



## Original Article

# Influence of Patch Shape on Mallard Nest Survival in Northern Iowa

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**ABSTRACT** Reproductive success of mallards (*Anas platyrhynchos*) is influenced by distribution and amount of wetlands and grasslands on the landscape during the breeding season. Most studies of mallard reproductive success have been conducted in areas with high wetland densities and large tracts of grasslands. We investigated nest survival of mallards in intensively cropped northern Iowa, USA, where wetland and grassland habitats were highly fragmented. We radiotracked female mallards nesting during 1998–2000 and located 318 nests in 6 types of land cover. Overall daily survival rate of nests was  $0.945 \pm 0.003$  standard error (SE), corresponding to an estimated nest survival rate of 0.14. Hen success (i.e., the probability that an individual female will hatch a nest in one of her attempts) averaged  $0.28 \pm 0.03$  SE. We used a model selection approach to examine covariates that might affect nest survival. Perimeter-to-area ratio (PAR) of the nest patch was the most important predictor of daily nest survival, with nest survival decreasing with increasing PAR. A greater percentage of nests hatched (18%) in habitats with low perimeter-to-area ratios (e.g., pastures, hayfields, Conservation Reserve Program fields, and managed grasslands) compared with habitats with high PAR (11%) such as drainage ditches, road-side ditches, fencerows, and waterways. Managing habitat in this region to increase mallard nest survival will be challenging, given the propensity of mallards to nest in linear habitats. If the climate change projections materialize in the 21st century, the southeastern portion of the Prairie Pothole Region could become a much more important breeding area for midcontinent mallards. Published 2016. This article is a U.S. Government work and is in the public domain in the USA.

**KEY WORDS** *Anas platyrhynchos*, hen success, nest survival, patch size, perimeter-to-area ratio, Prairie Pothole Region, predation, telemetry, waterfowl.

Mallard (*Anas platyrhynchos*) breeding ecology has been extensively studied in the Prairie Pothole Region (PPR) of the northern United States and Canada (Batt et al. 1992, Howerter et al. 2014). Most of the research, however, has been carried out in the central and northern portions of this extensive ecoregion (Cowardin et al. 1985, Greenwood et al. 1995, Reynolds et al. 2001, Stephens et al. 2005, Arnold et al. 2007, Walker et al. 2013, Howerter et al. 2014). In the southern portion of the PPR, intensive agricultural practices have resulted in the loss of 99% of shallow-basin wetlands and

99.9% of the presettlement prairie (Bishop et al. 1998, Smith 1998). The current landscape is dominated by row crops and contains highly fragmented patches of grassland and wetland habitat. Only a few studies of mallard nesting ecology have been conducted in this region and those occurred prior to the 1990s (Humburg et al. 1978, Ohde et al. 1983).

Reproductive success of ducks is influenced by the number and distribution of wetlands during the breeding season (Pospahala et al. 1974, Cowardin et al. 1995, Sorenson et al. 1998, Stephens et al. 2005, Walker et al. 2013), as well as the amount and distribution of grasslands on the landscape (Reynolds et al. 2001, Arnold et al. 2007). Nest survival of ducks in the PPR declines along a gradient, with the lowest rates occurring in the eastern and southern regions (Pospahala et al. 1974, Klett et al. 1988, Reynolds et al. 2001, Arnold et al. 2007). This gradient largely reflects the geographical variation in agricultural development, wetland drainage, wetland–grassland habitat fragmentation, and

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predator communities. There is also a strong climatic gradient from northwest to southeast, with cooler and drier conditions in the northwestern portion of the PPR (Millett et al. 2009); evaporation generally exceeds precipitation across most of the PPR (Niemuth et al. 2014). However, Iowa, USA, generally has a positive water balance with higher annual precipitation (Niemuth et al. 2014). Currently, the most productive areas for waterfowl nesting in the PPR are intermediate zones between the wetter areas in the southeast and the drier areas in the northwest (Ballard et al. 2014). Global-climate-change models suggest the southeastern portion of the PPR will experience increased precipitation levels in future decades, while the regions to the north and west may experience increased drought (Johnson et al. 2005, 2010; Millett et al. 2009; Portmann et al. 2009; Ballard et al. 2014).

The effect of habitat fragmentation and patch size on avian nest survival has been extensively studied (Hoover et al. 1995, Lahti 2001, Chalfoun et al. 2002, Stephens et al. 2004), including waterfowl nesting in the PPR (Pasitschniak-Arts et al. 1998, Sovada et al. 2000, Horn et al. 2005). In general, studies at the landscape scale reported negative effects of fragmentation on nest survival (Stephens et al. 2004). Additionally, predation was more prevalent when fragmentation occurred at the landscape scale, but the effects of patch size on reproductive success remain equivocal (Stephens et al. 2004, Eichholz and Elmberg 2014). For example, Pasitschniak-Arts and Messier (1996) found that nest survival was similar between large and small plots. In the Canadian Parklands, nest survival increased with the proportion of herbaceous cover in the landscape (i.e., larger patches of grassland) and decreased with increasing habitat edge density (i.e., more fragmentation; Howerter et al. 2014). Duck-nesting habitat in the southern portion of the PPR is highly fragmented, with lower wetland densities and fewer grassland acres available for nesting (Johnson et al. 2010). It is unclear how successful mallards will be at reproducing in this fragmented habitat if climate change increases the extent and duration of droughts in the northwest portion of the PPR and increasing numbers of breeding ducks use the southeast portion of the PPR (Johnson et al. 2005, Hagy et al. 2014).

Nest survival is only one vital parameter in the life history of mallards. Understanding which life history stages influence population growth rates is important for conservation (Crowder et al. 1994, Heppell et al. 1994). For birds in general, mean elasticity of adult survival was larger than mean elasticity of fecundity (Sæther and Bakke 2000). However, for mallards in the Canadian Parklands, a stage-based projection model indicated nest survival was the single vital rate to which populations were most sensitive, with nest survival more important at lower nest-survival rates (Howerter et al. 2014). Thus, nest survival may be an appropriate vital rate for monitoring mallard populations.

We examined nest survival of mallards in the intensively farmed southern portion of the PPR where wetland and grassland habitats are highly fragmented. Wetland restoration projects by the Iowa Department of Natural Resources,

USA, have been ongoing in this area since 1987. Our goal was to determine reproductive success of female mallards in this highly altered agriculturally dominated landscape. We assessed 1) how nest survival and hen success rates (i.e., the probability that an individual female will hatch a nest in one of her attempts) in the southeast PPR compared with nest survival and hen success in other areas of the PPR; 2) if the size and shape of the patches in which mallards nested influenced nest survival; and 3) whether nest survival in isolated patches was influenced by the proximity of the patch to large grassland-wetland complexes.

## STUDY AREA

The Eagle Lake Wetland Complex (ELWC), a project area of the North American Wetlands Conservation Act of 1989, was located in the eastern half of the Iowa PPR in Hancock and Winnebago counties in north-central Iowa. The 26,400-ha study area was composed of predominately agricultural fields with some Wildlife Management Areas, Waterfowl Production Areas, and Conservation Reserve Program fields. Most of the grasslands on Waterfowl Production Areas and Conservation Reserve Program fields, totaling approximately 530 ha, were established in the mid-1980s (Fletcher and Koford 2003). The dominant grasses were smooth brome (*Bromus inermis*), switchgrass (*Panicum virgatum*), and big bluestem (*Andropogon gerardii*). There were 7 wetland complexes (seasonal, semipermanent, and permanent wetlands) on public land (Fletcher and Koford 2003).

We obtained monthly precipitation totals from the Iowa Environmental Mesonet website (<http://mesonet.agron.iastate.edu/>) for Forest City, Iowa, the closest weather station to the study area. The 1951–2013 mean total October to June precipitation was 52 cm. The study area received 68 cm, 70 cm, and 48 cm October to June precipitation in 1997–1998, 1998–1999, and 1999–2000, respectively.

## METHODS

We trapped female mallards using decoy traps and net-guns from 12 April to 7 May 1998, 5 April to 27 April 1999, and 3 April to 21 April 2000. We fitted all mallards with U.S. Geological Survey (USGS) leg bands and abdominally implanted radiotransmitters (A2310 transmitters weighing 19 g; Advanced Telemetry Systems, Isanti, MN, USA, and IMP150 transmitters weighing 21 g; Telonics, Mesa, AZ, USA) following surgical techniques described by Olsen et al. (1992). All trapping and handling of mallards followed animal welfare protocols approved by the Iowa State University Committee on Animal Care (Protocol numbers 3-8-3844-3-Q and 3-8-3847-1-Q) with appropriate permits from Iowa Department of Natural Resources and USGS.

To find mallard nests, we attempted to locate females between 0600 and 1300 hours when females were most likely to be at their nests (Gloutney et al. 1993). We assumed that females located at the same upland location for 3 consecutive days were nesting and located nests by triangulating from a distance of approximately 20 m (White and Garrott 1990). We checked nest locations daily by radio signal to determine whether the nests were still active. When we determined

nesting activity had been terminated at the site, based on absence from the upland location for 3 consecutive days for laying birds, we visited each nest to ascertain its fate and recorded its location using a hand-held GPS. To minimize the potential effects of nest visitation on nest survival, we did not approach nests closer than 10 m until nesting concluded (Major 1990).

We obtained infrared aerial photographs of the entire study area in 1998 and 1999 from the U.S. Fish and Wildlife Service Habitat and Population Evaluation Team (Fergus Falls, MN, USA) and georeferenced and digitized them using ArcInfo–ArcView Geographical Information System (GIS) software (ESRI, Redlands, CA, USA). We defined a patch as a contiguous, relatively homogenous, discrete area whose boundaries were easily discerned (Wiens 1976). We distinguished 2 broad categories of patches—linear and block. Linear patches included roadside ditches, drainage ditches, fencerows, waterways, terraces, and other narrow patches <15 m wide; we classified all other patches as block. We classified nesting sites as either in block or linear patches and into 1 of 6 patch types (Table 1).

We determined landscape metrics of nests by overlaying nest locations on our land-cover maps in GIS. We checked all locations to ensure that the map unit was the same as the type in which the bird actually nested. We measured patch size (ha), distance to nearest grassland (m; zero used when nests were located in grasslands), and distance to nearest wetland edge (m) of the nest locations in the GIS. We also computed the perimeter-to-area ratio (PAR, m/ha) of each patch by dividing the patch perimeter by the area of the patch. Our 2 broad categories of patches—linear and block—reflected the extremes in the PAR gradient. We performed a 2 × 2 contingency table analysis and computed a Cochran-corrected chi-square value to compare the proportion of nests that hatched in block and linear habitats.

**Table 1.** Land-cover types used by nesting mallards on the Eagle Lake Wetland Complex study area in north-central Iowa, USA, during 1998–2000.

Patch type	Description
Block habitat	
Crop	Row crop, cornfields, and soybean fields
Grassland	Conservation Reserve Program land, grasslands on state, county-owned wildlife management areas or federally owned waterfowl production areas, grass fields actively grazed by livestock
Hay	Either alfalfa or alfalfa ( <i>Medicago</i> spp.)–brome ( <i>Bromus</i> spp.) mixed hayfields on private land
Odd	Small ( $\bar{x}$ < 1 ha) unmanaged grass areas including idle pastures and abandoned farmsteads
Wetland veg.	Emergent wetland vegetation
Linear habitat	Areas between water in the drainage ditch and the adjacent crop field (i.e., drainage ditch, fencerows [both wooded and herbaceous]), the area between the road surface and adjacent crop fields (i.e., road ditches), grass strips planted in crop fields to abate soil erosion (e.g., waterways).

We modeled daily nest survival (DSR) using the nest survival model in Program MARK (White and Burnham 1999, Dinsmore et al. 2002). We used Akaike’s Information Criterion for small sample sizes (AIC<sub>c</sub>) to select the most parsimonious model from a set of *a priori* candidate models (Burnham and Anderson 2002, Dinsmore and Dinsmore 2007). We checked for uninformative parameters within models by noting where model likelihood did not change between nested models and  $\Delta AIC_c$  increased <2 and eliminated them from consideration (Burnham and Anderson 2002, Arnold 2010). We used a hierarchical approach to model selection. For our first model set, we compared models of time trends to see whether DSR varied over the nesting season. We compared models of constant survival over the nesting season, a linear trend of survival over the nesting season, and a quadratic trend over the nesting season (Dinsmore et al. 2002). In addition, our first model set incorporated annual variation in DSR. We used the best temporal model (from the set described above) to test habitat and landscape factors that may affect mallard nest survival. We selected PAR, distance to nearest wetland, distance to nearest grassland, patch size, and patch type as *a priori* covariates. We tested for correlation and did not include in the same model variables with  $|r| > 0.7$  (i.e., patch size and PAR). We estimated nest survival and associated standard error during a 35-day nesting period using our most parsimonious model and the delta method (Seber 1982, Klett et al. 1988, Powell 2007). We used the “best model” rather than model average as a result of using the logit link in the nest survival models (Cade 2015).

Hen success has been defined as the probability that an individual female will hatch a nest in one of her attempts (Cowardin and Johnson 1979). We were able to calculate hen success because our birds were radiomarked and we assumed that we were able to observe all nest attempts (McPherson et al. 2003). Cowardin and Johnson (1979) modeled the relationship between hen success and nest survival with the equation  $H = fP_{\text{exp}}[f(1 - P)^2]$  where H is hen success, P is nest survival, and f is nesting effort. We had data on both hen success and nest survival, so we were then able to calculate nesting effort (f)—the probability that a hen will attempt  $\geq 1$  nest.

## RESULTS

We captured 171 female mallards (54, 69, and 48 in 1998, 1999, and 2000, respectively) and located 318 nests (90, 138, and 90 nest in 1998, 1999, and 2000, respectively), of which 47 (15%) hatched (Table 2). Mallards nested in patches of 6 different land-cover types (Table 1). Forty-six percent of nests were located in linear habitats and 36% of nests were located in grasslands. The median patch size in which female mallards nested was 2.50 ha (range = 0.03–147.50 ha). Seventy-five percent of nests were in patches <10.3 ha. The mean PAR of nest patches was 1,416 m/ha (min = 56 m/ha, max = 10,128 m/ha). Both patch area and PAR varied by land-cover type (Fig. 1). Croplands had the largest patch area and the smallest PAR, while linear habitats had the smallest patch area and the largest PAR.

**Table 2.** Fate of 318 mallard nesting attempts on the Eagle Lake Wetland Complex study area in north-central Iowa, USA, during 1998–2000.

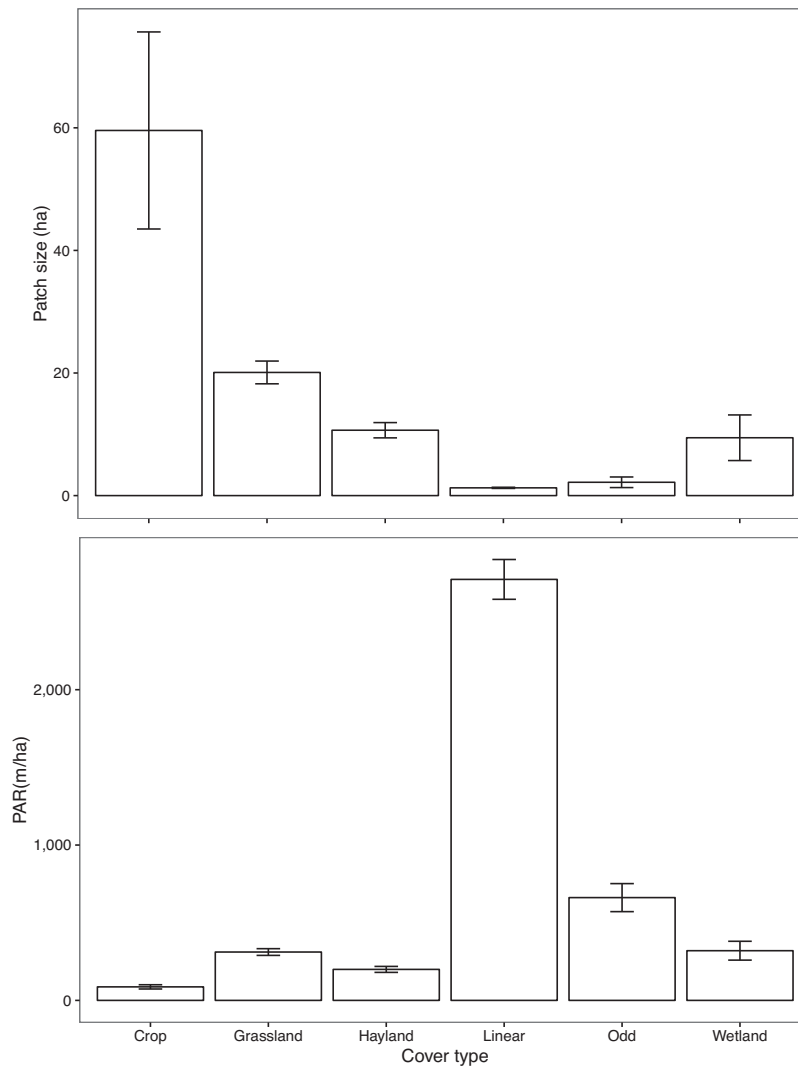
Fate	Year					
	1998		1999		2000	
	Block	Linear	Block	Linear	Block	Linear
Abandoned			4		1	3
Depredated <sup>a</sup>	24	43	41	51	23	31
Destroyed <sup>b</sup>			3	2	1	1
Hatched	9	9	12	4	8	5
Female killed		3	4	3	2	1
Unknown	2		13	1	10	4
Total nest attempts	90		138		90	

<sup>a</sup> Nest depredated by a predator.

<sup>b</sup> Nest lost as a result of any failure other than depredated (i.e., flooded, mowing, farm machinery, etc.).

The first stage of model selection identified 4 competing models describing time trends in mallard nest survival at the ELWC in north-central Iowa during 1998 to 2000 (Table 3). The model containing Constant survival was

the most parsimonious; therefore, we used this model for the next phase of the analysis. The second stage of our model selection analysis resulted in a set of 3 competing models (Table 3). The model containing Constant survival



**Figure 1.** Mean  $\pm$  1 standard error (SE) for patch size (top panel) and perimeter-to-area ratio (PAR; bottom panel) for land-cover types used by nesting mallards in the Eagle Lake Wetland Complex in north-central Iowa, USA, during 1998–2000.

**Table 3.** Nest survival model selection results for mallard nests located in the Eagle Lake Wetland Complex in north-central Iowa, USA, during 1998–2000. Covariates in the models included: constant survival over the nesting season, linear survival over the nesting season, quadratic survival over the nesting season, year, perimeter-to-area ratio (PAR), distance to the nearest wetland (Wetland), distance to the nearest grassland (Grass), the land-cover type where a nest was located (Patch Type), the area of the patch where a nest was located (Patch Size), and the broad patch category (Block vs Linear). Models Constant survival + Patch size and Constant survival + Block vs Linear were *post hoc* models.

Model	AIC <sub>c</sub> <sup>a</sup>	ΔAIC <sub>c</sub> <sup>b</sup>	w <sub>i</sub> <sup>c</sup>	K <sup>d</sup>	Deviance
Constant survival	1,506.11	0.00	0.33	1	1,504.11
Linear survival	1,506.94	0.83	0.22	2	1,502.94
Constant survival + Year	1,507.20	1.09	0.19	3	1,501.19
Linear survival + Year	1,508.08	1.97	0.12	4	1,500.07
Quadratic survival	1,508.94	2.83	0.08	3	1,502.94
Quadratic survival + Year	1,510.08	3.97	0.05	5	1,500.07
Constant survival + PAR	1,502.99	0.00	0.33	2	1,498.99
Constant survival + PAR + Wetland	1,504.15	1.16	0.18	3	1,498.15
Constant survival + PAR + Grass	1,504.95	1.95	0.12	3	1,498.94
Constant survival + PAR + Wetland + Grass	1,506.02	3.03	0.07	4	1,498.01
Constant survival + PAR + Patch type	1,506.73	3.74	0.05	7	1,492.71
Constant survival + Grass	1,506.77	3.78	0.05	2	1,502.77
Constant survival + Wetland	1,507.91	4.92	0.03	2	1,503.91
Constant survival + PAR + Wetland + Patch type	1,508.02	5.02	0.03	8	1,491.98
Constant survival + Patch type	1,508.35	5.36	0.02	6	1,496.33
Constant survival + PAR + Wetland + Grass + Patch type	1,509.99	7.00	0.01	9	1,491.95
Constant survival + Patch size	1,508.05	5.05	0.03	2	1,504.04
Constant survival + Block vs Linear	1,505.89	2.90	0.08	2	1,501.88

<sup>a</sup> AIC<sub>c</sub>—Akaike’s Information Criterion for small sample sizes.

<sup>b</sup> ΔAIC<sub>c</sub>—AIC<sub>c</sub>—minimum AIC<sub>c</sub>.

<sup>c</sup> w<sub>i</sub>—Akaike model wt.

<sup>d</sup> K—the no. of parameters in the model including the intercept.

and PAR was among the top models and the most parsimonious of the competing models. The PAR of the nest patch was the most important predictor of DSR ( $\beta = -9.18 \times 10^{-5}$  on the logit scale, 95% CI =  $-1.68 \times 10^{-4}$  to  $-1.55 \times 10^{-5}$ ), with the DSR decreasing with increasing PAR (Fig. 2). A model containing patch size had little model weight ( $w_i = 0.03$ ; Table 3), and the parameter estimate overlapped 0 ( $\beta = -9.16 \times 10^{-8}$  on the logit scale, 95% CI =  $-7.83 \times 10^{-7}$  to  $5.99 \times 10^{-7}$ ). Models that included distance to nearest wetland and distance to nearest grassland had  $\Delta AIC_c < 2$  (Table 3); however, parameter estimates also overlapped 0 ( $\beta_{\text{wetland}} = 1.55 \times 10^{-4}$  on the logit scale, 95% CI =  $-5.24 \times 10^{-4}$  to  $8.33 \times 10^{-4}$ ;  $\beta_{\text{grassland}} = -2.10 \times 10^{-4}$  on the logit scale, 95% CI =  $-5.61 \times 10^{-4}$  to  $1.41 \times 10^{-4}$ ).

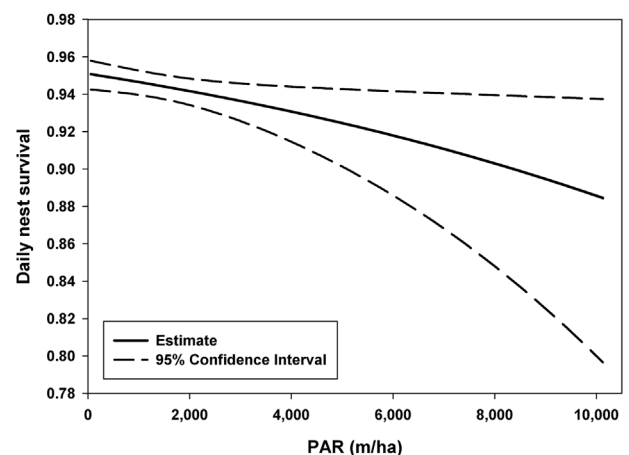
The overall DSR in our study was  $0.945 \pm 0.003$  SE or estimated 0.14 survival over the 35-day nest period (from the model with Constant survival + PAR using the mean value of PAR). We developed the *post hoc* model Constant survival + Block vs Linear, but it had less support than the model Constant survival + PAR. Additionally, parameter estimate overlapped 0 ( $\beta_{\text{Block vs Linear}} = 0.09$ , 95% CI =  $-0.058$ – $0.433$  on the logit scale). We found about equal numbers of nests in block ( $n = 157$ ) and linear patches ( $n = 161$ ); however, a greater percentage of nests in block habitat hatched (18%) compared with nests in linear habitat (11%;  $\chi^2_1 = 4.96$ ,  $P = 0.026$ ; Table 2).

Based on our models, nest survival was similar among years in the study and varied from 0.11 to 0.17 (DSR was  $0.951 \pm 0.006$ ,  $0.938 \pm 0.005$ , and  $0.948 \pm 0.006$  in

1998–2000, respectively). Hen success was 0.33, 0.23, and 0.27 in 1998, 1999, and 2000, respectively. Based on the model of Cowardin and Johnson (1979), nesting effort was 0.99, 0.99, and 0.91 for 1998, 1999, and 2000, respectively.

## DISCUSSION

We found that PAR had the most influence on nest survival of the covariates we considered. We found that configuration or shape of the nesting patches within the landscape was more important than patch size. The models with the



**Figure 2.** Daily nest survival estimates plotted against perimeter-to-area ratio (PAR) values for mallards in the Eagle Lake Wetland Complex in north-central Iowa, USA, during 1998–2000. Daily nest survival estimates were calculated with the model containing Constant Survival + PAR. The dashed lines represent the 95% confidence interval of the estimate.

addition of various patch types did not improve the deviance from the model with only PAR; so were noninformative covariates (Burnham and Anderson 2002, Arnold 2010). Our *post hoc* model with patch size was also not a competitive model. Previous studies in the PPR indicated that patch edge was an important influence on mallard nest success (Horn et al. 2005, Howerter et al. 2014). Howerter et al. (2014) found that nest survival declines with increasing habitat edge density in their long-term study in the Canadian portion of the PPR. The effect of edge on nest survival on birds in general is confusing; however, there appears to be some consensus that the effect is greater when occurring in highly fragmented landscapes, as is the case in our study (Lahti 2001, Horn et al. 2005, Eichholz and Elmberg 2014).

Mallards selectively nest in linear areas (Cowardin et al. 1985). Supporting this finding, we found large numbers of nests in roadside ditches and other linear patches. We also found that survival of nests from linear patch types was lower than those in blocks. If a substantial fraction of the mallard nesting population continues to select linear patches, overall nest survival rates may be negatively affected by the lower nest survival rates found in linear patches. Clark and Shutler (1999) found support for directional selection by mallards indicating proportionally greater nest failure at one end of their habitat gradient.

Contrary to our expectations, which were based on the findings of Kuehl and Clark (2002), we did not find a relationship between DSR and distance to grassland patches. One explanation for the lack of a relationship could be the small number of nests that were located far from grassland patches. The vast majority (76%) of nests were within 500 m of a grassland block. There are almost no wetlands outside of the managed grassland areas in the ELWC, which may have encouraged mallards to nest close to these grassland patches.

Nest survival in upland-nesting ducks is highly variable in space and time (Walker et al. 2013). Mallard nest survival in the Dakotas and Minnesota has ranged from 0.06 to 0.20 during the 1960s and the 1980s (Shaffer and Newton 1995), and averaged 0.11 from 1982 to 1985 in the PPR in Canada (Greenwood et al. 1995). Our estimate of annual mallard nest survival in this study was 0.14 during 1998–2000. The ELWC had very little grassland habitat outside of the public lands, which comprised approximately 5% of the study area (Fletcher and Koford 2003). Considering this lack of grassland habitat, it may be surprising that the estimated nest survival was not lower. In 1984–1985, Fleskes and Klaas (1991) estimated 0.09 annual nest survival (Mayfield method) at Union Slough National Wildlife Refuge, located approximately 30 km west of the ELWC. Their methods, however, included periodic visits to the nest sites to determine nest fates, which may have negatively influenced daily survival; whereas, we only approached the nest sites after we determined that nesting activity had been terminated.

Most studies of duck nest survival in the PPR have been conducted using standard nest searching methods (i.e., cable or chain drags), with nest sites visited by the investigator immediately after the female is flushed from the nest and

multiple times thereafter to determine the fate of the nest (Klett et al. 1986). We believe that by using radiomarked females and close proximity triangulation, we were able to avoid these confounding effects by never getting close to the nest until after the nesting activity had been terminated. Our nest survival results might therefore be somewhat higher, and possibly more representative than other studies that did not use these techniques. Additionally, an assumption of nest survival using standard nest searching techniques is that the nests monitored are a representative sample of the nests in the population. This assumption is seldom met because not all potential nesting habitats are searched in proportion to their availability. We used radiomarked mallards trapped wherever they were available throughout the study area to locate the nests that we monitored. Unless there was some bias introduced in our trapping methods, the sample of marked females should have been representative of the nesting female population using the study area and reduced bias due to poor *a priori* assumptions of nesting habitat (Daw et al. 1998, Powell et al. 2005, Peterson et al. 2015). Finally, the use of radiomarked females permitted us to find subsequent nesting attempts if a nest failed. This is critical for estimating population productivity and furthermore allowed us to calculate hen success for females that nested on the study area (Thompson et al. 2001, Peak and Thompson 2014, Peterson et al. 2015).

Hen success was high in our study area, averaging 27%. It should be noted that this is a conservative estimate of hen success for the radiomarked population because some of the marked hens that did not hatch nests on the study may have hatched nests after they left the study area. We did not have the resources to search for radiomarked females that left the study area. In a study in central North Dakota, USA, hen success was calculated to average 15% during 1977–1980 (Cowardin et al. 1985). We were able to independently determine both hen success and nest survival; therefore, we were also able to calculate yearly nesting effort. We found lower nesting effort during 2000, when October to June precipitation was below average, than in the 2 years when precipitation was above the long-term mean. This supports the view of Cowardin et al. (1985) that nesting effort is a function of water conditions.

Mallard reproduction and recruitment depend on the presence of herbaceous perennial vegetation for nesting and shallow wetlands for feeding (Krapu et al. 1997, 2000, 2006). In the eastern PPR, nest survival may have a more consistent relationship to perennial vegetation than in other areas of the PPR as a result of more consistent and often more abundant precipitation (Walker et al. 2013). According to global climate model projections, conditions in the Northern Great Plains will be warmer and drier (Millett et al. 2009), which will likely affect the number and quality of wetlands in the area (Poiani and Johnson 1993, but see Sofaer et al. 2016). Under drought conditions, ducks are often displaced or do not attempt to nest at all (Batt et al. 1992). Portmann et al. (2009) analyzed trends in precipitation data from 1950 to 2006 and found the greatest increases in mean daily precipitation were in the southeastern region of the PPR.

If the climate change projections materialize in the 21st century, the southeastern portion of the PPR could become a much more important breeding area for midcontinent mallards.

## MANAGEMENT IMPLICATIONS

Our findings suggest that PAR influenced mallard nest success, which suggests that the configuration or shape of nesting patches on the landscape may be more important than the size of the patches themselves. Adding wetland–grassland habitat areas to the intensively farmed region of north Iowa, particularly when expanding existing habitat complexes, will improve mallard production in the region. If climate change results in wetlands becoming drier in the western and central PPR (Johnson et al. 2005, 2010; Millett et al. 2009; but see Sofaer et al. 2016), restoration of additional wetlands and associated upland habitat in the southeastern portion of the PPR may become increasingly important. Because the effects of climate change remain uncertain, wildlife managers can continue to focus on land acquisition and wetland restoration in the southern portion of the PPR to hedge against the potential negative effects of climate change on wetland habitats in other parts of the PPR.

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