RESEARCH ARTICLE

Landscape heterogeneity and the effect of environmental conditions on prairie wetlands

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Abstract Populations can vary considerably in their response to environmental fluctuations, and understanding the mechanisms behind this variation is vital for predicting effects of environmental variation and change on population dynamics. Such variation can be caused by spatial differences in how environmental conditions influence key parameters for the species, such as availability of food or breeding grounds. Knowing how these differences are distributed in the landscape allows us to identify areas that we can expect the highest impact of environmental change, and where predictions on population dynamical effects will be most precise. We evaluated how wetland dynamics in the North-American prairies (pond counts; a key parameter for several waterfowl populations) were related to spatial and temporal variation in the environment, as measured by weather variables, primary productivity and phenology derived from annual normalized difference vegetation index (NDVI) curves, and agricultural composition of the landscape. Spatial and temporal variation in pond counts were closely related to these environmental variables. However, correlation strength and predictive ability of these environmental variables on wetland dynamics varied considerably across the study area. This variation was related to landscape characteristics and to the spatial scaling of the wetland dynamics, such that areas with late onset of spring, low spring temperature, high primary productivity, and high proportion of cropland had more predictable and spatially-homogenous dynamics. The success of predicting environmental influences on wetlands from NDVI measures derived from satellite images indicates they will be useful tools for assessing effects of changing landscape and climatic conditions on wetland ecosystems and their wildlife populations.

Keywords Agricultural influence · Climate effect · Environmental phenology · NDVI · North American prairie · Landscape variation · Spatial heterogeneity · Waterfowl · Wetland ecology

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Introduction

The influence of landscape heterogeneity on population processes is commonly recognized, and understanding this influence has increased our knowledge about mechanisms affecting dynamics and extinction of spatially distributed populations (Hanski and Gilpin 1996; Tilman and Kareiva 1997; Illius and O'Connor 2000; Fryxell et al. 2005; Cromsigt et al. 2009; Oliver et al. 2010). Spatially separated populations commonly differ in responses to similar and simultaneously experienced environmental conditions (Bjørnstad et al. 1995; Sæther et al. 2003, 2008; Herfindal et al. 2006; Grøtan et al. 2009), and such differences typically increase in magnitude with increasing distance among populations (Grøtan et al. 2005; Sæther et al. 2007). Explanations for spatial heterogeneity in population responses to environmental conditions includes strength of density dependence (Grøtan et al. 2009), variation in environmental conditions (Herfindal et al. 2006; Grøtan et al. 2008), and non-linear relationships between environment and vital rates (Laakso et al. 2004; Oliver et al. 2010). Understanding the details of interactions between demographic responses and measurable aspects of the environment remains a key challenge in applied ecology (Benton et al. 2006).

Geographical variation in effects of environmental conditions on important resources such as food or breeding sites, presents a significant challenge to explanations of population dynamical processes. Given the rapid environmental change that many populations experience today, we need to know how the landscape conditions and key population parameters are linked to environmental variation. Only then we can know in what areas we can expect changes to the most impacted populations, and understand how precision of predictions varies spatially. Consequently, if not incorporated into population models, spatial variation in responses to environmental variation may lead to imprecise predictions about environmental change on populations, particularly over large heterogeneous areas. However, to successfully account for landscape heterogeneity in predictions of environmental change on populations demands data with high spatial and temporal resolution in order to capture the fine-scale heterogeneity that characterises many landscapes.

The use of remotely sensed data has proven a powerful way to describe environmental conditions over large areas (Pettorelli et al. 2011). Satellite-derived data sources provide time series that are continuous in their spatial extent and provide more direct measures of environmental conditions, such as primary productivity or phenology that can be linked to ecological mechanisms (Stoms and Hargrove 2000; Herfindal et al. 2006; Karlsen et al. 2006; Pettorelli et al. 2011). Although satellite-derived data often are indices of terrestrial vegetation (e.g. the normalized difference vegetation index, NDVI; Verstraete et al. 1996), several data sources show promise for indexing landscape-level of wetlands (Adam et al. 1998; Beeri and Phillips 2007; Wright and Gallant 2007; Zoffoli et al. 2008). Derivates of these indices, such as timing of the onset of spring, or length of growing season, provide measures related to environmental phenology which can affect reproductive performance of birds (Visser et al. 2004).

The mid-continental prairies of North America contain an expansive matrix of grasslands and wetlands within an agriculturally dominated landscape that provides important habitat for a number of wildlife species. For example, more than half of all North American ducks breed in this region (Smith et al. 1964; Crissey 1969). The area has high spatiotemporal variation in environmental conditions, and some of the most abundant species that breed there show strong spatial gradients in the proportion of variation in population sizes that can be explained by environmental conditions, both among species and among populations of the same species (Sæther et al. 2008). Numbers of prairie wetlands vary with weather conditions (Larson 1995), and this has caused concern for potential effects of climate change on wildlife population sizes (Bethke and Nudds 1995; Sorenson et al. 1998). Much of this region has been converted to agriculture, which can have major impacts on wetlands by changing hydrological conditions (van der Kamp et al. 1999). This combined susceptibility to weather conditions and agricultural practices has prompted calls for landscape-level monitoring of prairie wetlands to detect long-term trends (Conly and van der Kamp 2001). Aerial surveys for waterfowl and wetlands (ponds) conducted by the US Fish and Wildlife Service and Canadian Wildlife Service (Smith 1995) currently provide one of the best programs to monitor wetland availability over the entire prairie region. However, we need to know more about the spatio-temporal dynamics of wetlands and how they relate to environmental

variation to be able to make predictions on effects of climate change on wetland ecosystems. If satellite-derived environmental variables successfully describe and predict spatio-temporal dynamics of wetlands, they will complement ongoing landscape-level wetland monitoring programs.

In this study, we combine pond counts with measures of environmental phenology and productivity from annual NDVI-curves, climate variables, and agricultural landscape composition to explain the spatio-temporal dynamics of pond counts. We address two interrelated questions: (1) how is spatial and temporal variation in wetland numbers related to variables measuring environmental conditions and agricultural composition over the prairies; and (2) is the spatial variation in the correlation strength and predictive ability of these environmental variables related to the landscapes' environmental conditions and agricultural composition? The first question addresses what environmental variables might be used to predict wetland dynamics, whereas the second question addresses whether we can identify landscape characteristics with high predictability. We addressed these questions at three different spatial resolutions, and evaluated the appropriate spatial scale to relate wetland dynamics to environmental conditions, and consequently also the scale at which wetland bird dynamics should be evaluated and managed.

Methods

Pond counts

Data on pond counts were obtained from the May Waterfowl Breeding Population and Habitat Survey conducted by the U.S. Fish and Wildlife Service and the Canadian Wildlife Service, which provides counts of breeding waterfowl and wetlands from a large section of North America from South Dakota to Alaska (Smith 1995). The survey has been conducted annually in May since 1955, and includes counts of waterfowl species and wetlands (referred to as 'ponds') observed from aircraft flying at a speed of ~150 km/h and a height of 30–50 m above ground level. Data from the survey is organized within three spatial units. The survey route follows 400-m wide transects that are composed of 28.8 km sections (referred to as 'segments'). These segments are aggregated into longer continuous series (referred to as 'transects') consisting of 2–11 segments oriented in an east–west direction. Transects are in turn aggregated into larger geopolitical units with similar habitat and duck densities (referred to as 'strata'). Ponds counted include seasonal and permanent ponds, both artificial and natural, that are expected to persist for >3 weeks beyond the survey date. Ground-based waterfowl and wetland surveys are conducted concurrently at a subsample of the aerial survey transects, and are used to correct the aerial counts for potential detection errors (Smith 1995). While other metrics of wetland abundance and conditions exist, such as pond area, these annual pond counts are the only regional-scale data available at present and therefore provide the best data for assessing long-term hydrologic trends and predicting waterfowl breeding success (Conly and van der Kamp 2001).

We used data from 1982 to 2001 to ensure overlap between data on pond counts and other data sources. Pond counts were recorded at the segment level, and these values were used directly. We aggregated the annual pond counts at transect and stratum levels by averaging over all segments within transects or strata. Averaging was preferred over sum, because the number of segments differ by transects and strata. Pond counts and mean pond counts at all three scales were ln-transformed (adding 1 to all values due to segments with no ponds) prior to all analyses to normalize residuals from linear analyses and to reduce heteroscedasticity.

Environmental variables

We calculated nine environmental variables related to productivity, phenology, weather, and agricultural composition (Table 1). Based on bimonthly values of NDVI, we calculated six measures related to environmental phenology and productivity: onset of spring, derived spring-NDVI, peak time of NDVI, peak value of NDVI, onset of autumn, and integrated NDVI. NDVI is a measure of photosynthetic activity, and is derived from the ratio of red to near-infrared light reflected by vegetation on the ground and captured by the sensor of the satellite, where NDVI = (NIR − RED)/(NIR + RED), and NIR and RED are the amounts of near-infrared and red light, respectively.

We used the Global Inventory Modelling and Mapping Studies (GIMMS) NDVI data set from the

Advanced Very High Resolution Radiometer (AV-HRR) onboard the US National Oceanic and Atmospheric Administration satellite series 7, 9, 11, 14, 16 and 17. Source for this data set was the Global Land Cover Facility, www.landcover.org. This NDVI dataset has been corrected for drift in preflight calibration coefficients, view geometry, volcanic aerosols, and other effects not related to vegetation change (Pinzon et al. 2005; Tucker et al. 2005). The GIMMS data set has 8×8 km^2 spatial resolution and is composed of the maximum NDVI values for bimonthly periods between July 1981 and December 2006. Accordingly, there are 2 half-month composites per month, from day 1 to 15 and from day 16 to the month's end.

To estimate the onset and end of the growing season (onset of spring and autumn), we applied a pixel-specific threshold method described by Karlsen et al. (2006). With this method, a 21-year mean NDVI value and a mean of peak NDVI values were computed for each pixel. The onset of spring was defined as the date (day number) of each year when 0.8 of the mean NDVI value was surpassed, and the onset of autumn as the date when the NDVI value decreased below 0.7 of the mean peak NDVI value. A derived spring-NDVI was computed as the difference of the NDVI value at onset of spring and the 15-day period before onset, and can serve as a measure of the speed of plant development during spring. For removing outliers in the NDVI time series a 3 pixel long median filter window was applied. The NDVI-measures were assigned to survey segments that lay within pixel boundaries. In some pixels, high proportions of open water due to presence of large lakes, barren ground, or other non-vegetated areas resulted in annual NDVI-curves that did not allow estimation of reasonable values of environmental phenology. These pixels were omitted from the data, and segments located within these pixels were excluded from the analyses (3.4 % of the segments were omitted).

Weather variables known to affect wetland availability were derived from high-resolution gridded data (CRU TS 2·1; Mitchell and Jones 2005) and assigned to survey segments. We calculated two weather variables: spring temperature (°C) as the average for March and April, and total winter (January–April) precipitation (mm) (Larson 1995).

We obtained data on agricultural landscape composition from US and Canadian agricultural censuses, which were conducted every 5 years and provided information on local agricultural conditions as reported by farmers (US Department of Agriculture 2009; Statistics Canada 2009). We extracted a single measure from the censuses representing intensively managed agricultural lands. Proportion cropland was derived for each reporting unit by summing the total area devoted to row crops, summerfallow, hayland, and pastured cropland, and dividing by the total area of each reporting unit (Podruzny et al. 2002). We excluded cities and towns and water bodies >1 km^2 from areas within survey units. Survey segments that were located within boundaries of reporting units were then assigned a value of proportion cropland. Values for years between surveys were obtained by linear interpolation.

Table 1 Environmental variables related to variation in pond counts over the prairie-parkland region of North America

Variable (abbr.)	Description
Proportion cropland (prop. crop.)	Total area devoted to row crops divided by total area of each reporting unit in Census of Agriculture
Winter precipitation (winter prec.)	Total accumulation of precipitation for January–April prior to the pond count in each year (mm)
Spring temperature (spring temp.)	Average daily temperature (°C) for March and April
Onset of spring (os)	Day number in year when 0.8 of the pixel's mean NDVI value was surpassed
Derived spring NDVI (dn)	Difference of NDVI values at onset of growing season and at 15-day period before onset. Can serve as a measure of rapid plant development during spring
Peak time (pt)	Day number in year when the NDVI reaches its highest value
Peak value (pv)	NDVI value at peak time
Onset of autumn (oa)	Day number in year when 0.7 of the pixel's mean peak NDVI value was surpassed.
Integrated NDVI (in)	Sum of NDVI-values between onset of spring and onset of autumn. Can serve as a measure of primary productivity

Variable abbreviations are given in parentheses

Statistical analyses

In all analyses, we chose a univariate approach with respect on the influence of environmental variables on spatial and temporal variation in pond counts. While multiple regression models might have resulted in better predictive models, univariate analyses avoided the problem with multi-colinearity (Graham 2003), and allowed us to compare the relative explanatory power of individual variables. Nonetheless we fitted multiple linear regressions with ln(pond counts) as dependent variable and the environmental variables as explanatory, but this did not qualitatively affect the results. We therefore chose to present results from univariate analyses to best assess the explanatory power of individual variables.

Large-scale spatial and temporal dynamics in pond counts

We first evaluated how pond counts and the nine environmental variables co-varied spatially across the prairie-parkland region and temporally over the study period (1982–2001). To examine spatial variation, we averaged variables over the study period at each spatial unit. We present the spatial variation only for the transect level (results were similar if we averaged over the segment or stratum level). Temporal variation in pond counts and environmental variables over the whole study area was assessed by averaging the variables at the segment unit for each year. Spatial and temporal relationships between pond counts and mean values of environmental variables were analyzed with linear models where each environmental variable was added as a linear term or as a second order polynomial (quadratic term). We also applied generalized additive models (GAM; Woods 2006) to evaluate non-linearity in the patterns. The significant non-linear patterns suggested for some of the relationships were well captured by the quadratic models. We therefore do not present the GAM results further.

Annual dynamics in pond counts and relationships with landscape characteristics

We assessed the influence of environmental variables on annual pond counts at three spatial resolutions (segment, stratum and transect) using a similar approach developed for time series analyses of population dynamics (Sæther et al. 2004; Engen et al. 2005). For each spatial unit j, a regression was run between ln-transformed pond counts at year k, u_{jk}, and each of the environmental variables i at year k, y_{ijk} (Eq. 1):

$$u_{jk} = \beta_{ij} y_{ijk} + w_{ij} \tag{1}$$

where w_{ij} is the intercept for the regression at spatial unit j and environmental variable i. β_{ij} represent the effect of environmental variable i on pond counts at the spatial unit j.

The proportion of total variance in pond counts that was explained by an environmental variable y_i at spatial unit j, ρ_{ij}, was calculated as:

$$\rho_{ij} = \mathrm{var}(\beta_{ij} y_{ij}) \Big/ \sigma_j^2 \tag{2}$$

where σ_j^2 is the variance in ln(pond frequency) at spatial unit j.

We used β_{ij} and ρ_{ij} from the three spatial resolutions to evaluate whether their ability to explain variation in pond counts was related to climate and landscape composition of an area, that is, if environmental variables had more explanatory power for pond counts dynamics in areas with particular characteristics. Specifically, we tested whether β_{ij} and ρ_{ij} varied systematically with mean values of four a priori selected variables: spring temperature (a weather variable potentially affected by climate change), proportion cropland (representing anthropogenic modification of the landscape), onset of spring (related to phenology), and integrated NDVI (measure of primary productivity).

Results

Large-scale spatial patterns in pond counts

Average pond counts during the study period were greatest in the north-eastern part of the study area, particularly near the border of Manitoba and Saskatchewan (Fig. 1). Greater proportions of cropland occurred in central and eastern portions of the Canadian and US prairies, respectively. All nine environmental variables showed strong spatial co-variation (Table 2), and an environmental gradient was apparent that extended along a southwest–northeast axis over the study region (Fig. 1).
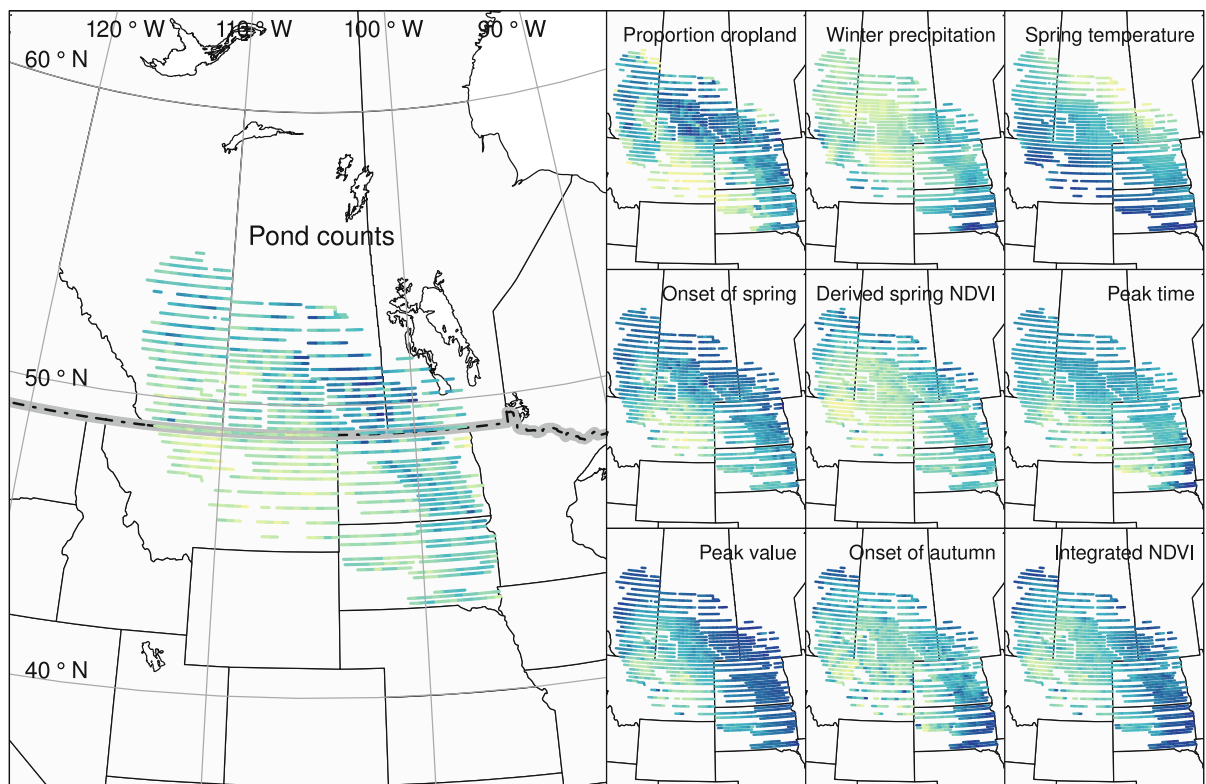
Fig. 1 Mean values of pond counts and nine environmental variables in the Prairie Pothole Region of North America, 1982–2001. *Yellow* are low values whereas *dark blue* represent high values. For explanation of the variables, see Table 1

Spatial variation in pond counts was positively related to proportion of cropland, onset of spring, derived spring NDVI, peak time, peak value, and integrated NDVI, while it was negatively related to spring temperature (all $P < 0.05$ at all spatial levels; Fig. 2). Pond counts were only weakly correlated with winter precipitation (Fig. 2), and not significant at transect level ($t = 1.22$, df $= 138$, $P = 0.224$) or stratum level ($t = 0.50$, df $= 22$, $P = 0.625$). Similarly, the relationship with onset of autumn was not significant at the stratum level ($t = 1.59$, df $= 22$, $P = 0.125$), but had a significant squared term at all levels (Fig. 2).

There was some evidence for non-linearity in relationships between ln-transformed pond counts and some environmental variables (onset of spring, derived spring NDVI and peak time, Fig. 2). All significant quadratic terms had negative sign (Fig. 2), indicating either that effects of environmental variables on pond counts flattened out at high values of environmental variables (e.g. onset of spring and peak time at the transect level; Fig. 2), or that highest pond counts were found in areas with intermediate levels

(e.g. derived spring NDVI and onset of autumn; Fig. 2).

Large-scale temporal dynamics in pond counts

Mean values for pond counts and environmental variables based on the entire study area varied widely over the study period (Fig. 3), with peak NDVI value, onset of autumn, and integrated NDVI having significant positive trends over the period (Table 2). Years with high spring temperature were associated with early onset of spring (Table 2). Moreover, seasons with high productivity tended to have later peak of NDVI values and onsets of autumn (Table 2). Annual values of proportion cropland and winter precipitation were not significantly correlated with the other environmental variables (Table 2).

Linear models confirmed that region-wide mean pond counts were positively related to onset of spring ($t = 2.41$, df $= 18$, $P = 0.027$), peak value ($t = 2.38$, df $= 18$, $P = 0.029$) and onset of autumn ($t = 2.12$, df $= 18$, $P = 0.048$), but not to other environmental

Table 2 Temporal (above the diagonal) and spatial (below the diagonal) correlations among pond counts and environmental variables, 1982 to 2001

	Pond counts	Prop. crop.	Winter prec.	Spring temp.	os	dn	pt	pv	oa	in
Year	0.443	−0.438	−0.140	−0.038	0.045	0.014	0.358	0.641*	0.539*	0.650*
Pond counts		−0.391	0.192	−0.366	0.487*	0.238	0.266	0.462*	0.439	0.378
Prop. crop.	0.506*		0.059	0.149	−0.279	−0.151	0.052	−0.205	−0.161	−0.088
Winter prec.	0.046	0.045		−0.299	0.239	0.169	−0.202	0.287	0.131	0.150
Spring temp.	−0.623*	−0.437*	0.278*		−0.717*	−0.255	−0.277	−0.257	−0.240	0.003
os	0.575*	0.684*	0.049	−0.791*		0.572*	0.344	0.320	0.402	0.088
dn	0.367*	0.246*	0.446*	−0.534*	0.730*		0.125	0.064	0.256	0.145
pt	0.404*	0.585*	0.193*	−0.463*	0.643*	0.469*		0.374	0.810*	0.611*
pv	0.563*	0.501*	0.488*	−0.569*	0.776*	0.883*	0.579*		0.723*	0.813*
oa	0.128	0.075	0.687*	−0.038	0.275*	0.675*	0.596*	0.637*		0.900*
in	0.303*	0.191*	0.721*	−0.192*	0.423*	0.814*	0.515*	0.857*	0.909*	

Temporal correlations are based yearly values averaged over all segments, $N = 20$ years. Spatial correlations are based on variables averaged over all years at the transect level, $N = 140$ transects. For variable abbreviations, see Table 1
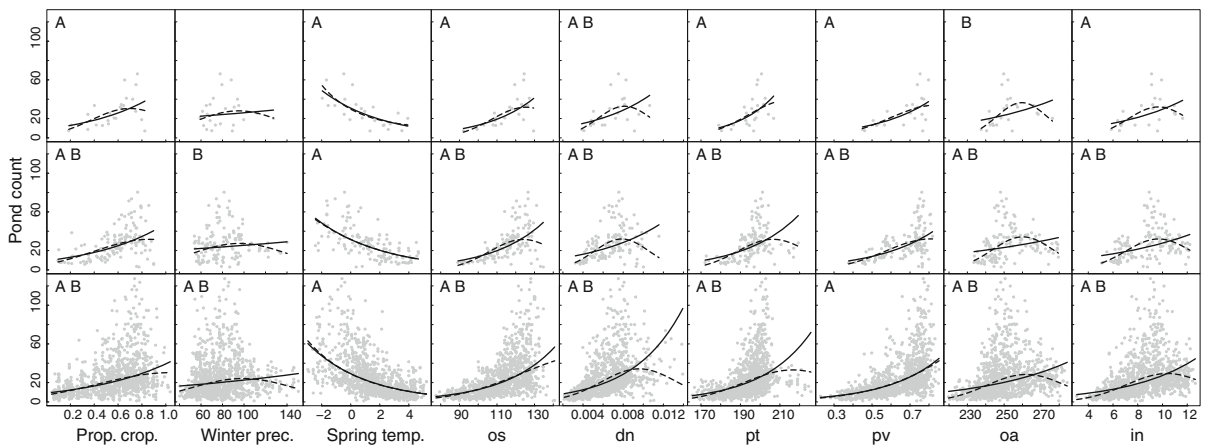
* $P < 0.05$

Fig. 2 Relationships between mean pond counts and mean values of nine environmental variables at three spatial levels, 1982–2001. The *upper panel* gives the relationship at the stratum level, the *mid panel* at the transect level, and the *lower panel* at the segment level. *Solid lines* show the predicted relationship from a log-linear model (A indicates significant log-linear relationship, $P < 0.05$), while *dashed lines* give predicted relationship for a log-linear model with a quadratic term (B indicates that the quadratic term was significant, $P < 0.05$), with ln-transformed pond counts all models. Variables' abbreviations are given in Table 1

variables (all $P > 0.078$, Fig. 4). Only derived spring NDVI was significantly related to annual mean pond counts in a non-linear way (squared term: $t = −2.28$, df = 17, $P = 0.036$, all other $P > 0.159$; Fig. 4). The relationship suggested that highest pond counts occurred in years with intermediate values of derived spring NDVI (Fig. 4).

Relationships between pond dynamics and landscape characteristics

Stratum-based models indicated that annual pond counts were positively associated with integrated NDVI, derived spring NDVI, onset of spring, onset of autumn, peak value, and winter precipitation, and
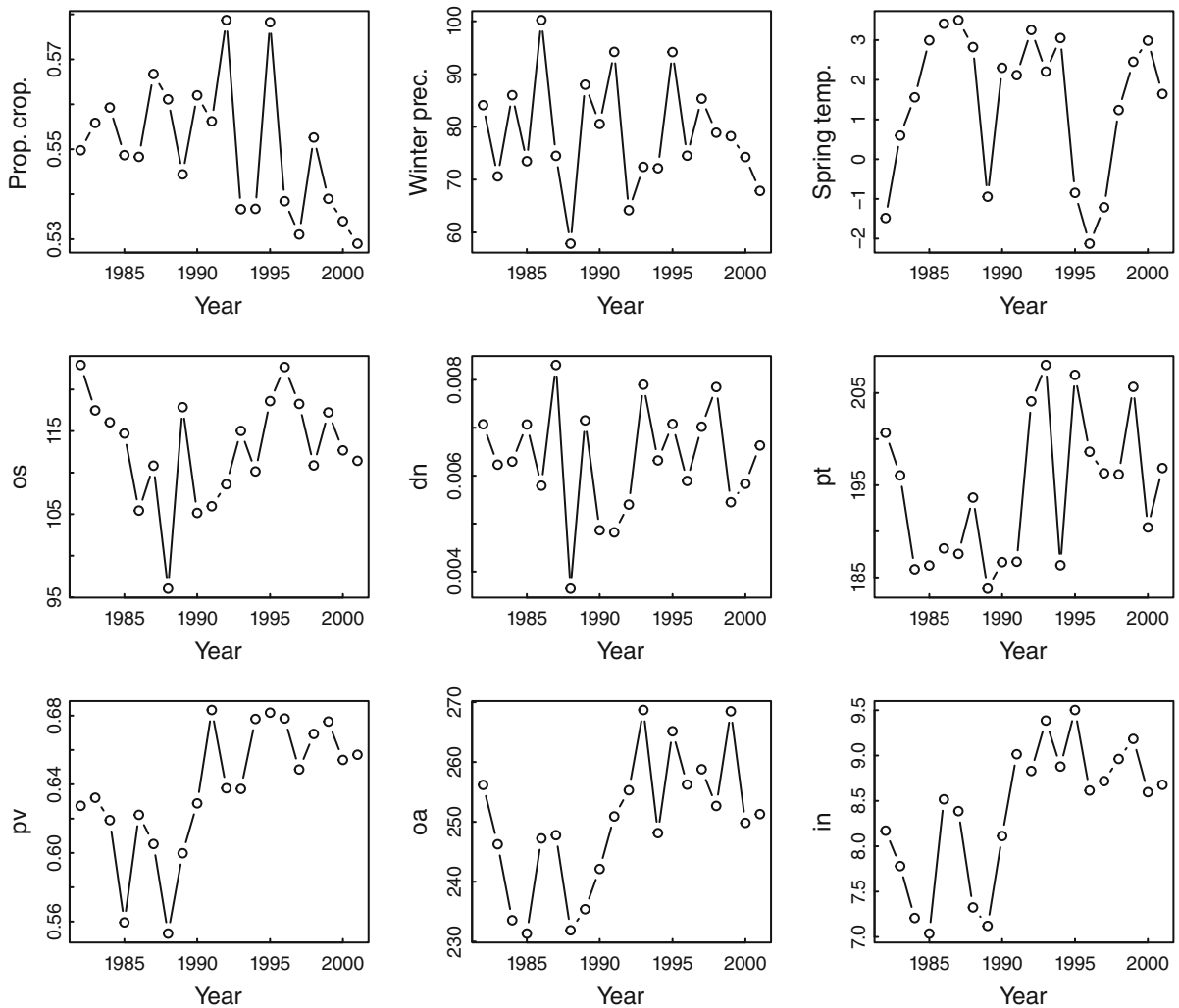
Fig. 3 Temporal variation in pond counts and environmental variables averaged over all segments in the study area, 1982–2001. For variables' abbreviations, see Table 1

negatively associated to spring temperature. Estimated β values for these environmental variables were consistent with respect on signs of the β values across all strata (Table 3). In quadratic models, the quadratic terms tended to be equally distributed with respect on sign (Table 3), suggesting little evidence for non-linear relationships between pond counts and most environmental conditions. However, spring temperature had a high proportion (79 %) of positive quadratic terms, and winter precipitation had negative quadratic terms at 84 % of the strata. Transect- and segment-specific models supported results from the stratum-level models (Table 3).

The amount of variance in pond counts explained by environmental variables at each spatial unit, ρ_{ij}, was highest at the stratum level, somewhat lower at the transect level, and considerably lower at the segment level (Table 3). The NDVI-variables related to environmental phenology had highest mean ρ_{ij} values. Among linear models, highest mean ρ_{ij} was obtained by onset of spring (mean = 0.189) and onset of autumn (mean = 0.187) at the stratum level. The quadratic regressions had somewhat higher ρ_{ij}, and also here onset of autumn and onset of spring were the environmental variables explaining highest amounts of variation in pond counts (Table 3).
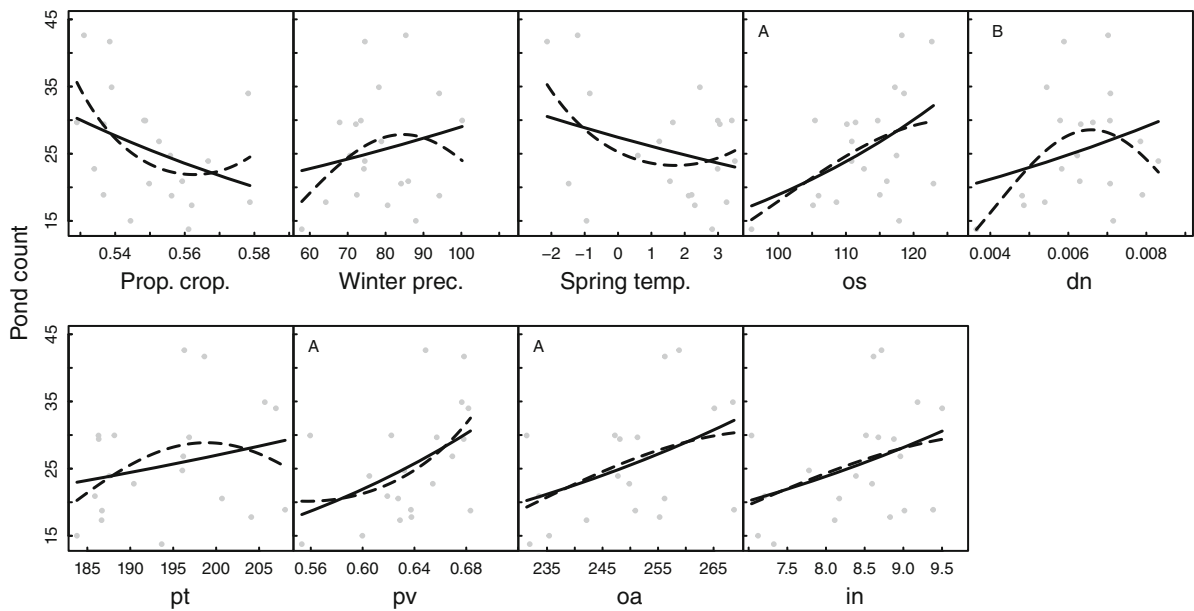
Fig. 4 Relationships between annual mean measures of pond counts and nine environmental variables, averaged over the entire study area, 1982–2001. *Solid lines* show the predicted relationship from a log-linear model (*A* indicates significant log-linear relationship, $P < 0.05$), while *dashed lines* give predicted relationship for a log-linear model with a quadratic term (*B* indicates that the quadratic term was significant, $P < 0.05$). Pond counts were ln-transformed in all models. Variables' abbreviations are given in Table 1

Landscape characteristics and effects of environmental conditions on pond counts

The landscape influence on the ability of environmental variables to predict variation in pond counts (ρ_{ij}) did not differ qualitatively between the three spatial scales. The finer scales had larger noise around the fitted lines, but also more power to detect non-linear patterns. Still, the strength of the relationships did not differ considerably. We therefore present results only from the stratum level. The variation in pond counts explained by environmental variables (ρ_{ij}) was related to landscape characteristics as described by mean values of integrated NDVI, onset of spring, spring temperature, and proportion cropland (Fig. 5). In general, mean spring temperature had fewer significant relationships with ρ_{ij} than the other three landscape characteristics. Only ρ_{ij} from variables extracted from the annual NDVI-curves gave significant linear relationships with the landscape characteristics (Fig. 5). There was also evidence for non-linear patterns between ρ_{ij} and some of the landscape characteristics. In particular, highest ρ_{ij} for derived spring NDVI was found in areas with intermediate

values of mean onset of spring, and proportion cropland (Fig. 5). The other significant non-linear relationships indicated that the pattern levelled out at high or low values of the landscape characteristic (Fig. 5).

Discussion

Spatial heterogeneity in landscape characteristics promotes differences in the environmental effects on populations (Sæther et al. 2007), which can elicit differences in their properties, such as life history traits (Herfindal et al. 2006) or population dynamical processes (Miller 2000; Forcey et al. 2007; Sæther et al. 2008; Grøtan et al. 2009). Wetland abundance influences reproduction in several wildlife species (e.g. waterfowl; Johnson and Grier 1988; Rotella and Ratti 1992; Bethke and Nudds 1995; Krapu et al. 1997; Drever 2006; Drever et al. 2007). We confirmed that spatial and temporal variation in pond counts ('pond dynamics') on the North-American prairies can be explained by environmental variables related to weather, phenology, and agricultural practices, where

Table 3 Summary statistics for proportion of variance in pond counts explained of environmental variable i at spatial unit j (ρ_{ij}; $\bar{\rho}$ = mean value) and parameter values (β; $\bar{\beta}$ = mean value) for models of annual dynamics of pond counts, at the three spatial levels

| Environmental variable	Statistic	Log-linear			Squared log-linear		
		Stratum	Transect	Segment	Stratum	Transect	Segment
Prop. crop.	$\bar{\rho}$	0.094	0.123	0.104	0.159	0.214	0.183
	Proportion $\beta > 0$	0.250	0.257	0.421	0.625	0.564	0.545
	$\bar{\beta}$	−7.229	−7.621	−1.913	430.0	291.5	−75.86
Winter prec.	$\bar{\rho}$	0.145	0.135	0.115	0.187	0.180	0.174
	Proportion $\beta > 0$	0.917	0.907	0.898	0.167	0.193	0.329
	$\bar{\beta}$	0.008	0.008	0.008	−0.0001	−0.0001	−0.0001
Spring temp.	$\bar{\rho}$	0.101	0.104	0.091	0.133	0.139	0.135
	Proportion $\beta > 0$	0.042	0.050	0.133	0.792	0.743	0.657
	$\bar{\beta}$	−0.065	−0.073	−0.074	0.018	0.017	0.016
os	$\bar{\rho}$	0.189	0.180	0.133	0.234	0.231	0.183
	Proportion $\beta > 0$	0.917	0.907	0.856	0.458	0.400	0.427
	$\bar{\beta}$	0.023	0.023	0.016	−0.00007	−0.00004	−0.00008
dn	$\bar{\rho}$	0.156	0.147	0.121	0.211	0.206	0.185
	Proportion $\beta > 0$	0.958	0.950	0.856	0.333	0.357	0.401
	$\bar{\beta}$	93.18	93.60	74.43	−12192	−9402	−4411
pt	$\bar{\rho}$	0.131	0.110	0.094	0.230	0.194	0.160
	Proportion $\beta > 0$	0.625	0.721	0.636	0.417	0.357	0.380
	$\bar{\beta}$	0.012	0.010	0.007	−0.0007	−0.0005	−0.0003
pv	$\bar{\rho}$	0.151	0.152	0.116	0.240	0.208	0.174
	Proportion $\beta > 0$	0.875	0.879	0.813	0.625	0.564	0.477
	$\bar{\beta}$	4.188	4.076	2.869	5.598	8.772	−3.757
oa	$\bar{\rho}$	0.187	0.157	0.116	0.240	0.208	0.174
	Proportion $\beta > 0$	0.917	0.879	0.800	0.500	0.450	0.458
	$\bar{\beta}$	0.015	0.014	0.010	0.0001	0.00002	−0.0001
in	$\bar{\rho}$	0.137	0.124	0.103	0.185	0.176	0.166
	Proportion $\beta > 0$	0.875	0.843	0.802	0.583	0.400	0.459
	$\bar{\beta}$	0.159	0.154	0.120	−0.006	−0.014	−0.017

For variables abbreviation, see Table 1

phenology-related variables obtained from satellite-derived NDVI data had the highest explanatory power. More importantly, we showed large spatial variation in the extent to which these environmental variables explained pond dynamics. This variation in predictability of wetland dynamics was linked to landscape characteristics, which allowed us to describe the types of landscapes for which we can expect more precise predictions on population consequences of environmental change. These landscapes had greater productivity (high integrated NDVI values), later onset of spring, and higher proportions of cropland. Consequently, we were able to identify variables that best

explained temporal variation in wetland abundance, and to pinpoint areas where we can best predict wetland abundance in relation to environmental changes.

Variables intended to index environmental phenology based on satellite-derived data can be confounded with changes in vegetation that result from agricultural practices (Walker and Mallawaarachchi 1998; Pouliot et al. 2009). For example, ploughing can influence the estimation of onset of spring, whereas estimates of onset of autumn can be affected by harvesting. Indeed a shift occurred over the study period from summer-fallow to continuous cropping over much of the Prairie

Fig. 5 Relationships between the ability of environmental variables to explain variation in pond frequency (ρ) and mean environmental values within units at the stratum level. *Solid lines* give the predicted linear relationships between response (square root of ρ) and mean values for environmental variables, where *A* indicates that the slope had $P < 0.05$. *Dashed lines* give the predicted quadratic relationship, and *B* indicates that the quadratic term had $P < 0.05$. For Variables' abbreviations, see Table 1
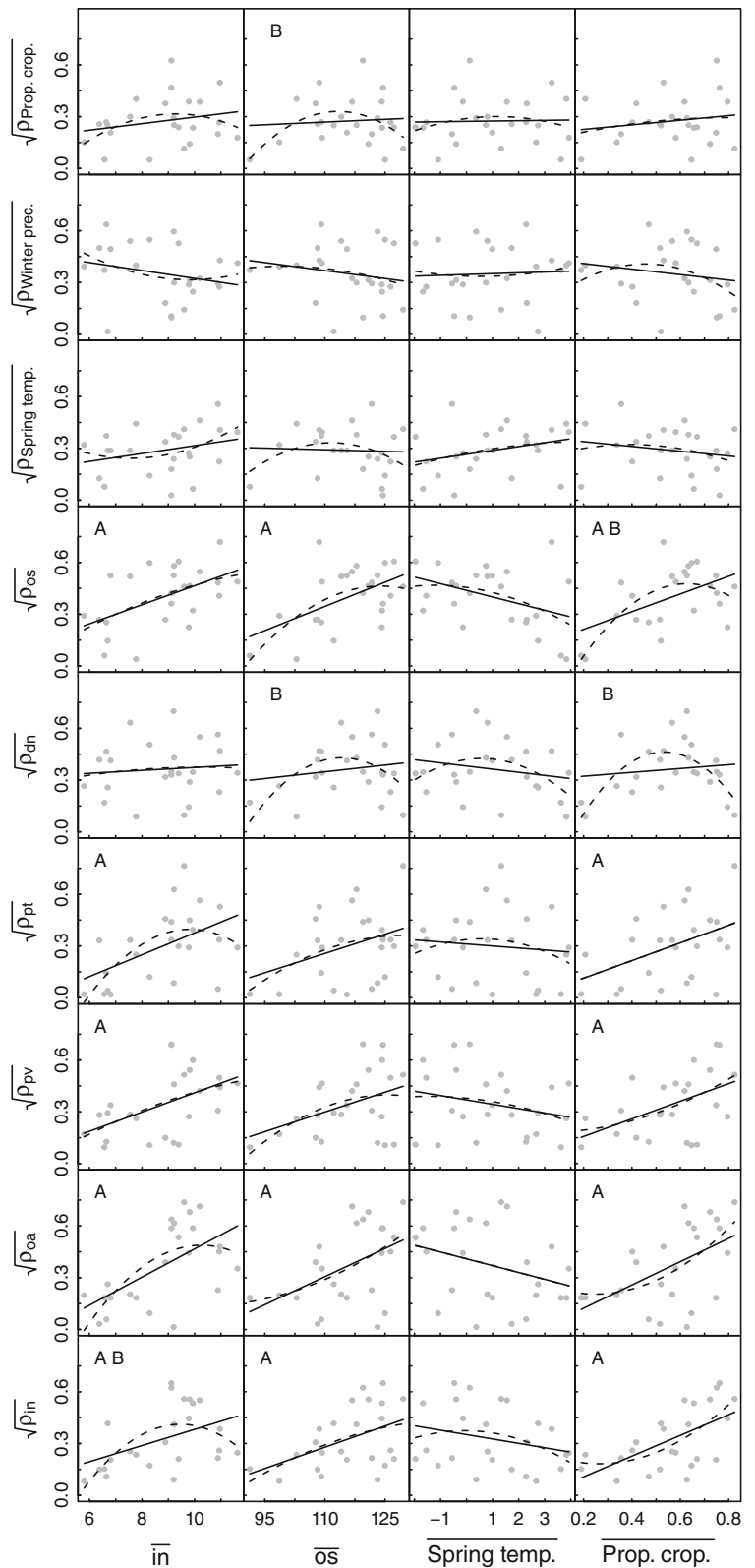
Pothole Region (Podruzny et al. 2002), indicating an increase in the frequency of ploughing. We found a close spatial relationship between proportion of cropland and NDVI-derived values of onset of spring, and times of peak values (Table 2). However, we believe these correlations likely reflect the historical agricultural encroachment that occurred predominantly on the most productive parts of the region (Bethke and Nudds 1995), rather than reflecting contemporary processes. First, the temporal relationships between proportion cropland and environmental conditions were much weaker than the spatial covariation (Table 2). Second, whereas the spatial relationships between pond counts and onset of spring and agricultural areas were both positive (Fig. 2), the analogous temporal relationship was positive only for onset of spring, and was negative with proportion cropland (Fig. 4). Similar contrasting spatial and temporal effects on pond counts were present among proportion cropland and several environmental variables. It is therefore apparent that the relationship between temporal dynamics in pond counts and environmental variables is not solely related to temporal changes in agricultural practices, but reflects annual variation in environmental conditions that will also influence wetland availability and wildlife populations.

The proportion of variation explained (ρ_{ij}) is a ratio between the strength of the relationship between pond counts and environmental variables and the overall variance in pond counts at spatial unit j (σ_j^2) (Eq. 2). The observed positive relationships between ρ_{ij} and mean values for environmental variables (Fig. 5) may have thus resulted either from stronger relationships between pond counts and environmental variables, or from differences in σ_j^2. Moreover, the heterogeneity of a landscape can influence how precisely we can estimate variation in pond counts explained by environmental variables. For example, in homogenous landscapes the influence of an environmental condition can be similar in all locations, which makes a more homogenous response to temporal variation in the environment. Analyses of these factors at the stratum level (see Appendix I in Electronic Supplementary Material) suggested that the variance in pond counts was positively related to mean values of integrated NDVI, onset of spring, and proportion of cropland, and negatively related to mean spring

temperature. However, the heterogeneity of environmental conditions within a stratum, as measured by spatial scaling of environmental conditions, was not related to ρ_{ij}. Instead, spatial scaling of pond dynamics within a stratum was positively related to the ability of environmental variables to explain temporal variation in pond counts. Consequently, strata with a high variance in pond counts also had the highest amounts of variation explained by environmental variables, and were more homogenous with respect on the spatial variation in pond counts (Appendix I in Electronic Supplementary Material).

The timing of May Waterfowl Breeding Population and Habitat Survey is meant to overlap primarily with the breeding season of Mallard (*Anas platyrhynchos*), a duck species that nests early in the season, and thus the relationship between environmental variables and pond counts could vary among areas and years due to differing phenological changes in pond type and availability. Pond counts are comprised of both permanent (permanent ponds over the season) and seasonal or semi-permanent (ponds that dry out during late summer) ponds, and therefore some of the patterns we observed may be partly explained by interactions between pond counts, pond hydroperiod, precipitation, and timing of spring. For example, in late wet springs, pond counts may be comprised of higher proportions of seasonal ponds relative to early springs when some temporary ponds have dried by the time the survey takes place. In such springs, ponds of different types may coalesce into single entities, resulting in a nonlinear 'hump-shaped' relationship between pond counts and precipitation (Fig. 2). Numbers of semi-permanent and seasonal ponds are strongly correlated ($r = 0.75$; Niemuth et al. 2010), which suggests that pond counts early in spring provide good estimates for the wetland abundance later in summer. Further, we found similar relationships between pond counts and timing of both spring and autumn (Table 3), suggesting the overall relationships are robust relative to interannual differences that may result from the timing of the survey. Untangling such correlations among pond counts and climate variables may require detailed hydrological studies conducted at local scales (Conly and van der Kamp 2001).

Landscape characteristics and the ability to predict pond counts

The fraction of variation in pond counts explained by environmental variables varied between <0.001 and 0.584 at stratum, and <0.001 and 0.684 at transect scales. This spatial heterogeneity in the relationship between pond counts and environmental conditions complicates estimation of effects of environmental conditions on population growth rates (Sæther et al. 2008), because the signal between environmental conditions and population responses will also differ spatially. We were able to relate the predictability of pond counts (ρ) to specific landscape characteristics, where ρ of several variables were positively related to mean values of onset of spring, primary productivity, and proportion of cropland (Fig. 5). The high predictive value of variables based on NDVI likely resulted because the spatial resolution of these data is fine enough to capture the heterogeneity of the landscape, and provides insight into the complex mechanisms that generate spatio-temporal dynamics in pond counts. For example, considering onset of spring, one of the best predictors of pond counts at all spatial scales (Table 3), areas with a late onset of spring had higher mean pond counts than areas with early onset of spring (Fig. 4), greater variation in pond counts (Fig. A1 in Electronic Supplementary Material), and higher proportions of explained variation (Fig. 5), compared to areas with an earlier onset of spring. Further, pond counts in areas with late onset of spring also had greater spatial scaling, suggesting that ponds vary in greater synchrony over larger distances (Fig. A3 in Electronic Supplementary Material). Accordingly, onset of spring influences both the spatial and temporal variation in pond counts, in addition to explaining spatial variation in how wetland dynamics are related to environmental conditions.

A strong connection thus exists between the mean and variance of pond counts and the effect of the environmental conditions, and in particular environmental conditions described by the NDVI-variables. Sites with higher mean pond counts were also more inherently variable and had a stronger environmental influence than sites with low mean pond counts. In particular, we found that areas with a late onset of spring, high primary productivity and high proportion cropland had higher annual variation in both environmental conditions and pond counts than areas with earlier onset of spring, lower primary productivity and less agricultural land. These differences are likely caused by the underlying geomorphology that determines the ability of basins to retain water and their relationship to agriculture. Flat areas are expected to contain more shallow basins that dry out more often due to evapo-transpiration (Euliss et al. 2004), and thus be under tighter environmental control, as well as be more amenable to ploughing. Further, productivity of prairie wetlands is linked to their temporal variability because the periodic drawdown of wetlands allows oxidation of sediments and release of nutrients once wetlands are re-flooded (Euliss et al. 1999). This link between productivity and temporal variability has been identified as a vital component of wetland ecosystems that allows high population abundance and diversity of species (Nudds et al. 2000; Euliss et al. 2004), and understanding the processes that maintain this link will be key to effective conservation.

Spatial scales of variation in pond counts

When exploring ecological relationships, it is important to consider the spatial scale of the processes (Wiens 1989; Levin 1992; Donaldson and Nisbet 1999). Data on pond counts were collected at a rather fine scale (the segment level), and aggregated into larger units (transects and stratum). Aggregation introduces the risk of losing information about heterogeneity in the landscape (Wiens 1989). However, relationships between pond counts and environmental conditions were remarkably consistent over all three spatial scales, such that even the coarsest scale, the stratum level, captured the landscape heterogeneity that shapes differences in wetland dynamics within the prairie system. Further, we found greater variability and noise around predicted relationships at the finer scales (Fig. 2), which also suggest that coarser scales could be used when making predictions on environmental and management influences on landscapes or populations. For waterfowl in the North American prairies, the strata level represented by geopolitical boundaries may appropriately capture differences among populations generated by heterogeneity in the landscape.

Implications for predictions of climate change on wetland ecosystems

Prairie wetlands are highly vulnerable to projected climate warming (Johnson et al. 2005, 2010), and the

strong negative correlations between pond counts and spring temperature, as well as the positive association between pond counts and winter precipitation (Fig. 2), support the concern for wildlife populations depending on these wetlands. Further, climate change may also result in mismatches between timing of breeding and emergence of food resources (Visser et al. 2004). We found that late springs tend to have high primary productivity and high pond counts. Early springs can thus be expected to have low May pond counts, and these habitat-related effects may exacerbate or even overshadow effects of increased temperatures and altered phenology on populations (Drever and Clark 2007; Pearce-Higgins et al. 2009). Further, the links between these variables vary across the landscape, which makes it difficult to make predictions on a general basis. We also showed how environmental variables and landscape characteristics based on NDVI obtained from satellite images can provide an important source of data for modelling effects of environmental variation on wetland abundance. Although NDVI was developed primarily as an index of terrestrial conditions, it appears to hold promise for understanding variability in wetland ecosystems. We anticipate that it will similarly prove important for predicting how wetland-dependent wildlife populations respond to environmental change.

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