local control leading to site level variability in how environmental stochasticity contributes to population change. Not only did we find apparent randomness in the location where any given species was strongly affected by environmental stochasticity (though never in the core), we also failed to detect evidence that the effect of environmental stochasticity increased linearly from the core to the periphery. Thus, different suites of species may be strongly affected by the environment even at adjacent sites. Furthermore, the degree to which any individual species is affected by the environment may differ among adjacent sites. Together, these results suggest that the factors that ultimately affect population growth in a density independent manner are those that vary at fine spatial scales (i.e. the ~24 km transect segments we analysed). One strong influence we did not measure was underlying geology; in the PPR moraine landforms are spatially discontinuous but correlated with duck abundances (Ducks Unlimited Canada, personal communication; see also Browne *et al.*, 2009). Moraines may be a better indicator of habitat quality than any feature or combination of features that may vary along core-to-periphery gradients.

The fact that we did not find a fine scale relationship between environmental stochasticity and position on a core-periphery gradient is somewhat consistent with the findings of Sæther *et al.* (2008). Using the same prairie duck data, Sæther *et al.* (2008) found a latitudinal gradient (south > north) in population fluctuations and, for some species, a latitudinal gradient in process variance, which encompasses both demographic and environmental stochasticity. Our analysis suggests that the latitudinal differences that Sæther *et al.* (2008) observed may be driven by patterns in the southwest rather than the south as a whole. More generally, then, one cannot ignore longitudinal variation especially in systems structured by both latitudinal (temperature) and longitudinal (precipitation) climatic gradients. Furthermore, Sæther *et al.* (2008) suggested that latitudinal differences in population dynamics may be driven by latitudinal differences in wetland shape and agricultural practices.



**Figure 3** The weight of evidence for each of eight structural equation models. The models relate the magnitude of environmental stochasticity to the distance of a site to the geographic centre of the Prairie Pothole Region (PPR) and to the abundance of a site. We constructed eight separate models that reflect different ways of linking the three variables. Each individual link is labeled A, B, or C as shown in Figure 1. The model indicated by an 'X' is the null model whereby none of the variables are linked to each other. We calculated the Bayesian Information Criterion for each model, which we converted to the model weights shown here. The data are presented as means  $\pm$  95% credible intervals for 2000 model iterations, each corresponding to an independent posterior draw of environmental stochasticity values. Asterisks indicate the model upon which we made inferences.

**Table 1** Coefficients from the selected structural equation model for each species. We show the coefficients for the two links included in the species models (see also Fig. 1). Link B relates environmental stochasticity to a site's abundance. Link C relates a site's abundance to the distance of the site from the centre of the Prairie Pothole Region. We do not include link A – the direct relationship between environmental stochasticity and distance from the centre of the PPR – because the link was not included in any of the selected structural equation models. The coefficients in link B are estimated along with their 95% credible intervals from 2000 draws of the posterior distribution of environmental stochasticity. The uncertainties in link C are 95% confidence intervals because the values of abundance and distance to the centre of the PPR are fixed across all posterior draws

Species	Links included in selected model	Parameters			
		Link B		Link C	
		Environment (Intercept)	Abundance	Abundance (Intercept)	Distance
Am. Wigeon	C	-5.28 [-7.54, -3.09]	0	0.609 [0.416, 0.803]	-0.000980 [-0.000558, -0.00140]
BW Teal	BC	-5.67 [-9.87, -2.01]	0.0363 [-0.0105, 0.0765]	2.14 [1.23, 3.05]	0.00282 [0.000844, 0.00480]
Canvasback	C	-3.55 [-4.50, -2.56]	0	0.417 [0.267, 0.567]	-0.000948 [-0.000620, -0.00127]
Gadwall	B	-5.22 [-9.15, -1.50]	0.0109 [-0.0294, 0.0354]	2.46 [2.09, 2.82]	0
GW Teal	B	-2.72 [-3.03, -2.39]	0.136 [0.0118, 0.215]	-0.179 [-0.221, -0.137]	0
Scaup	B	-3.37 [-4.96, -2.65]	0.0147 [-0.0242, 0.0645]	1.03 [0.827, 1.24]	0
Mallard	B	-5.02 [-9.20, -1.35]	0.00322 [-0.0240, 0.0234]	10.1 [9.28, 10.9]	0
Pintail	B	-4.73 [-7.96, -1.79]	0.0346 [-0.0410, 0.0973]	1.40 [1.23, 1.58]	0
Shoveler	B	-5.11 [-8.79, -1.51]	0.0466 [-0.00676, 0.102]	1.21 [1.03, 1.38]	0
Redhead	X	-3.06 [-3.76, -2.59]	0	0.819 [0.669, 0.968]	0

Certainly the latter has also a longitudinal component: a greater proportion of upland habitat has been converted to agriculture in the east than the west (Samson *et al.*, 2004).

The only environmental variable we actually included in our models was wetland availability (*sensu* Viljugrein *et al.*, 2005; Sæther *et al.*, 2008). We did so in order to remove its effect and

focus our interpretation on less obvious but potentially very influential environmental drivers of population change, such as those mentioned above. Yet because the particular environmental variables that best characterize marginal environments might differ for different regional 'peripheries', we chose to quantify them collectively as environmental stochasticity. An alternative

perspective would have been to use wetland availability to predict carrying capacity, or, at least allow carrying capacity to vary over time. Doing so might have given a more realistic picture of how abundance tracks wetland availability (Fowler & Pease, 2010). When wetlands are included as an additive density independent term, they explain very little of the variation in duck numbers (Sæther *et al.*, 2008; Feldman *et al.*, unpublished). If, however, temporal variability in carrying capacity shifts the variation in counts away from the environment and toward density dependence, then the periphery might actually correspond to sites of strong density regulation in fluctuating environments rather than stochastic variation around a long-term equilibrium population.

### Importance of dispersal to population dynamics

Metapopulation and source-sink perspectives posit dispersal as a key process creating geographic structure in population dynamics: individuals are thought to disperse from productive environments toward the periphery, creating gradients in abundance and susceptibility to environmental change (Pulliam, 1988; Guo *et al.*, 2005). That we did not find these patterns suggests an alternative type of dispersal dynamic that better corresponds to what is known about duck migration. When returning from their wintering grounds, prairie ducks are not necessarily philopatric and there may be some geographic or habitat related bias in where they settle (Johnson & Grier, 1988). For example, if wetland availability is low due to drought conditions, individuals are known to fly over southern breeding grounds and settle farther north (Hansen & McKnight, 1964; Smith, 1970; Derksen & Eldridge, 1980; Johnson & Grier, 1988). Hence, southern populations may be particularly affected by emigration and northern populations by immigration, with the extent of the effect dependent on temporal climatic variability. Thus dispersal might exacerbate the environmental differences between the core and periphery, which creates an apparent mismatch between how populations respond to environmental change and the actual underlying environmental gradients.

Past studies showing core-periphery patterns in population dynamics have revealed how population size is the link between range position and response to environmental variability (Curnutt *et al.*, 1996; Williams *et al.*, 2003). In our study, none of the species followed this causal pathway. Instead, we found some support for an inverse relationship between abundance and the influence of environmental stochasticity regardless of the underlying spatial pattern of abundance. Furthermore, our results support the finding that in any species assemblage, only a few will show core to periphery gradients in abundance (Sagarin & Gaines, 2002). In our study, only two of the ten species (American Wigeon and Canvasback) conformed to the pattern. Critically, though, because low abundant populations are not all at the periphery, extinction risk due to random environmental fluctuations may be tempered by the possibility of rescue from nearby high abundant populations. Even at the periphery, patchy responses to environment means that greater environ-

mental change (e.g. climate change) will not lead to a contraction in occupancy across the Prairie Pothole Region.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

**Appendix S1** R code to impute missing wetland data and prepare duck and wetland data for analysis in OpenBUGS.

**Appendix S2** OpenBUGS code for the conditionally autoregressive Ricker model of population dynamics.

**Appendix S3** Priors used for all stochastic nodes in MCMC modeling of duck population dynamics.

**Appendix S4** Spatial variation in the magnitude of environmental stochasticity for each of the 10 duck species.

**Appendix S5** Spatial variation in abundance, Breeding Bird Survey counts averaged from 1961–2012.

## BIOSKETCH

This project emerged from a collaboration between biologists at Trent University and Ducks Unlimited Canada. Together, our aim is to improve our understanding of how ducks respond to global environmental change given the potential for strong density dependence in the regulation of their abundance. We will use such an understanding to improve management and ensure that ducks and their habitat are conserved well into the future.

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