

# Time-lagged variation in pond density and primary productivity affects duck nest survival in the Prairie Pothole Region

JOHANN WALKER,<sup>1,4</sup> JAY J. ROTELLA,<sup>2</sup> SCOTT E. STEPHENS,<sup>1,5</sup> MARK S. LINDBERG,<sup>3</sup> JAMES K. RINGELMAN,<sup>1</sup>  
CHRISTINE HUNTER,<sup>3</sup> AND AARON J. SMITH<sup>1,6</sup>

<sup>1</sup>Great Plains Regional Office, Ducks Unlimited, 2525 River Road, Bismarck, North Dakota 58503-9011 USA

<sup>2</sup>Department of Ecology, Montana State University, Bozeman, Montana 59717 USA

<sup>3</sup>Department of Biology and Wildlife and Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska 99775 USA

**Abstract.** The Prairie Pothole Region (PPR) is the primary breeding region for most species of North American dabbling ducks (*Anas* spp.). Conservation of these species is guided in part by knowledge of relationships between nest survival probability and habitat features. Positive relationships between duck nest survival and amount and configuration of herbaceous perennial vegetation have been observed in previous studies, but these 2- to 4-year studies might not have adequately characterized the temporal effect of wet–dry episodes on nest survival. Over an eight-year period, we studied nest survival of five species of ducks in the PPR relative to spatial and temporal variation in pond density, primary productivity, and hydrologic status of wetlands, soil, and vegetation on 52 study sites selected to span a gradient of spatial variation in proportion of herbaceous perennial vegetation and in number of wetland basins. We observed the fate of 12 754 nests. Consistent with past studies, 90% of nests that failed to hatch were destroyed by predators. Nest survival probability was positively related to current-year pond density and primary productivity, negatively related to pond density and primary productivity during the previous two years, and positively related to the number of wetland basins on the study site. Predicted relationships between nest survival and proportion or configuration of herbaceous perennial vegetation in the surrounding landscape were not supported. For mallard (*Anas platyrhynchos*), median estimated nest survival probability ranged from 0.02 (SE = 0.01) to 0.22 (SE = 0.02). Estimated nest survival was greatest on sites with numerous wetland basins that had transitioned from dry, unproductive conditions to wet, productive conditions in the previous 1–2 years. Our results were consistent with time-lagged responses of food webs to resource pulses in a broad array of ecosystems. Our study highlighted the importance of wetland basins and wet–dry episodes to duck nest survival in the PPR. Current habitat conservation efforts focus on landscapes with numerous wetland basins and a high proportion of herbaceous perennial vegetation. Our results suggest that future conservation efforts should focus on preserving high-density wetland complexes across as large a geographic extent as possible even in cropland-dominated landscapes.

**Key words:** agricultural landscapes; Anatidae; conservation planning; demographic rates; nest success; predator–prey; resource pulses.

## INTRODUCTION

The Prairie Pothole Region (PPR) encompasses 770 000 km<sup>2</sup> of the north-central United States and south-central Canada and provides breeding habitat for an estimated population of 15.8 million (range: 9.3 million–24.2 million) upland-nesting dabbling ducks (*Anas* spp.; Zimpfer et al. 2009). Landscapes of the PPR are characterized by variable densities of glacially formed depressional wetland basins distributed through-

out a mosaic of privately owned agricultural land managed for production of annual crops, livestock, and livestock forage (van der Valk 1989, Johnson et al. 1994). The defining feature of the PPR climate is episodes of wetness and drought that typically last from 2 to 10 years, and these episodes can be associated with two- to eightfold changes in precipitation, drought indices, and number of wetland basins containing ponded water as the environment transitions between wet and dry states (Shapley et al. 2005, Millett et al. 2009, Zimpfer et al. 2009). The PPR is becoming warmer and wetter (Millett et al. 2009), and the frequency and intensity of wet–dry episodes is projected to increase during the next century (Johnson et al. 2010). In this dynamic agricultural environment, millions of dollars are expended annually to conserve productive wetland and grassland habitat for breeding ducks and thereby assure their sustained abundance, and guidance for these

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<sup>4</sup> E-mail: jwalker@ducks.org

<sup>5</sup> Present address: National Headquarters, Ducks Unlimited Canada, Stonewall, Manitoba R0C 2Z0 Canada.

<sup>6</sup> Present address: Equinox Analytics, P.O. Box 2479, Bismarck, North Dakota 58502-2479 USA.

efforts is provided by knowledge of relationships between demographic rates and environmental variables describing habitat quality (Prairie Pothole Joint Venture 2005, Prairie Habitat Joint Venture 2008).

Parameters associated with reproductive success, particularly nest survival probability, determine the growth rate of duck populations in the PPR across species representing a range of variation in life-history traits (Hoekman et al. 2002, Koons et al. 2006), and thus relationships between nest survival and habitat quality provide insight into population dynamics and a basis for conservation efforts. Nest survival is highly variable in space and time. Analysis of data from nest survival studies across the PPR during 1937–2000 showed that nest survival averaged 0.21 but varied from less than 0.01 to greater than 0.80 among sites and years (Drever et al. 2004). Some of the among-site variation in nest survival of ducks in the PPR is related to spatial variation in agricultural intensity at landscape scales. For example, studies conducted on multiple sites for 2–4 years have shown that nest survival is negatively related to the amount of cropland in the surrounding 26.8 km<sup>2</sup> (Greenwood et al. 1995) and positively related to the amount of herbaceous perennial vegetation in the surrounding 10.4 km<sup>2</sup> (Reynolds et al. 2001), 40.1 km<sup>2</sup> (Horn et al. 2005), and 41.4 km<sup>2</sup> (Garrettson and Rohwer 2001, Stephens et al. 2005). Most nest failures are caused by predators (Sargeant et al. 1993, Pieren and Rohwer 2010), thus observations of increased probability of nest destruction in intensively cropped landscapes are thought to result from functional and numerical responses of nest predators to the effects of agricultural intensification (Phillips et al. 2003, Horn et al. 2005, Stephens et al. 2005).

The current understanding of nest survival of ducks in the PPR relative to landscape-level spatial variation in agricultural intensity has been formed from relatively short-term studies. Within a landscape, however, temporal variation in nest survival probability can be substantial. For example, nest survival ranged from 0.05 to 0.30 within a single study site during one 16-year investigation (Higgins et al. 1992), and variation in nest survival among years exceeded variation among sites in a 4-year study of 17 sites (Greenwood et al. 1995). In the PPR, temporal variation in precipitation can result in substantial pulses of productivity within landscapes particularly during transitions from dry to wet conditions (Lynch 1984, Murkin et al. 1997, Euliss et al. 2004). Pulsed variation in productivity has been shown to have substantial effects on food webs across a broad array of taxa and ecosystems (Sears et al. 2004, Yang et al. 2010). Transitions from dry to wet (or wet to dry) conditions in the PPR may indirectly affect behavior, abundance, and community composition of nest predators and induce time-lagged variation in nest survival regardless of agricultural intensity. Longer-term multi-site studies of nest survival that facilitate investigation of more complicated spatial and temporal patterns (Ste-

phens et al. 2005, Gunderson et al. 2007) are needed to expand knowledge of reproductive success of birds in agricultural landscapes and support improved conservation planning for breeding ducks in the dynamic environment of the PPR.

To evaluate the potential effects of wet–dry episodes and agricultural intensity on duck nest survival at a broad spatial and temporal scale, we conducted an 8-year research project on 52 sites in the PPR of North and South Dakota, USA. The main objective of our study was to assess support for predictions about relationships between nest survival and covariates describing landscape-level spatial and temporal variation in pond density (i.e., number of wetland basins containing ponded water), primary productivity, and wetness (i.e., hydrologic status of soil, vegetation, and wetlands) across a range of spatial variation in the amount of herbaceous perennial vegetation, amount of edge between cropland and herbaceous perennial vegetation, and number of wetland basins.

## METHODS

### *Study area*

We studied nest survival of Blue-winged Teal (*Anas discors*), Gadwall (*A. strepera*), Mallard, Northern Pintail (*A. acuta*), and Northern Shoveler (*A. clypeata*) in the PPR of North and South Dakota, USA, during 2002–2009. The study area was centered approximately 12 km west of Turtle Lake, North Dakota, at 101°02'40" W, 47°31'35" N (Fig. 1). Our study sites were not part of the United States Fish and Wildlife Service Four Square Mile Survey of breeding duck pairs (Reynolds et al. 2006). Upland land cover and land use across the study area was a mosaic of agricultural land composed primarily of cultivated cropland used to produce small grains and row crops (57%) and herbaceous perennial vegetation used for livestock forage (34%). The remaining 9% of the land area comprised idled perennial vegetation retired from crop production and enrolled in the United States Department of Agriculture Conservation Reserve Program (7%) and farmyards, farmsteads, and associated planted nonnative tree cover (2%; U.S. Fish and Wildlife Service, unpublished data). Density of wetland basins averaged 13 basins/km<sup>2</sup> (range: 1–195 basins/km<sup>2</sup>; U.S. Fish and Wildlife Service 2010). Grassland and wetland loss averaged 0.4% per year and 0.025% per year, respectively, during the study period (Stephens et al. 2008; U.S. Fish and Wildlife Service, unpublished data). In the climate zone nearest the center of our study area (North Dakota Climate Zone 5), average temperature during our study varied from –16°C to –4°C in January, 3°C to 9°C in April, and 18°C to 23°C in July, annual precipitation averaged 450 mm (range: 313 mm–565 mm), and the June Palmer Hydrologic Drought Index ranged from –2.29 (moderate drought) in 2002 to 3.82 (very moist) in 2009 (all data from the National Oceanic and Atmospheric

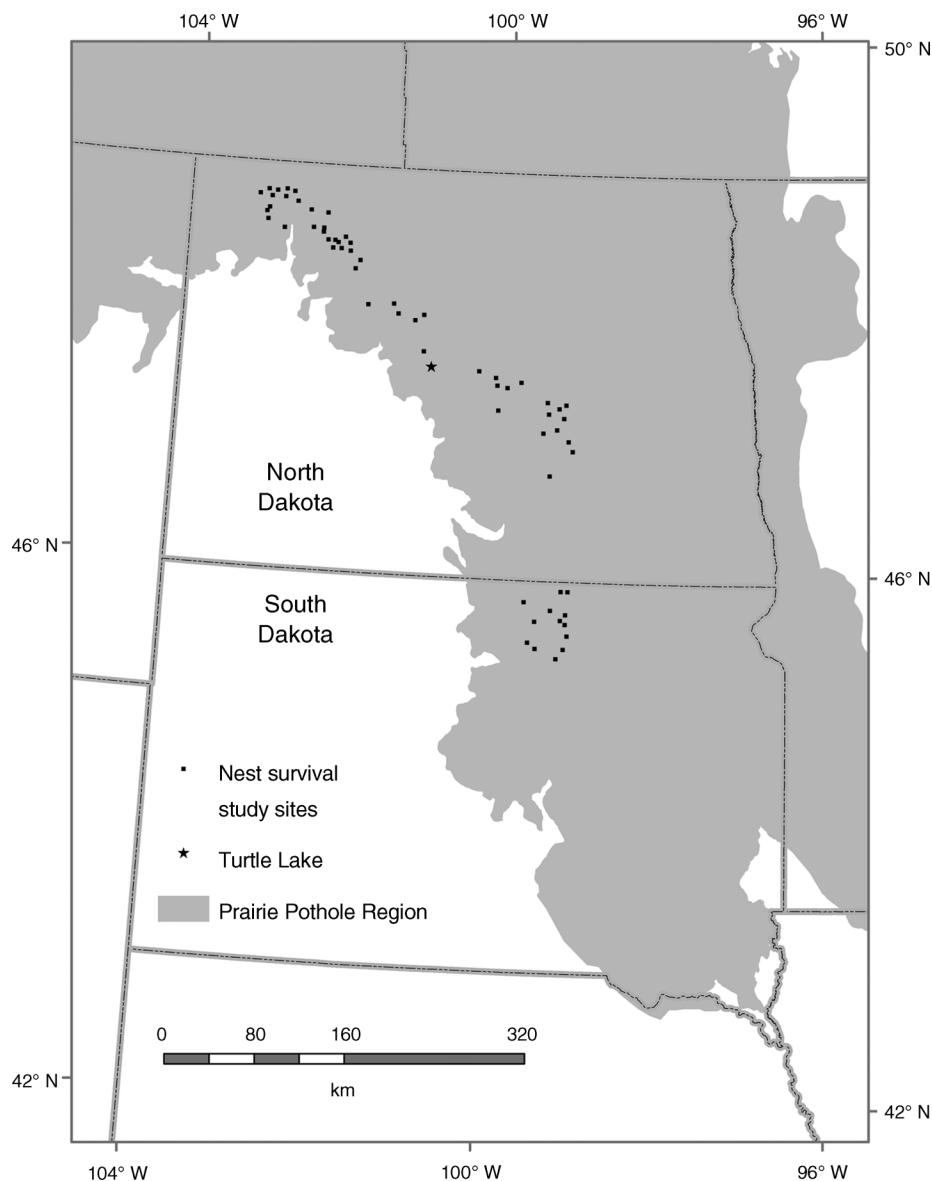


FIG. 1. Location and extent of the Prairie Pothole Region in North and South Dakota, USA, and locations of study sites used for investigation of nest survival relative to spatial and temporal variation in landscape-level habitat covariates. The geographic center of the study area was located 12 km west of Turtle Lake, North Dakota.

Administration National Climate Data Center).<sup>7</sup> May pond numbers across the PPR of North and South Dakota ranged from 797 755 in 2005 to 1 832 145 in 2009 (Zimpfer et al. 2009).

#### Data collection

We collected nest data on a sample of 10.4-km<sup>2</sup> sites selected according to (1) the proportion of herbaceous perennial vegetation in a 41.4-km<sup>2</sup> area including and immediately surrounding the site and (2) the number of wetland basins on the site (Stephens et al. 2005).

<sup>7</sup> <http://www.ncdc.noaa.gov>

Heterogeneity in agricultural intensity in the PPR at landscape scales is well indexed by the proportion of upland habitat composed of herbaceous perennial vegetation (Reynolds et al. 2001, Stephens et al. 2005) or its near complement (proportion of cropland [Greenwood et al. 1995]), and the number of breeding pairs in a given landscape is positively related to the number of wetlands (Cowardin et al. 1995). Selection criteria for candidate sites were calculated using U.S. Fish and Wildlife Service classified land cover (U.S. Fish and Wildlife Service, unpublished data), National Wetlands Inventory (NWI) data (U.S. Fish and Wildlife Service 2010), and the Spatial Analyst extension in

ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, California, USA). Sites were then randomly selected from the pool of potential sites with the objective of maintaining a sample of 9–27 sites during every year of the study while adding new sites as needed to compensate for sites that were dropped from the sample due to variation in funding and access to privately owned lands. To prevent overlap, site centroids were required to be at least 3.2 km apart.

All-terrain vehicles and chain-drag techniques (Klett et al. 1986) were used to locate duck nests. Nest searches were conducted from 07:00 to 14:00 during late April through early July (Klett et al. 1986, Gloutney et al. 1993). On each site, 3.3–5.2 km<sup>2</sup> representing 35–100% of total grassland area was completely searched for nests at least three times in each year that the site was included in the study. Cultivated land was not searched.

When a nest was found, we recorded date, species, number of eggs, and nest age. Nest age was determined by candling several eggs from each nest (Weller 1956). The geographic coordinates of the nest were recorded with a handheld global positioning systems receiver and nests were marked by a fiberglass rod (1 × 100 cm) placed in the ground approximately 5 m north of the nest. Marked nests were then revisited approximately every 5–7 days until the eggs either hatched, were destroyed by a predator, were abandoned by the nesting female, or the nest failed for unknown reasons (Klett et al. 1986). Nest status (active or failed), number of days of incubation, and apparent cause of failure (given failure) were recorded at each visit. Following standard practice in nesting studies, any nest that was abandoned by its attending female between the time when we discovered the nest and our next visit to the nest was excluded from analysis because of concerns that investigator activity may have caused the abandonment (Klett et al. 1986).

#### *Calculation of covariates and sample statistics*

Site- and year-specific pond density indices were derived from May pond counts taken from the FWS cooperative breeding pair and habitat survey (Smith 1995) within the study area. Segment-level (~4.45 km<sup>2</sup>) pond counts were downloaded from the USFWS Division of Migratory Bird Management Migratory Bird Data Center. Using ArcGIS 9.3, the pond count value for each segment was assigned to a point location at the center of each linear transect segment. These point locations were used to model an inverse-distance-weighted spatial interpolation surface of average pond density in May for each year (Podruzny et al. 2002). A site- and year-specific pond density covariate (hereafter pond density) was then assigned by intersecting the site centroid with the interpolated year-specific pond density index layer. Thus, pond density represented a site- and year-specific index of the density of wetland basins and other depressions containing ponded water in May.

Site- and year-specific values of covariates describing primary productivity and wetness were derived from National Aeronautics and Space Administration's moderate resolution imaging spectrometer (MODIS) sensors housed on the Terra and Aqua satellites. All MODIS data sets were obtained from the USGS Land Processes Distributed Active Archive Center (LP DAAC) data pool file transfer service.<sup>8</sup> Modeled gross primary productivity (GPP; MOD17A2 [Running et al. 2004]) data sets (1 km<sup>2</sup>) were downloaded for the MODIS sinusoidal grid tile (H11v04) covering all of the study sites. Twenty-three scenes were collected at 8-day intervals within the growing/nesting season (days 89–273 of the year, with 1 January = day 1) each year from 2000 to 2009. MODIS GPP was selected as the productivity covariate for use in the nest survival analysis based on its demonstrated relationship to primary productivity on the ground (Turner et al. 2005, 2006). The GPP value assigned to a study site in a specific year was the maximum GPP (hereafter primary productivity) observed during April–July on the 1-km<sup>2</sup> pixel nearest the center of the study site in the corresponding MODIS data set. In the nest survival analysis, each nest on a given site in a given year was therefore represented by a single value. ERDAS Imagine software (ERDAS, Norcross, Georgia, USA) was used to calculate the normalized difference water index (NDWI), which described combined surface water, soil moisture, and water content of vegetation (Gao 1996). Calculation of this index followed the same spatial and temporal coverage pattern as primary productivity. Site-year-level values of NDWI (hereafter wetness) were calculated as the sum of the NDWI measurements taken from the 0.5-km<sup>2</sup> MODIS pixel nearest the center of the study site during the April–July nesting season in a given year.

Covariates describing spatial variation in the amount and configuration of herbaceous perennial vegetation were calculated from a U.S. Fish and Wildlife Service land cover data set (30-m resolution; U.S. Fish and Wildlife Service, *unpublished data*). We used Definiens eCognition Developer v.7 software (Definiens Developer, Munich, Germany) to combine similar land cover pixels into patch-level objects. We then calculated the proportion of upland area composed of herbaceous perennial vegetation in the 41.4-km<sup>2</sup> landscape surrounding and centered on the study site (hereafter perennial cover) based on the sum of the area of patch-level objects classified as herbaceous perennial vegetation divided by the sum of the area of patch-level objects classified as upland. We calculated the amount of edge between cropland and herbaceous perennial vegetation on the study site (hereafter edge) as the sum of shared perimeter between patch-level objects classified as perennial vegetation and patch-level objects classified

<sup>8</sup> <https://lpdaac.usgs.gov/lpdaac>

as cropland. To develop a covariate describing spatial variation in the number of wetland basins on the study sites (hereafter basin count), we used ArcGIS to count all NWI wetland basins (U.S. Fish and Wildlife Service 2010) with centroids that fell within the boundaries of each site. Rules and spatial scales of measurement for basin count, edge, and perennial cover were chosen based on the results of a previous study of nest survival conducted on some of the same sites used in our study (Stephens et al. 2005).

Summary statistics for the nest sample and the covariates provided a basis for checking model assumptions, comparison to other studies, and model selection. We calculated the proportion of nests in the sample by species, the proportion of failed nests that were destroyed by predators, the proportion of failed nests that were abandoned between discovery and the first visit, and the effective sample size. Effective sample size (ESS) was calculated as the sum of (1) the number of days that nests were known to have survived and (2) the number of visit intervals that ended in failure (Rotella et al. 2004). ESS was used to calculate penalty terms for model selection criteria. To assess possible multicollinearity, we examined pair plots of correlations and estimated variance inflation factors (VIF) of the covariates with the AED package (Zuur et al. 2007) in R 2.10.0 (R Development Core Team 2010). To evaluate the range of variation in environmental conditions captured by our study design, we calculated the observed range of the environmental covariates among site and year combinations.

#### *Hypotheses and predictions*

Our multi-site, multi-year observational study design allowed us to effectively assess complicated patterns in nest survival over time across a broad cross-section of agricultural landscapes in the PPR. It also allowed us to make inferences at a useful scale for conservation planning. However, it did not allow us to fully identify causal mechanisms. Evidence from smaller-scale predator removal studies, however, indicates that a suite of mid-sized generalist mammalian predators, particularly red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), and striped skunk (*Mephitis mephitis*), is responsible for most duck nest failure in the PPR (reviewed in Pieron and Rohwer 2010). Our predictions about relationships between nest survival and our measured covariates were therefore based on hypothesized patterns of variation in nest survival of ducks given plausible functional and numerical responses of nest predators to (1) landscape-level spatial and temporal variation in pond density, primary productivity, and wetness and (2) landscape-level spatial variation in proportion of herbaceous perennial vegetation, amount of edge between herbaceous perennial vegetation and cropland, and number of wetland basins.

Survival rate of duck nests could be related to spatial and temporal variation in current-year pond density,

primary productivity, and wetness through functional responses of nest predators to variation in availability of preferred foraging sites and primary prey. We predicted that nest survival would be negatively related to current-year pond density and wetness based on results of past research on predator behavior, which indicated that wetlands are activity centers for nest predators (Kuehl and Clark 2002, Phillips et al. 2003). Because pond density was measured in May and wetness was measured across the nesting period, we thought that these variables provided a useful contrast between the relative effects of early and sustained wet conditions within a season. We predicted that nest survival would be positively related to primary productivity in the current year. We based this prediction on past results that indicate that (1) small mammals, amphibians, insects, and seeds compose the primary diet of generalist mammalian predators of duck nests (Azevedo et al. 2006, Brook et al. 2008); (2) primary prey resources likely increase with primary productivity (Chase et al. 2000, Heisler-White et al. 2008, Warne et al. 2010); and (3) positive relationships between nest survival and abundance of microtine rodents have been observed in smaller-scale studies (Ackerman 2002, Brook et al. 2008). Thus, on sites with higher primary productivity, we expected generalist nest predators to destroy a lower proportion of nests because of the abundance of other food types.

Because transitions from dry to wet conditions in the PPR can be associated with a substantial pulse of productivity (Murkin et al. 1997, Euliss et al. 2004), sustained periods of increased pond density, primary productivity, and wetness following a pulse could lead to sustained periods of higher prey availability and a positive numerical response by nest predators over relatively short (1–2-year) periods (Gunderson et al. 2007). We therefore predicted a negative relationship between nest survival and pond density, primary productivity, and wetness in the previous two years (Drever et al. 2004, Yang et al. 2010). We considered 1- and 2-year time lags appropriate to both the number of trophic levels of interest in our study (two trophic levels; Yang et al. 2010) and the life-history of the suite of mammalian nest predators in the PPR (Sargeant et al. 1993, Drever et al. 2004).

Our predictions about nest survival relative to land use and land cover were based directly on past research. In general, survival probability of bird nests and young in agricultural landscapes tends to decrease with intensity of land use along a gradient from idled perennial vegetation to annually cultivated cropland (Peterjohn 2003, Whittingham and Evans 2004). Based on previously conducted landscape-scale studies of duck nest survival (Greenwood et al. 1995, Reynolds et al. 2001, Stephens et al. 2005) and species composition, distribution, and relative abundance of nest predators in the PPR (Sargeant et al. 1993), we predicted a positive relationship between nest survival and perennial cover

and a negative relationship between nest survival and edge. We predicted a negative relationship between nest survival and basin count, because wetland basins are highly productive features in the PPR landscape (Murkin et al. 1997) and may provide preferred foraging sites for nest predators regardless of whether they contain ponded water (Phillips et al. 2003). We based this prediction on two ideas: (1) that predators might be more abundant in productive landscapes with abundant wetland basins and (2) that, on average, nests would be located closer to wetland basins in landscapes with more abundant wetland basins (Stephens et al. 2005).

Variation in nest survival among species and with nest age is commonly observed in duck nesting studies. We expected Blue-winged Teal to have the largest nest survival probability and Mallard the smallest nest survival probability (Stephens et al. 2005, Pieron and Rohwer 2010). We expected to observe a positive relationship between survival probability and nest age (Klett and Johnson 1982, Emery et al. 2005, Stephens et al. 2005, Grant and Shaffer 2012), possibly because of changes in incubation behavior and nest defense during the nesting period (Forbes et al. 1994) or alternatively because nests initiated in relatively secure locations tend to survive longer (Dinsmore et al. 2002).

#### *Model selection and parameter estimation*

To quantify support for our predictions, we used penalized likelihood criteria to select top-ranked models from a set of candidate models (Burnham and Anderson 2002). We selected covariates based on past research and ecological hypotheses with clear predictions, and thus we viewed all possible combinations of the covariates as credible alternatives. We selected among competing models by conducting two rounds of model selection, which began with ranking the 512 candidate models defined by the nine site- and year-specific time-lagged pond density, primary productivity, and wetness covariates. Then, we added the site-specific basin count, edge, and perennial cover covariates to each model in the subset of pond density, primary productivity, and wetness models that received support from the data in the first round of model evaluation and ranked the models defined by this step. The total number of models in the analysis was thus  $512 + m \times 7$  where  $m$  was the number of models in the subset of top-ranked models identified in the first round of model selection. To account for expected species- and nest-age-related variation in survival, every model included a separate intercept term for each of the five study species and a shared slope term that described a linear relationship between nest survival and nest age common to all of the study species.

Model coefficients and log-likelihoods were estimated using the nest survival module in program MARK 6.0 (White and Burnham 1999) via R 2.10.0 and the contributed R package RMark 1.9.6 (Laake 2010). The nest survival module in program MARK uses a

generalized linear model with logit-link function and binomial errors to estimate daily nest survival probability (DNS) as a linear function of the various combinations of the covariates described by the candidate models: that is,  $\text{logit}(\text{DNS}_{ij}) = \beta_0 + \sum_k \beta_k x_{ijk}$  where the  $\beta_k$  represent coefficients to be estimated and the  $x_{ijk}$  represent nest( $i$ )- and day( $j$ )-specific values of  $k$  covariates (Dinsmore et al. 2002). To facilitate estimation, we rescaled covariate values to similar magnitudes.

The logit-linear model of DNS with binomial errors is valid given the following assumptions (Dinsmore et al. 2002): (1) nest age at discovery is measured accurately, (2) nest fate is determined correctly, (3) nest visits do not influence survival, and (4) given the covariates, the binomial model of DNS fits the data. The first three model assumptions were addressed by the data collection protocol. Nest ages were correctly classified to within 3–4 days by candling (Weller 1956, Klett et al. 1986), and projected hatch dates derived from candling were largely consistent with observed hatch dates in our study. Destroyed nests were identified by the presence of broken, partially consumed eggs and disturbed nest materials and successful nests were identified by the presence of detached embryonic membranes, thus errors in classification of nest fate were probably rare (Klett et al. 1986). To minimize the potential effect of nest visits on survival, nest visits took place in the afternoon when females were most likely to be absent (Gloutney et al. 1993), nest visits were short in duration (<5 minutes), and observers approached nests from various directions to avoid creating trails to nests. Finally, nests that were abandoned between discovery and the first visit, presumably due to investigator disturbance, were not included in the analysis.

As is common in studies employing generalized linear models to estimate daily nest survival probability, the assumption of adequate model fit, which encompasses both extra-binomial variation (overdispersion caused by heterogeneity and lack of independence) and missing covariates (apparent overdispersion), was more challenging to address. To our knowledge, there is no currently available approach to account for lack-of-fit in nest survival models that is both unbiased and computationally practical for data sets comprising 1000s of nests (Dinsmore et al. 2002, Sturdivant et al. 2007, Schmidt et al. 2010). As an alternative, we evaluated the sensitivity of our results to increasing levels of overdispersion by adjusting observed model selection criteria and sampling variances by an overdispersion factor ( $c$ ). We estimated the overdispersion factor ( $\hat{c}$ ) from our data as the deviance of the top-ranked model divided by the residual degrees of freedom and regarded it as an upper bound for  $c$  because this estimator is known to be positively biased for finite samples (McCullagh and Nelder 1989:118; Dinsmore et al. 2002). We then evaluated changes in model selection criteria and 95% confidence intervals of parameter

estimates as we allowed the overdispersion factor to vary from 1 (no overdispersion) to  $\hat{c}$ .

Primary sampling units in our study (i.e., nest histories) were repeated within sites and years. We therefore assessed the robustness of our site- and year-level inferences to potential nest-level pseudoreplication (Hurlbert 1984, Johnson 2002) by testing for potential changes in our results given a large reduction in sample size. Specifically, we graphically compared the magnitude, direction, and precision of the coefficients from the top-ranked model in our analysis of nest histories in Program MARK with analogous coefficients estimated from a model that used weighted site- and year-level estimates of DNS (from a model without covariates) as response data. Weights were proportional to the ESS associated with a given site and year combination (Reynolds et al. 2001). We predicted that if our results were robust to pseudoreplication, results would be similar for both models.

We used differences in model-specific values of Schwarz' Bayesian information criterion ( $DBIC_i = BIC_i - BIC_{\min}$ ) to rank competing models (Schwarz 1978). We assumed equal prior weight among models (Link and Barker 2006), and we considered models with  $DBIC_i \leq 10$  (Raftery 1995) to represent a subset of models that received at least minimal support from the data. We used the parameter estimates from the top-ranked model and the observed covariate values to estimate the probability of a mallard nest surviving from initiation to hatching (hereafter, nest success). We chose to estimate nest success for mallards because they were the most broadly distributed and thoroughly studied species in our study. The average mallard nest is exposed to mortality for 35 days (Klett et al. 1986: Table B-1). We calculated nest success from DNS in two steps. First, we calculated estimates of DNS for each day of the nesting period ( $\widehat{DNS}_{ij}$ ) using the estimated intercept for mallards, the age of the nest on each day (from 1 to 35), and the covariate values of interest. Then, we calculated nest success as

$$\widehat{NS} = \prod_{j=1}^{35} \widehat{DNS}_{ij}.$$

To assess the potential ecological impact of the covariates, we compared ratios of nest success estimates (hereafter probability ratios) across a range of variation in a covariate with other covariates held constant (Agresti 2007:27). Because we could not choose the observed levels of primary productivity and pond count, we calculated probability ratios using (1) the minimum and maximum values and (2) the fifth and 95th percentile values of the covariates, which allowed us to better assess the effect of large changes in the environment. We used the delta method to estimate the sampling variance of nest success and probability ratios (Seber 1982:7).

## RESULTS

We sampled 52 study sites during 2002–2009. The number of sites sampled per year ranged from 9 to 26. Number of years per site ranged from 1 to 8, and 25 sites were sampled in two or more years. Our sampling design produced a range of covariate conditions across sites and years, and VIFs indicated that the full set of covariates could be included in candidate models (Table 1). We discovered and monitored 12 754 nests, which resulted in an effective sample size of 123 935. The most abundant nesting species was Mallard (30% of the sample) followed by Blue-winged Teal (26%), Gadwall (26%), Northern Shoveler (10%), and Northern Pintail (8%). Nearly 90% of failed nests exhibited evidence of destruction by predators. Less than 2% of failed nests were associated with abandonment between discovery and the first visit.

In the first round of analysis, the subset of supported models that described nest survival given current and recent variation in pond density, primary productivity, and wetness was generally consistent with our overall hypotheses, but contradicted some of our specific predictions. There were seven models in the subset of supported models, and the top-ranked model ( $DBIC = 0$ ) included pond density<sub>*t*</sub>, pond density<sub>*t*-2</sub>, primary productivity<sub>*t*</sub>, primary productivity<sub>*t*-2</sub>, and wetness<sub>*t*-1</sub> (where *t* is the current year, *t* - 1 is the previous year, and *t* - 2 is two years ago). The six models within 10 DBIC of the top-ranked model included pond density<sub>*t*</sub> (six models), pond density<sub>*t*-2</sub> (six models), primary productivity<sub>*t*</sub> (six models), primary productivity<sub>*t*-1</sub> (four models), primary productivity<sub>*t*-2</sub> (five models), wetness<sub>*t*-1</sub> (two models), and wetness<sub>*t*-2</sub> (three models). Consistent with our predictions, all estimated coefficients for primary productivity<sub>*t*</sub> were positive, and all estimated coefficients were negative for all time-lagged variables. Contrary to our predictions, all estimated coefficients for pond density<sub>*t*</sub> were positive.

In the second round of analysis, we evaluated 49 models that resulted from combining the basin count, edge, and perennial cover covariates with each of the seven models from the first round of model selection (Appendix A: Table A1). In the top-ranked model, DNS was positively related to basin count, pond density<sub>*t*</sub>, and primary productivity<sub>*t*</sub> and was negatively related to pond density<sub>*t*-2</sub>, primary productivity<sub>*t*-1</sub>, and primary productivity<sub>*t*-2</sub> (Table 2, Fig. 2). There were five other models within 10 DBIC of the top-ranked model in this subset. These models included basin count (five models), edge (one model), pond density<sub>*t*</sub> (five models), pond density<sub>*t*-2</sub> (five models), primary productivity<sub>*t*</sub> (five models), primary productivity<sub>*t*-1</sub> (three models), primary productivity<sub>*t*-2</sub> (five models), wetness<sub>*t*-1</sub> (two models), and wetness<sub>*t*-2</sub> (one model). Two models were very similar to the top-ranked model in terms of structure, number of parameters, and support ( $DBIC = 2$  and  $DBIC = 3$ ; Table 2). Together, these three models indicated some uncertainty about the relationship of

TABLE 1. Range of observed values and variance inflation factors (VIF) for landscape-level environmental covariates used to parameterize models of daily nest survival probability of upland-nesting ducks on 52 10.4-km<sup>2</sup> study sites in the Prairie Pothole Region in North and South Dakota, USA, during 2002–2009.

Covariate	Units	Range	VIF
Basin count	no. wetland basins	10–374	1.2
Edge	m	0–47 880	1.9
Perennial cover	none	0.16–0.98	2.0
Pond density <sub><i>t</i></sub>	no. ponds/km <sup>2</sup>	1–36	1.9
Pond density <sub><i>t</i>-1</sub>	no. ponds/km <sup>2</sup>	1–32	3.1
Pond density <sub><i>t</i>-2</sub>	no. ponds/km <sup>2</sup>	1–32	3.1
Primary productivity <sub><i>t</i></sub>	g C/m <sup>3</sup>	119–448	2.1
Primary productivity <sub><i>t</i>-1</sub>	g C/m <sup>3</sup>	119–474	2.6
Primary productivity <sub><i>t</i>-2</sub>	g C/m <sup>3</sup>	158–448	2.3
Wetness <sub><i>t</i></sub>	none	–3.92–0.16	2.1
Wetness <sub><i>t</i>-1</sub>	none	–3.84 to –0.68	2.4
Wetness <sub><i>t</i>-2</sub>	none	–3.84 to –0.15	2.3

Notes: Basin count was the number of wetland basins on the study site, edge was the total length of edge between herbaceous perennial vegetation and annually cultivated cropland on the study site, perennial cover was the proportion of upland area composed of herbaceous perennial vegetation in the 41.4-km<sup>2</sup> landscape centered on the study site, primary productivity was an index of the maximum gross primary productivity on the study site during April–July, wetness was the sum of the normalized difference water index (NDWI; Gao 1996) values measured weekly on the study site during April–July, and pond density was a spatially interpolated index of the average density of wetland basins containing ponded water on the study site. Values of basin count, edge, and perennial cover varied spatially and were represented by a single value for each study site. Pond density, primary productivity, and wetness varied both spatially and temporally and were evaluated for each study site in the current year (*t*) and the two previous years (*t*–1 and *t*–2). These covariates were represented by three values for each of the 161 site and year combinations. Variation among current and previous values of pond density, primary productivity, and wetness was due to inclusion of sites that were studied in a single year.

nest survival to primary productivity<sub>*t*-1</sub>, wetness<sub>*t*-1</sub>, and wetness<sub>*t*-2</sub>. Primary productivity<sub>*t*-1</sub> was included in two of three top-ranked models, wetness<sub>*t*-1</sub> was included in one of three, and wetness<sub>*t*-2</sub> was included in one of three. Counter to our predictions, models including perennial cover and edge received little or no support. The highest-ranked model including edge was 9 DBIC from the top-ranked model, and the highest-ranked model including perennial cover was 12 DBIC from the top-ranked model. In these models, estimated logit-scale coefficients

for edge and perennial cover were 0.016 (SE = 0.011) and 0.010 (SE = 0.054), respectively.

Although there was some model selection uncertainty, we based our inferences on the top-ranked model from the second round of model selection because the magnitude and direction of coefficients in this model was similar to the same coefficients in other models that received material support from the data (Table 2). The overdispersion factor ( $\hat{c}$ ) estimated from the top-ranked model was 2.89. When we increased *c* from 1 to 3, model

TABLE 2. Estimated differences in Bayesian information criterion (DBIC<sub>*i*</sub> = BIC<sub>min</sub> – BIC<sub>*i*</sub>), logit-scale coefficients (mean), and standard errors of estimated coefficients (SE) from three top-ranked models of daily nest survival probability of upland-nesting ducks relative to time-lagged landscape-level variation in environmental covariates.

Covariate	DBIC = 0		DBIC = 2		DBIC = 3	
	Mean	SE	Mean	SE	Mean	SE
Blue-winged Teal	2.619	0.086	2.307	0.107	2.399	0.114
Gadwall	2.508	0.088	2.191	0.109	2.281	0.116
Mallard	2.380	0.085	2.067	0.106	2.157	0.114
Northern Pintail	2.538	0.093	2.224	0.113	2.311	0.120
Northern Shoveler	2.532	0.091	2.214	0.112	2.305	0.118
Nest age	0.031	0.001	0.031	0.001	0.031	0.001
Basin count	0.067	0.014	0.057	0.014	0.064	0.014
Pond density <sub><i>t</i></sub>	0.354	0.057	0.372	0.056	0.376	0.057
Pond density <sub><i>t</i>-2</sub>	–0.668	0.069	–0.656	0.070	–0.632	0.070
Primary productivity <sub><i>t</i></sub>	0.181	0.025	0.167	0.024	0.191	0.025
Primary productivity <sub><i>t</i>-1</sub>	–0.099	0.023			–0.099	0.023
Primary productivity <sub><i>t</i>-2</sub>	–0.138	0.028	–0.184	0.025	–0.129	0.028
Wetness <sub><i>t</i>-1</sub>			–0.083	0.021		
Wetness <sub><i>t</i>-2</sub>					–0.065	0.022

Note: Empty cells indicate that the covariate associated with that row was not included in the model associated with that column.

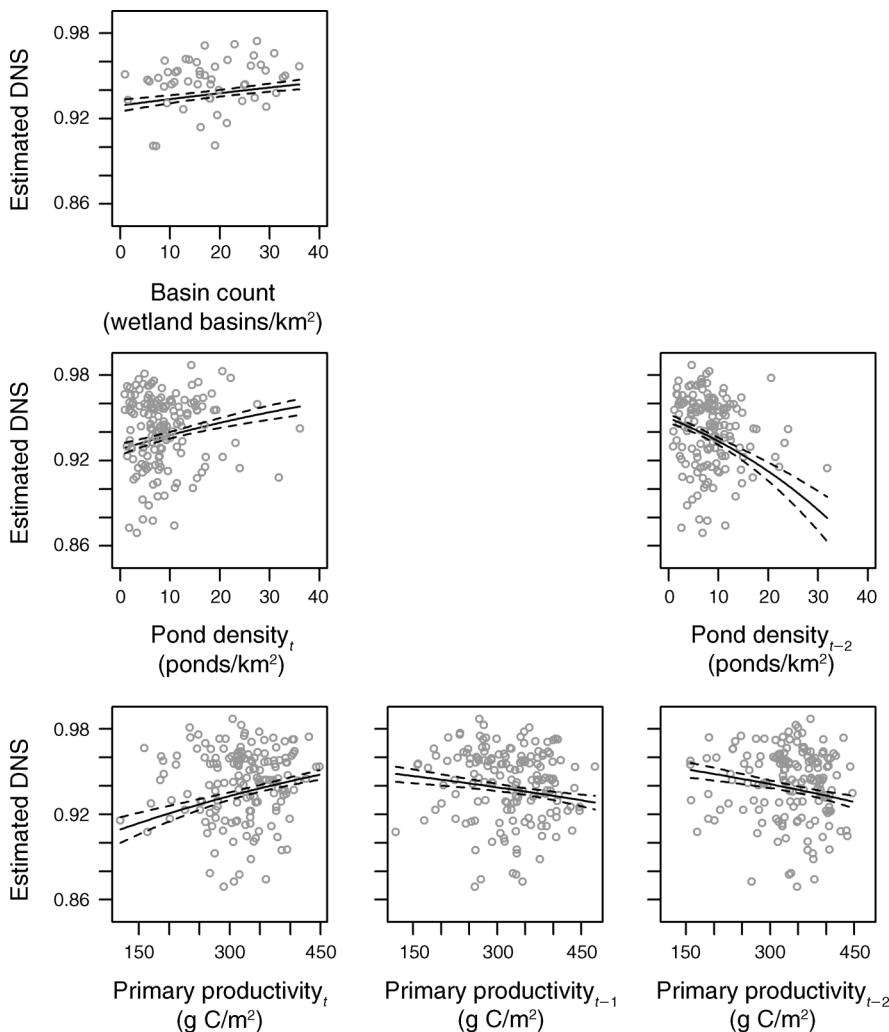


FIG. 2. Daily nest survival probability (DNS) of upland-nesting ducks relative to time-lagged landscape-level environmental covariates. Solid lines represent estimated average DNS across the range of variation in a covariate with all other covariates held constant at their median values. Dashed lines are 95% confidence limits. Points are estimates of average site-specific (basin count) or site- and year-specific (primary productivity and pond density) DNS from a model without covariates. Subscripts on primary productivity and pond density indicate values for the current year ( $t$ ), the previous year ( $t - 1$ ), or two years previous ( $t - 2$ ).

ranks did not change. DBIC for the three top-ranked models was 0, 1, and 7 given  $c = 2$ , 0, and 1, and 9 given  $c = 3$ . As expected, confidence intervals of model parameter estimates widened as  $c$  increased. With  $c = 2$ , 95% CIs of logit-scale parameter estimates in the best model were 41% wider on average (range 33%–43%), and with  $c = 3$  they were 72% wider on average (range 67%–74%), but 95% CIs did not overlap zero at any level of  $c$  tested (Appendix B: Fig. B1). This analysis provided evidence that our inferences were robust to potential overdispersion in the nest sample. Our analysis of the 161 weighted site- and year-specific DNS estimates as a function of the environmental covariates in the top-ranked model indicated that even under an approximately 79-fold reduction in sample size (i.e., from 12 754 to 161), our results were largely unchanged. The precision of the estimates was reduced, but the

magnitude and direction of estimated coefficients was similar in both models (Appendix B: Fig. B1). VIFs associated with the site- and year-specific covariates in the top-ranked model were 1.1, 1.6, 1.6, 1.8, 1.7, and 1.9 for basin count, pond density $_t$ , pond density $_{t-2}$ , primary productivity $_t$ , primary productivity $_{t-1}$ , and primary productivity $_{t-2}$ , respectively. Estimated pairwise correlations were positive for all covariates and ranged from 0.05 to 0.60 (Fig. 3).

Model-based estimates of nest success ( $\widehat{NS}$ ) varied by a factor of 11.0 (SE = 3.4) among sites and years. Median  $\widehat{NS}$  was 0.10 (SE = 0.01) on a site where pond density $_t$ , pond density $_{t-2}$ , primary productivity $_t$ , primary productivity $_{t-1}$ , and primary productivity $_{t-2}$  were 12 ponds/km $^2$ , 11 ponds/km $^2$ , 380 g C/m $^3$ , 450 g C/m $^3$ , and 400 g C/m $^3$ , respectively. Minimum  $\widehat{NS}$  of 0.02 (SE = 0.01) was estimated on a site where pond density $_t$ , pond

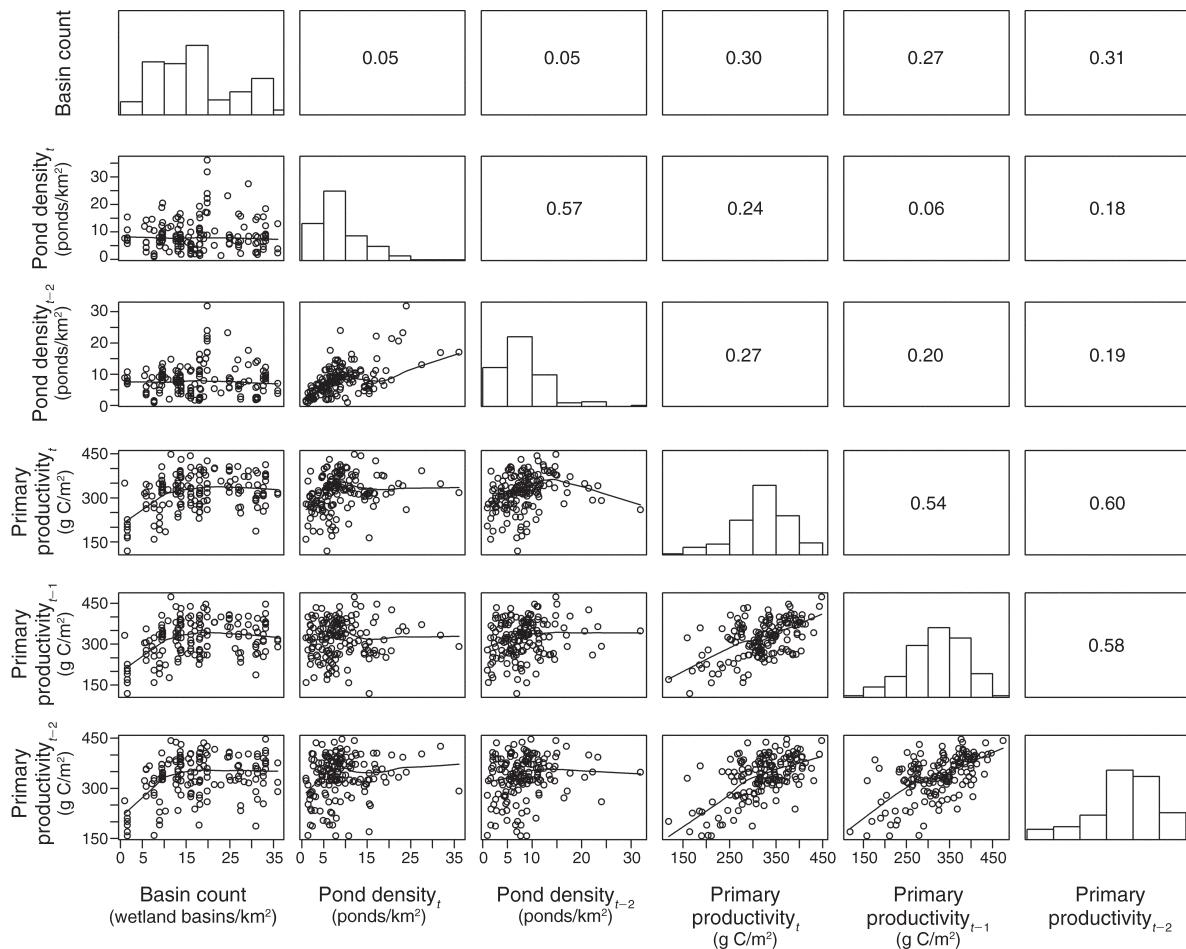


FIG. 3. Histograms (main diagonal), paired scatterplots (left below diagonal), and two-way Pearson correlation matrix (right above diagonal) for covariates contained in the top-ranked ( $DBIC = 0$ , where  $DBIC$  is the difference in Bayesian information criterion [ $DBIC_i = BIC_i - BIC_{\min}$ ]) model of nest survival probability of upland nesting ducks in the Prairie Pothole Region of North and South Dakota during 2002–2009. Covariate names are located above each histogram. Orientation follows matrix conventions. For example, the top- and right-most panel shows the two-way correlation coefficient between primary productivity<sub>*t-2*</sub> and basin count, and the bottom- and left-most panel is the paired scatterplot of basin count (*x*-axis) and primary productivity<sub>*t-2*</sub> (*y*-axis). Lines on scatterplots are means of local regression (LOESS) functions applied to covariate pairs.

density<sub>*t-2*</sub>, primary productivity<sub>*t*</sub>, primary productivity<sub>*t-1*</sub>, and primary productivity<sub>*t-2*</sub> were 24 ponds/km<sup>2</sup>, 31 ponds/km<sup>2</sup>, 260 g C/m<sup>3</sup>, 350 g C/m<sup>3</sup>, and 350 g C/m<sup>3</sup>, respectively. Maximum  $\widehat{NS}$  of 0.22 ( $SE = 0.02$ ) was estimated on a site where pond density<sub>*t*</sub>, pond density<sub>*t-2*</sub>, primary productivity<sub>*t*</sub>, primary productivity<sub>*t-1*</sub>, and primary productivity<sub>*t-2*</sub> were 15 ponds/km<sup>2</sup>, 5 ponds/km<sup>2</sup>, 340 g C/m<sup>3</sup>, 310 g C/m<sup>3</sup>, and 250 g C/m<sup>3</sup>, respectively.

Analysis of probability ratios indicated that nest success was more sensitive to variation in pond density and primary productivity than to the number of wetland basins on a site (Fig. 2). Across the observed range of a given covariate with other covariates held constant at their median values, probability ratios ranged from 1.7 ( $SE = 0.2$ ) to 13.9 ( $SE = 5.0$ ). Estimated nest success ( $\widehat{NS}$ ) increased by a factor of 1.7 ( $SE = 0.2$ ) over the observed range of basin count. Over the observed range of pond density<sub>*t*</sub> and pond density<sub>*t-2*</sub>,  $\widehat{NS}$  increased by a factor of

2.9 ( $SE = 0.5$ ) and decreased by a factor of 13.9 ( $SE = 5.0$ ), respectively. Over the observed range of primary productivity<sub>*t*</sub>,  $\widehat{NS}$  increased by a factor of 4.4 ( $SE = 0.9$ ). Nest success decreased by factors of 2.1 ( $SE = 0.4$ ) and 2.3 ( $SE = 0.4$ ) over the observed range of primary productivity<sub>*t-1*</sub>, and primary productivity<sub>*t-2*</sub>.

With the largest and smallest 10% of observed values trimmed from the distribution, probability ratios for current and recent pond density and primary productivity ranged from 1.6 ( $SE = 0.1$ ) to 2.7 ( $SE = 5.0$ ). Across 90% of the observed range of pond density<sub>*t*</sub> (3–20 ponds/km<sup>2</sup>) and pond density<sub>*t-2*</sub> (2–16 ponds/km<sup>2</sup>),  $\widehat{NS}$  increased by a factor of 1.8 ( $SE = 0.2$ ) and decreased by a factor of 2.7 ( $SE = 0.3$ ), respectively. Across 90% of the observed range of primary productivity<sub>*t*</sub> (230 g C/m<sup>3</sup>–410 g C/m<sup>3</sup>),  $\widehat{NS}$  increased by a factor of 2.2 ( $SE = 0.2$ ). Nest success decreased by factors of 1.6 ( $SE = 0.2$ ) and 1.7 ( $SE = 0.2$ ) across 90% of the observed range of

primary productivity<sub>*t*-1</sub> (200–430 g C/m<sup>3</sup>), and primary productivity<sub>*t*-2</sub> (230–420 g C/m<sup>3</sup>).

#### DISCUSSION

Our study expanded the existing understanding of variation in a key demographic rate of a ground-nesting bird population in a dynamic agricultural environment. We observed positive relationships between nest survival and current-year primary productivity and pond density and negative relationships between nest survival and pond density and primary productivity in the two previous years. Transitions from dry to wet conditions were associated with large between-year increases in nest survival and provided evidence that intermittent variation in primary productivity may have been associated with resource pulses (Yang et al. 2010) that resonated through our study system, affecting nest predators and in turn affecting duck nest survival. Somewhat surprisingly given past work, we observed greater support for relationships between nest survival and variation in landscape-level spring pond density and primary productivity than for relationships between nest survival and intensity of agricultural land use as indexed by the amount and configuration of perennial grass cover in the landscape. Further, our results provided new evidence for a strong relationship between duck nest survival and wetlands and wetland dynamics with implications for habitat conservation strategies in the PPR.

There are several plausible explanations for the positive relationships between nest survival and current-year pond density and primary productivity that we observed. Spring pond density is positively related to the amount of snow accumulation in the previous winter (Fang and Pomeroy 2008). Greater snow accumulation is associated with lower survival, reproduction, and body condition of nest predators (Gehrt 2005, Bartoń and Zalewski 2007, Pitt et al. 2008). Primary productivity affects the availability of resources for consumers and affects the height and density of vegetation. Increased primary productivity may have led to increased abundance and availability of primary prey (Ackerman 2002, Brook et al. 2008). Alternatively, nests might have been better concealed from predators in years of vigorous plant growth (Chalfoun and Martin 2009). We speculate that, in years of high spring pond density, high primary productivity, or both, nest predators might be fewer, primary prey might be more abundant, and nest concealment might be improved leading to higher nest survival.

We hypothesize that negative relationships of nest survival to primary productivity and spring pond density in *t* - 1 and *t* - 2 could have resulted from shifts in predator distribution and abundance during wet-dry cycles. Numeric responses of mid-sized, generalist predators to increased abundance of prey are generally positive (Schmidt and Ostfeld 2008). A series of wet, productive years may result in increased predator abundance and higher rates of nest depredation in

subsequent years. Conversely, a series of dry years might result in decreased predator abundance and lower rates of nest depredation. The strong negative effect of pond density in *t* - 2 on nest survival through depredation could be driven by positive reproductive responses of multiple species of nest predators to periods of increased prey resources.

Our results were consistent with a large body of research on the effects of resource pulses on food webs in variable environments. In a meta-analysis of the effects of resource pulses based on 68 peer-reviewed studies, Yang et al. (2010) reported on one study conducted in an agricultural ecosystem and one study conducted in a wetland ecosystem. By providing evidence of an indirect, time-lagged relationship between reproductive success of alternate prey (ducks) and pulses of pond density and primary productivity across a broad gradient of landscape contexts, our study contributed new information about possible mechanisms of predator-prey dynamics in a wetland-rich agricultural ecosystem. Nearly every nest that failed to hatch was destroyed by predators, and the relationships that we observed between nest survival and pond density and primary productivity were largely consistent with existing knowledge of predator-prey dynamics in the PPR (Sargeant et al. 1993, Brook et al. 2008) and also with the effects of resource pulses observed in a broad cross-section of ecosystems (Sears et al. 2004, Yang et al. 2010). We appreciate the challenge of conducting intensive studies across broad spatial and temporal extents, but we suggest that multi-site, multi-year studies involving simultaneous measurement and manipulation of duck nests, primary prey (e.g., microtines), and nest predators would be a useful approach for further elucidating the mechanisms of the patterns we observed.

In contrast to past large-scale studies of nest survival of upland-nesting ducks in the PPR (Greenwood et al. 1995, Reynolds et al. 2001, Stephens et al. 2005), nest survival was relatively insensitive to the proportion or configuration of herbaceous perennial vegetation in our study. We thought that this unexpected result might have been an outcome of the greater temporal extent of our sampling effort, which allowed us to capture a broader range of spatial and temporal variation in nest survival and revealed that nest survival was, on average, unrelated to perennial vegetation during our study. However, if the magnitude and direction of the relationship between nest survival and perennial vegetation varied among years (see Stephens et al. 2005), then year-specific relationships could have been omitted by our additive models. Post hoc, exploratory analysis indicated that the relationship between nest survival and perennial cover varied among years in our study. Nonetheless, exploratory models including interactions between perennial cover and pond density or primary productivity received no support from the data (J. Walker, *unpublished analysis*). We think that together our exploratory analyses indicate that further investiga-

tion of hypotheses about how relationships between nest survival and perennial vegetation might interact with environmental conditions is warranted. Further, our study was conducted in the southwest PPR where precipitation is highly variable (Millett et al. 2009) and wet–dry cycles potentially have stronger effects on duck populations (Sæther et al. 2008). In environments like the eastern PPR, where precipitation is less variable, nest survival may possibly have a more consistent relationship to perennial vegetation.

By providing clear evidence of time-lagged relationships between nest survival and pond density in the PPR, our study further affirmed the overall importance of wetland basins and wet–dry episodes (Lynch 1984) to North American duck populations. Density of breeding pairs, nesting effort, and clutch size are positively correlated with wet pond area in the spring (Krapu et al. 1983, Reynolds et al. 2006). Nest survival probability was positively correlated with current May pond density in our study. Survival of breeding females is positively correlated with nest survival because most mortality of breeding females is associated with depredation during nesting (Arnold et al. 2012). Duckling survival probability is positively correlated with the amount of seasonal wetland habitat (Krapu et al. 2000, Pietz et al. 2003). Therefore, when a precipitation-driven pulse of increased pond density and productivity occurs following drought, the environmental potential for a large increase in the duck population is likely to be maximized.

Previous studies of nest survival in the PPR have provided conservation recommendations focused on protection and restoration of herbaceous perennial vegetation in landscapes with abundant wetland basins (Greenwood et al. 1995, Reynolds et al. 2001, Horn et al. 2005, Stephens et al. 2005). These recommendations may have under-valued cropland-dominated landscapes with abundant wetlands. Our results indicated that landscapes with relatively little herbaceous perennial vegetation and abundant wetland basins could be productive for nesting ducks during transitions between dry and wet conditions. The spatial extent of conserved habitat needed to sustain populations of relatively short-lived, highly mobile animals like our study species is positively related to the level of spatial and temporal variation in key environmental drivers (Verboom et al. 2010). Given projections of increased variation in climate in the PPR (Johnson et al. 2010), we suggest that cropland-dominated landscapes with abundant wetland basins are an important part of the PPR conservation portfolio and inclusion of these landscapes in future conservation plans would help to promote the long-term sustainability of North American duck populations.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Ranked models of daily nest survival of duck nests in the Prairie Pothole Region relative to environmental covariates ([Ecological Archives A023-055-A1](#)).

### Appendix B

Comparative assessment of the potential effects of nest-level overdispersion and site- and year-level pseudoreplication on estimated regression coefficients in the top-ranked covariate model ([Ecological Archives A023-055-A2](#)).