Temporal and multi-spatial environmental drivers of duck nest survival

RESEARCH ARTICLE

Temporal and multi-spatial environmental drivers of duck nest survival

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ABSTRACT
Nest survival is determined in part by a combination of large-scale environmental factors and local nest-site characteristics. Because predation is the primary cause of nest failure, those drivers likely operate by influencing predator abundance, behavior, and/or nest detectability. For example, fluctuations in landscape productivity have the potential to alter predator and prey abundance, whereas nest vegetation and patterns of nest spacing may influence predator behavior. We used 8 yr of site-specific environmental data coupled with data collected from 11,547 duck nests to evaluate the relative importance of large-scale and local factors on nest survival. We found that higher values of gross primary productivity, basins, and pond counts were associated with higher nest survival in a given year, but were associated with lower nest survival the following 2 yr. Taken in combination with the literature, our interpretation is that productive environmental conditions can result in time-lagged increases in predator abundance, leading to higher levels of nest predation in subsequent years. Local factors were generally less important than large-scale covariates in determining duck nest survival, but we found that nests laid earlier, in thicker vegetation, and with closer nearest neighbors had higher survival rates. However, as the season progressed, nests with closer nearest neighbors had lower survival rates (significant initiation date*distance interaction), suggesting predators may eventually aggregate in areas of higher nest density. Our results highlight the importance of both large-scale and local factors as they affect duck nest survival, and suggest several hypotheses about predator numerical and aggregative responses that are ripe for empirical testing.

Keywords: aggregative response, functional response, nearest neighbor, nest survival, numerical response, prairie pothole region, time-lagged

Promotores ambientales temporales y multi-espaciales de la supervivencia del nido de pato

RESUMEN
La supervivencia del nido está determinada en parte por una combinación de factores ambientales de gran escala y características locales del sitio del nido. Debido a que la depredación es la causa principal de fracaso del nido, estos condicionantes probablemente operan influenciando la abundancia y el comportamiento de los depredadores, y/o la detectabilidad del nido. Por ejemplo, las fluctuaciones en la productividad del paisaje tienen el potencial de alterar la abundancia de los depredadores y las presas, mientras que la vegetación del nido y los patrones de espaciamiento del nido pueden influenciar el comportamiento del depredador. Usamos 8 años de datos ambientales específicos de sitio junto con datos colectados de 11,547 nidos de pato para evaluar la importancia relativa de factores de gran escala y locales en la supervivencia del nido. Encontramos que los valores más altos de productividad primaria bruta, cuencas y conteos de estanques estuvieron asociados con una mayor supervivencia del nido en un año dado, pero estuvieron asociados con una menor supervivencia del nido los dos años siguientes. Basados en estos datos y en la literatura, nuestra interpretación es que las condiciones ambientales productivas pueden originar aumentos temporales desfasados en la abundancia de depredadores, llevando a niveles más altos de depredación del nido en los años subsecuentes. Los factores locales fueron generalmente menos importantes que las covariables de gran escala en determinar la supervivencia del nido de pato, pero encontramos que los nidos con puestas más tempranas, en vegetación más espesa y con vecinos cercanos más próximos tuvieron tasas de supervivencia más altas. Sin embargo, a medida que la estación progresa, los nidos con vecinos cercanos más próximos tuvieron tasas de supervivencia más bajas (interacción significativa día de inicio*distancia), sugiriendo que los depredadores pueden eventualmente agregarse en áreas de mayor densidad de nidos. Nuestros resultados subrayan la importancia tanto de los factores de gran escala como de los locales, ya que ambos afectan la supervivencia del nido de pato, y sugieren varias hipótesis sobre las respuestas numéricas y agregativas de los depredadores que están listas para una evaluación empírica.

Palabras clave: región de los baches de pradera, respuesta agregativa, respuesta funcional, respuesta numérica, retraso temporal, supervivencia del nido, vecino más cercano

INTRODUCTION

Ecologists are challenged to understand how factors at multiple scales interact to influence population abundance and community structure. At large scales, landscape composition (Horn et al. 2005, Stephens et al. 2005) and fragmentation (Stephens et al. 2003, Mutter et al. 2015) influence recruitment and even population persistence (Stratford and Stouffer 1999). Fluctuating environmental conditions over time, such as ocean oscillations (Flint 2013, Schmidt et al. 2014), snowfall (Drever et al. 2012), drought (Sorenson et al. 1998), and resource pulses (Wolff 1996) are also strong drivers of animal populations, and it can take years for their effects to percolate up through the trophic web (Clotfelter et al. 2007). Often, these large-scale processes act on populations and communities by influencing primary productivity, which elicits numerical responses (increases in population through reproduction) in consumers. This in turn increases predator abundance (Schmidt and Ostfeld 2003), which can lead to density-dependent feedbacks and trophic web interactions such as buffering (lower predation on a focal species when alternate prey increase, e.g., Ackerman 2002) or apparent competition (higher predation on a focal species when alternate prey increase, e.g., Holt 1977).

Many researchers have noted that large-scale processes can influence and even amplify local drivers of population regulation (Laurance et al. 2011), such as predator (Chalfoun et al. 2002, Phillips et al. 2004) and prey (Kotler 1984) behavior. Predator behaviors such as aggregative responses (i.e. behavioral shifts that result in predators congregating in areas of high prey density) typically occur over local scales, and the consequences for prey can be acute, although prey avoidance behavior can ameliorate these effects (Sih 1984, 2005; Hammond et al. 2007). Local factors that influence predator foraging success, as well as those large-scale factors that affect overall predator abundance, both have the potential to drive prey demographics. However, their relative importance is difficult to disentangle.

In North American waterfowl, there is convincing evidence that populations are regulated at large scales by factors such as density dependence (reviewed in Gunnarsson et al. 2013) and regional environmental conditions (Drever et al. 2012, Walker et al. 2013, Koons et al. 2014). Recent research has furthered our understanding of how interannual environmental variation such as precipitation and primary productivity influence duck recruitment and population fluctuations (Drever et al. 2012, Walker et al. 2013, Ross et al. 2015). At much smaller scales, nest-site vegetation (Crabtree et al. 1989, Skone et al. 2016), predator behavior (Larivière and Messier 1998, Phillips et al. 2004), and nest spacing (Ringelman et al. 2012, 2014; Ringelman 2014) influence nest survival, but the effects are

likely variable among geographies and species communities. Accordingly, there is an increasing focus on integrating large-scale and local factors in an attempt to identify the most important drivers of duck demographics (Stephens et al. 2003, Ross et al. 2015, Skone et al. 2016).

Walker et al. (2013) used data from 12,754 duck nests to demonstrate the importance of large-scale environmental variation on nest survival. They found that duck nest survival was positively related to pond numbers and primary productivity in the first year, but nest survival was negatively related to pond numbers and primary productivity in the previous year and two years previous. Walker et al. (2013) attributed these patterns to time-lagged numerical responses by nest predator populations. However, their analysis did not consider local factors that may plausibly affect nest detectability or predator behavioral responses to nest density (Larivière and Messier 1998, Ringelman et al. 2014). Therefore, we used some of the same data as Walker et al. (2013) to investigate the relative importance of large-scale environmental factors vs. local factors (nest vegetation, nest spacing, etc.) that may affect duck nest survival. We were especially interested in how nest spacing influenced survival, because the local density of active duck nests is potentially a primary determinant of predator foraging behavior and aggregative responses.

METHODS

Hypotheses, study design, study area, data collection protocols, and calculation of landscape-scale covariates are described thoroughly in Walker et al. (2013), and we present only a brief synopsis here. Between 2002 and 2009, duck nests were monitored on 52 sites (9–27 per year) in the prairie pothole region of North and South Dakota, USA. Sites were 10.4 km^2 and were selected based on the density of wetland basins (>100 per km^2) and the amount of perennial grass cover present (>20% grassland) (Stephens et al. 2005, Walker et al. 2013). On each site, 3–5 km^2 of grassland were searched 3 times per season between 0700 and 1400 hours (Gloutney et al. 1993) using a chain-drag (Klett et al. 1986). Duck nests were marked with a 1 m fiberglass rod placed 5 m north of the nest bowl (Hein and Hein 1996), and technicians recorded the date, species, nest location, and nest age determined by candling (Weller 1956). To measure nest concealment, a Robel measuring pole (marked in dm) was placed at the nest bowl and viewed from 4 m from each of the cardinal directions; the lowest visible number on the pole was recorded, and the 4 values were averaged (Robel et al. 1970). Robel measurements convey information about the biomass and structural complexity of vegetation near the nest, and are a useful measure of visual and potentially olfactory concealment from terrestrial predators (Robel et al. 1970). However, the influence of Robel measurements

on nest survival should be interpreted with caution because readings were taken when the nest was found, rather than when it was located by a predator. Nests were revisited every 5–7 days to determine nest fate. Nests that were abandoned by the next nest visit after they were found were assumed to be influenced by investigator disturbance and were censored. Nests for which there were no GPS coordinates ($n = 1,026$) were also excluded, leaving 11,728 nests for analysis.

Following Ringelman et al. (2014), we evaluated duck nest spacing using nearest-neighbor distances, which provides a measure of local nest clustering (Clark and Evans 1954) that may drive predator aggregative responses (Seymour et al. 2003, 2004). We selected nearest-neighbor distance as our correlate of local nest density to avoid imposing any anthropogenic bias on defining an appropriate radius around a nest within which to measure density (Ringelman et al. 2014). For each nest, we identified the nearest active neighboring nest: for depredated nests, we identified the nearest neighbor on the estimated depredation date, and for successful nests, the nearest neighbor at the midpoint of initiation and hatching (or the last day of nest monitoring) (Ringelman et al. 2014). Presumably, the presence of any duck nest, regardless of species, could drive aggregative responses in predators, so we included the nests of all species as potential neighbors for each focal nest. We discarded nests with no neighbors or those with neighbors >1,000 m away ($n = 181$), leaving 11,547 nests for analysis.

Year- and site-specific values of wetness and primary productivity were derived from the National Aeronautics and Space Administration's moderate resolution imaging spectrometer sensors, made available by the U.S. Geological Survey. Gross primary productivity (the amount of biomass produced during a fixed period of time; GPP) was estimated as the maximum GPP observed during an 8-day window during the duck nesting season (April–July) on the 1 km^2 pixel closest to the center of the study site (Walker et al. 2013). The normalized difference water index (NDWI) combined surface water and the water content of vegetation and soil; these values were summed across the nesting season at the nearest available pixel (0.5 km^2 in size) for each site and year to estimate wetness (Walker et al. 2013). As an estimate of general site quality, we used the National Wetlands Inventory layer in ArcGIS to enumerate wetland basins at each study site; this metric was static among years (Walker et al. 2013). In contrast, actual pond counts for each site and year were taken from the U.S. Fish and Wildlife Service annual survey of May ponds (Zimpfer et al. 2009). Unlike NDWI, pond counts represent an early-season point estimate of wetness of the wetland basins for each site-year. U.S. Fish and Wildlife Service land cover data (30 m resolution) were used to calculate the percentage of perennial grassland in the 41.4 km^2 landscape surrounding the study site and the sum of the shared perimeter (in meters) between grassland and cropland on the 10.4 km^2 study site ("edge") (Walker et al. 2013).

We used the nest survival module (Dinsmore et al. 2002) in program MARK (White and Burnham 1999) accessed through the RMark package (Laake 2013) to analyze our data. All covariates included in the modeling exercise were a priori supported as potentially having an influence on duck nest survival (Crabtree et al. 1989, Pieron and Rohwer 2010, Walker et al. 2013, Ringelman et al. 2014). We modeled the daily survival rate (DSR) as a function of species, nest age at time of discovery, various landscape- and local-level covariates, and ranked models based on AIC$_c$ score (Burnham and Anderson 2002). In our first analysis, we evaluated the influence of large-scale environmental drivers on nest survival: our global parameter set consisted of year- and site-specific basin numbers as well as pond counts, estimates of primary productivity, wetness, and 1- and 2-yr lag effects for these. All covariates could potentially influence duck nest survival, so we constructed models using all possible combinations of these factors. Our next analysis tested the effect of local variables on nest survival, and we included nest initiation date, Robel measurements at the nest, and nearest-neighbor distance. Previous research has demonstrated increased predator use of high-density nesting areas later in the season (Larivière and Messier 1998), so we added an initiation date*neighbor distance interaction term. We also included the percent of grassland and the amount of habitat edge because these variables can directly influence predator movements and functional responses (Pasitschniak-Arts and Messier 1995, Pasitschniak-Arts et al. 1998, Raquel et al. 2015). We selected the top-ranking local model and sequentially added quadratic terms for initiation date (Pieron and Rohwer 2010), Robel measurements (Clark and Shutler 1999), and neighbor distance to determine whether nonlinear effects improved model fit. Finally, we built a model that combined variables from our best-fitting large-scale and local models, and compared that to our first 2 analyses. To estimate the relative importance of each variable, we sequentially removed single variables from the combined model, and calculated odds ratios from the model weights of that full set of models. All analyses were conducted in R (version 3.4.1).

RESULTS

We included 11,547 nests from 162 site-years in our analysis: Mallards (*Anas platyrhynchos*) were the most numerous species (~3,500 nests), followed by Blue-winged Teal (*Spatula discors*) and Gadwall (*Mareca strepera*) (~3,000 nests each). There were fewer Northern Pintail

TABLE 1. Model selection results evaluating the relative influence of large-scale environmental metrics on duck nest survival, using data collected in the prairie pothole region, North and South Dakota, USA, 2002–2009. GPP refers to gross primary productivity, and NDWI is the normalized difference water index. Temporally lagged parameters are noted with subscripts. All models also contained parameters for species and the age of the nest at discovery. Not all models are shown.

Parameters	Deviance	AIC$_c$	ΔAIC$_c$	Weight
Basins + Ponds + Ponds$_{t-1}$ + Ponds$_{t-2}$ + GPP + GPP$_{t-1}$ + GPP$_{t-2}$ + NDWI + NDWI$_{t-1}$	33845.2	33875.2	0.0	0.417
Basins + Ponds + Ponds$_{t-1}$ + Ponds$_{t-2}$ + GPP + GPP$_{t-1}$ + GPP$_{t-2}$ + NDWI	33847.8	33875.8	0.7	0.298
Basins + Ponds + Ponds$_{t-1}$ + Ponds$_{t-2}$ + GPP + GPP$_{t-1}$ + GPP$_{t-2}$ + NDWI + NDWI$_{t-1}$ + NDWI$_{t-2}$	33845.1	33877.1	2.0	0.155
Basins + Ponds + Ponds$_{t-1}$ + Ponds$_{t-2}$ + GPP + GPP$_{t-1}$ + GPP$_{t-2}$ + NDWI + NDWI$_{t-2}$	33847.5	33877.5	2.4	0.128
Basins + Ponds + Ponds$_{t-2}$ + GPP + GPP$_{t-1}$ + GPP$_{t-2}$ + NDWI + NDWI$_{t-1}$ + NDWI$_{t-2}$	33856.4	33886.4	11.3	0.002
[null]	34369.6	34371.6	496.5	0.000

(*Anas acuta*) and Northern Shovelers (*Spatula clypeata*) (~1,000 nests each). In our first analysis, we evaluated all linear combinations of large-scale environmental variables in our global set. Model selection results supported inclusion of all terms except lagged metrics of NDWI (Table 1). We next analyzed the influence of local variables on duck nest survival. The top-ranked model accounted for 89% of model weights and supported the inclusion of all variables. Sequentially appending squared terms for initiation date, Robel, and nearest-neighbor distance to this top model did not improve model fit (all ΔAIC$_c$ = 2), and these variables were not considered further.

Finally, we combined parameters from our top-ranked large-scale model and our top-ranked local model, which resulted in substantial improvement in model fit (Table 2). As anticipated, model-averaged coefficients indicated that nest survival varied among species, and nests that were older when found had higher survival rates; models that failed to include these terms were 9.0×10^{21} and 9.5×10^{20} times less likely than the fully saturated model (Table 3). In terms of large-scale environmental drivers, nest survival was positively related to numbers of basins, ponds, and primary productivity, was negatively related to NDWI, and was negatively related to number of ponds and primary productivity in each of the previous 2 yr (Table 3). Odds ratios provided a measure of the relative importance of each variable in determining model fit. GPP was the most important large-scale variable (model containing GPP was 5.2×10^{21} more likely than one without it) and remained important as a lagged variable (odds ratios for GPP$_{t-1}$ and GPP$_{t-2}$ greater than 3.7×10^5). Including the number of ponds was more important for model fit than the number of basins or NDWI, but both of those current-year variables were more important determinants of nest survival than time-lagged pond counts (Table 3).

Parameter estimates for local variables indicated that nests initiated earlier in the season had higher survival rates (odds ratio: 1.7×10^{10}). Higher nest survival was also associated with larger Robel measurements and closer nearest neighbors (higher local density); models

that did not include these terms were 165 and 128 times less likely than the global model (Table 3). However, the survival benefit of having close neighbors reversed later in the season (initiation date*neighbor distance interaction term) and, as the season progressed, close neighbors were associated with lower nest success (Table 3, Figure 1). The effect of percent grassland and the amount of edge habitat on nest survival was equivocal, as parameter confidence intervals bounded zero (Table 3).

DISCUSSION

Many duck nesting studies use categorical variables of study area and year to control for landscape-level variation in environmental conditions and predator communities which ultimately influence nest survival (Skone et al. 2016). Our study helps diagnose the relative importance of specific environmental mechanisms that may underlie those site and year differences, while also examining covariates particular to individual nest sites. Predator abundance is often driven by large-scale environmental fluctuations (Schmidt and Ostfeld 2003), whereas predator behavior likely depends on prey density (Larivière and Messier 1998) and detectability (Nams 1997). Here, we used spatially explicit, long-term nesting data to model relationships between nest survival and habitat covariates that could potentially relate to numerical and behavioral responses of predators.

Our top-ranked model included all large-scale variables except NDWI$_{t-2}$. In addition, NDWI$_{t-1}$ was an uninformative parameter because including it did not improve model fit by >2 AIC. Higher year-specific values for basins, ponds, and GPP indicated favorable breeding conditions for ducks and had a positive influence on nest survival. Indeed, the strength of the relationship between environmental conditions and nest survival suggests an important role for bottom-up structuring of prairie communities. Highly productive landscapes with numerous wetlands are associated with increased availability and quality of nest sites (Johnson and Grier 1988) and may

TABLE 2. Model selection results evaluating the relative influence of large-scale environmental metrics and local site characteristics on duck nest survival, using data collected in the prairie pothole region, North and South Dakota, USA, 2002–2009. GPP refers to gross primary productivity, NDWI is the normalized difference water index, and Distance refers to nearest-neighbor distance. Temporally lagged parameters are noted with subscripts. All models also contained parameters for species and the age of the nest at discovery.

Model name	Parameters	Deviance	AIC_c	ΔAIC_c	Weight
Combined model	Basins + Ponds + $Ponds_{t-1}$ + $Ponds_{t-2}$ + GPP + GPP_{t-1} + GPP_{t-2} + NDWI + Initiation + Robel + Grass + Edge + Distance + Initiation*Distance	33788.4	33828.4	0.0	1.000
Top large-scale model	Basins + Ponds + $Ponds_{t-1}$ + $Ponds_{t-2}$ + GPP + GPP_{t-1} + GPP_{t-2} + NDWI	33847.8	33875.8	47.4	0.000
Top local model	Initiation + Robel + Grass + Distance + Initiation*Distance	34061.7	34085.7	257.3	0.000
[null]		34369.6	34371.6	543.2	0.000

increase the abundance of alternative prey which buffer duck nests from predation (Ackerman 2002). Interestingly, "wetness" as measured by NDWI had a negative effect on nest survival. NDWI integrates open water, soil moisture content, and green features, where more positive values indicate open water, and more negative values are typically non-water features such as vegetation. Thus, we interpret the negative effect of NDWI on nest survival as an indication that ducks nest more successfully in areas with green uplands and shallow emergent wetlands as opposed to large expanses of open (and likely more permanent) water.

The productive prairie conditions described above also provide predators with an abundance of prey, potentially leading to enhanced reproduction (O'Donoghue et al.

1997) and increases in predator populations the following season (Schmidt and Ostfeld 2003). Consistent with this hypothesis, all time-lagged variables in our model had a negative effect on nest survival. This is particularly noteworthy because our models controlled for the effect of current conditions at each site—this indicated that something from the past carried over across years to influence nest survival. Lagged increases in predator abundance seem logical, and may help explain the interannual density dependence in waterfowl productivity that is consistently observed at large scales (Gunnarsson et al. 2013). Other lagged mechanisms—for example, that females incur costs to future reproduction in years when they successfully nest—would more likely manifest in lower nesting propensity rather than lower nest success

TABLE 3. Model-averaged parameter estimates from an analysis of factors influencing duck nest survival, using data collected in the prairie pothole region, North and South Dakota, USA, 2002–2009. GPP refers to gross primary productivity, NDWI is the normalized difference water index, and Distance refers to nearest-neighbor distance. Temporally lagged parameters are noted with subscripts. Species codes refer to Gadwall (GADW), Mallard (MALL), Northern Pintail (NOPI), and Northern Shoveler (NSHO), with Blue-winged Teal as the reference species for the categorical variable. Confidence intervals (CIs) are 95% intervals from program MARK. Odds ratios compare model weights from the combined model to a model with the coefficient removed.

| Parameter	Coefficient	Lower CI	Upper CI	Odds ratio
Intercept	2.760246	2.486512	3.033979	
AgeFound	0.021362	0.017166	0.025558	9.0×10^{21}
SpeciesGADW	−0.138616	−0.210287	−0.066944	9.5×10^{20}
SpeciesMALL	−0.355867	−0.424921	−0.286813	
SpeciesNOPI	−0.170007	−0.273539	−0.066475	
SpeciesNSHO	−0.131156	−0.220460	−0.041852	
Basins	0.000662	0.000376	0.000947	11,780.3
Ponds	0.004050	0.002804	0.005297	4.2×10^5
GPP	0.002825	0.002279	0.003372	5.2×10^{21}
NDWI	−0.099373	−0.140189	−0.058557	28,118
$Ponds_{t-1}$	−0.003305	−0.004997	−0.001613	494.3
$Ponds_{t-2}$	−0.004171	−0.006060	−0.002282	3794.0
GPP_{t-1}	−0.001660	−0.002163	−0.001156	5.7×10^8
GPP_{t-2}	−0.001511	−0.002077	−0.000946	3.7×10^5
Initiation	−0.008069	−0.010353	−0.005786	1.7×10^{10}
Robel	0.035285	0.015377	0.055193	164.8
Distance	−0.000517	−0.000795	−0.000242	127.7
Initiation*Distance	0.000014	0.000006	0.000022	136.9
Grass	0.146153	−0.004402	0.296707	2.3
Edge	0.000002	−0.000000	0.000005	1.4
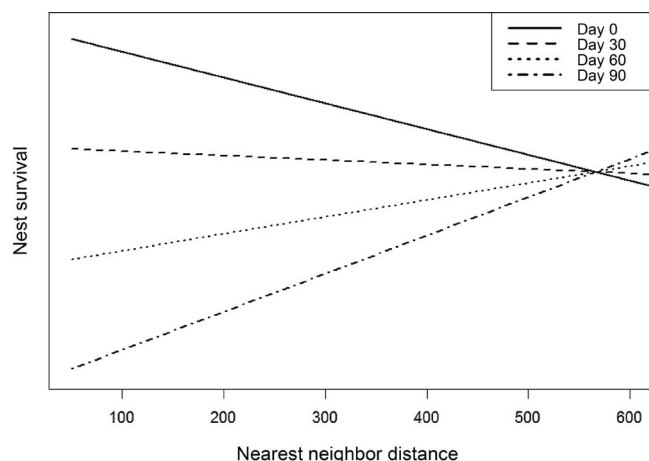
FIGURE 1. The interaction effect of initiation date and nearest-neighbor distance on survival of duck nests from the prairie pothole region, North and South Dakota, USA, 2002–2009. Coefficients for initiation date, nearest-neighbor distance, and their interaction were taken from the top-ranked model of duck nest survival, and all other parameters were held constant at zero; hence, the y axis is dimensionless. Parameter values for initiation date and nearest-neighbor distance chosen for this visualization were within the range empirically observed in the dataset.

(Devries et al. 2008). Productive years may not only increase overall predator populations in subsequent years, but could also shift community structure or lead to individual predators focusing more on duck nests as prey, though empirical data for these hypotheses are currently lacking.

In our models that included only local variables, inclusion of percent grassland and the amount of edge habitat was supported, but these variables were less meaningful in the combined model. We suggest this may have happened because those 2 parameters were static within a site-year; hence they provided a useful landscape context in the local-only model (soaking up some variance as a site-year categorical effect would) but were overwhelmed by more important temporally varying landscape metrics in the combined model. Overall, the top-ranked model of large-scale environmental variables was a better fit to the nest survival data than the top-ranked model of local variables. When we used a leave-one-out approach to estimate variable importance with odds ratios, we found that large-scale environmental variables were more important determinants of model fit than local covariates (except initiation date). In terms of nest survival, this suggests that environmental conditions in a given year (i.e. a "good" or "bad" year in terms of water and primary productivity) were more important than details of nest vegetation or spacing. If we interpret that large-scale, time-lagged variables are potentially related to increases in predator populations after the "good"

years, then it also follows that overall predator populations are more important determinants of duck nest survival than fine-scale factors that could influence predator foraging behavior and success (Ringelman 2014).

In concordance with most previous research (Clark and Shutler 1999, Raquel et al. 2015), at a local scale, nests initiated earlier in the season and those discovered in denser vegetation had higher survival rates. In our study, the relationship between nest survival and nearest-neighbor distance changed through the course of the season. Nests initiated within the first month of the season had higher survival rates when neighbors were close, but later nests with closer neighbors had lower survival rates (Figure 1). Earlier in the season, duck nests are a relatively rare prey item, therefore predation may be largely incidental; if this is the case, close neighboring nests help dilute predation risk (Ringelman et al. 2014). However, as the season progresses, more frequent encounter rates and formation of olfactory search images (Nams 1997) may cause duck nests to be specifically targeted by predators. Increases in predator density, activity, or efficiency in areas of higher nest density would result in lower nest survival. While this aggregative/behavioral response seems especially likely in foxes (Seymour et al. 2003), even incidental predators like striped skunks (*Mephitis mephitis*) have been shown to eventually concentrate their foraging activity in profitable patches (Larivière and Messier 1998, 2001).

Most studies of nesting waterfowl (and indeed, birds in general) show a negative relationship between initiation date and nest survival (Flint and Grand 1996, Grant et al. 2005, Arnold et al. 2007, Raquel et al. 2015), but that can vary by cover type (Emery et al. 2005). Our results incorporating nearest-neighbor distance suggest this pattern may be caused by predators aggregating in response to increases in local nest density. Nevertheless, some studies show a positive relationship between initiation date and nest survival (Grand 1995, Greenwood et al. 1995, Garrettson and Rohwer 2001). Those authors also implicate seasonal changes in predator foraging behavior and surmise that an increasing abundance of small mammals later in the season causes predators to switch from preying on duck nests; further research in this area is sorely needed (Ackerman 2002). Despite the fact that predator foraging strategies fundamentally depend on prey density (Fretwell and Lucas 1970), little attention has been given to explicitly modeling duck nest density through time at various spatial scales (but see Ringelman et al. 2016). Furthermore, the foraging behavior of nest predators has been studied at only coarse spatiotemporal scales (Phillips et al. 2004); there is little information (Larivière and Messier 2001) on changes in predator behavior that may indicate short-

or long-term learning (e.g., through Bayesian updating [Valone 2006]). Our results add to a growing literature suggesting that predator behavior can change seasonally, with important repercussions for grassland-nesting ducks. Taken in combination with what appears to be indications of time-lagged responses in predator populations as a result of environmental resource pulses, we recommend a renewed focus on predator ecology in the prairie pothole region.

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