

# Nest survival of piping plovers at a dynamic reservoir indicates an ecological trap for a threatened population

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**Abstract** In the past 60 years, reservoirs have reshaped riverine ecosystems and transformed breeding habitats used by the threatened piping plover (*Charadrius melodus*; hereafter plover). Currently, 29 % of the Northern Great Plains plover population nests at reservoirs that might function as ecological traps because reservoirs have more diverse habitat features and greater dynamics in water levels than habitats historically used by breeding plovers. We examined factors influencing daily survival rates (DSR) of 346 plover nests at Lake Sakakawea (SAK; reservoir) during 2006–2009 by evaluating multiple a priori models, and we used our best model to hindcast nest success of plovers during 1985–2009. Our observed and hindcast estimates of nest success were low compared to published estimates. Previous findings indicate that plovers prefer nest sites that are low relative to water level. We found that elevation of nests above the water level had a strong positive correlation with DSR because water levels of SAK typically increased throughout the nesting period. Habitat characteristics on the reservoir differ from those that shaped nest-site selection for plovers. Accordingly, extraordinary nest loss occurs there in many years, largely due to inundation of nests, and based on low fledging rates those losses were not compensated by potential changes in chick survival. Therefore, our example supports the concept of ecological traps in birds because it addresses quantitative assessments of habitat preference and productivity over

25 years (since species listing) and affects a large portion of the population.

**Keywords** Flooding · Productivity · Recruitment · Shorebird · Waterbird

## Introduction

Animals evolved the use of cues to select resources that optimize individual fitness (Hutto 1990; Martin 1998; Clark and Shutler 1999), but those cues are at least one step removed from the ultimate mechanism that influences fitness (Robertson and Hutto 2006). Land use changes have affected the composition and availability of habitat for many species around the globe (Foley et al. 2005). When habitats change from those under which a species evolved, resource-selection cues may no longer be informative for individuals to make optimal decisions, and thus “trap” animals into using sub-optimal habitats (hereafter ecological trap; see Schlaepfer et al. 2002). If species do not have adequate plasticity in resource-selection behavior then habitat change can result in a precipitous decline in recruitment or survival and can lead to extinction of populations (Schlaepfer et al. 2002). Although there have been countless papers purporting evidence of ecological traps, two recent literature reviews revealed that few studies on birds provide rigorous support (i.e., quantitative information about habitat preferences and fitness outcomes) for this ecological theory and none demonstrate ecological traps of a temporal and spatial magnitude sufficient enough to influence populations (Robertson and Hutto 2006; Part et al. 2007). Here we present evidence of an ecological trap where (1) a large portion of a threatened bird population uses a novel breeding habitat that is different from the

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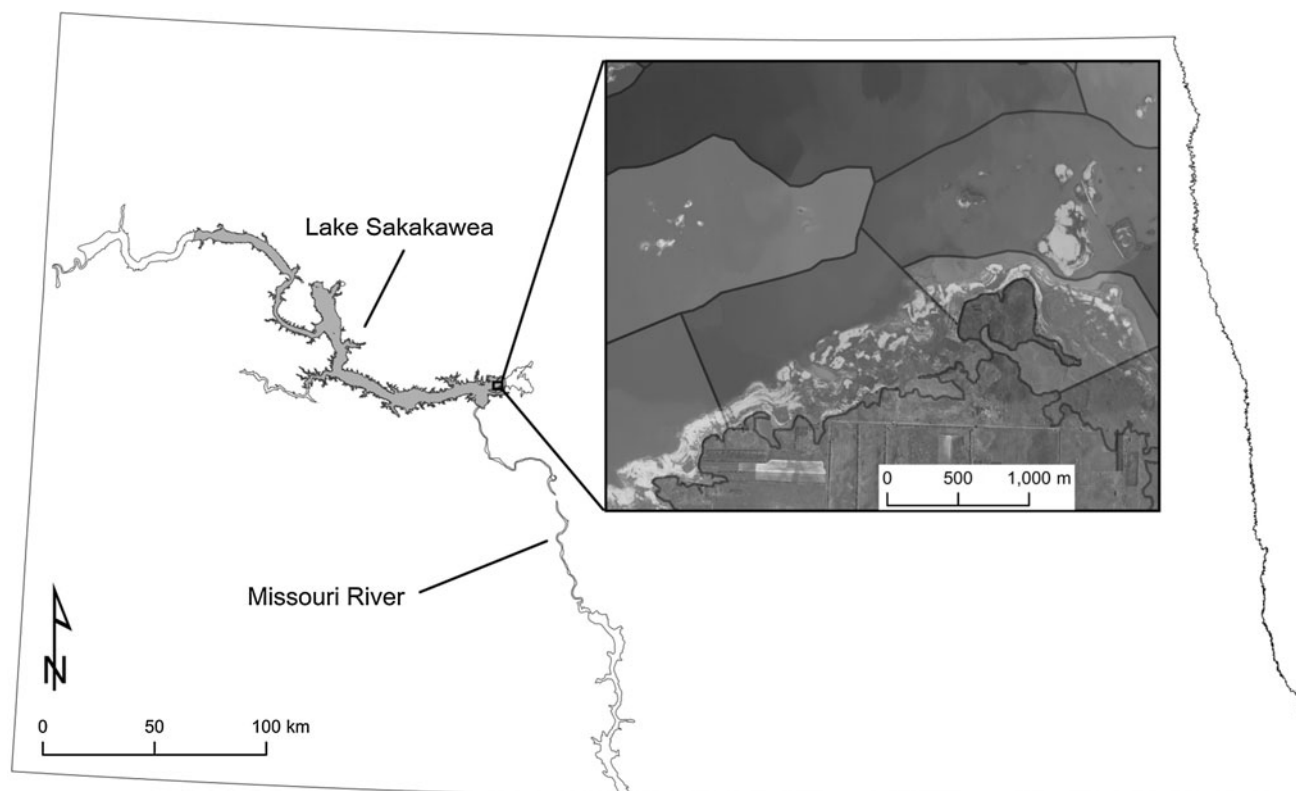
habitat where they evolved resource-selection behaviors; (2) the resulting use of resource-selection cues lead to precipitous reproductive failures; and (3) a predictive model indicates that these failures occurred in the majority of the past 25 years.

Piping plovers (*Charadrius melodus*; hereafter plovers) evolved nest-site selection behaviors while breeding at shorelines of alkali wetlands, sandbars on major rivers, and coastal beaches (Prindiville Gaines and Ryan 1988; Elliott-Smith and Haig 2004). Periodic fluctuations in water level maintain unvegetated conditions in these habitats. Plovers adapted their nest-site selection behaviors to capitalize on areas that are mostly devoid of vegetation, with sandy substrate sometimes broken up by larger sediments (Cairns 1982; Burger 1987; Prindiville Gaines and Ryan 1988; Espie et al. 1996). It is thought that open areas with coarse substrate facilitate nest defense behaviors and nest crypsis (Whittingham et al. 2002; Colwell et al. 2011; Anteau et al. 2012).

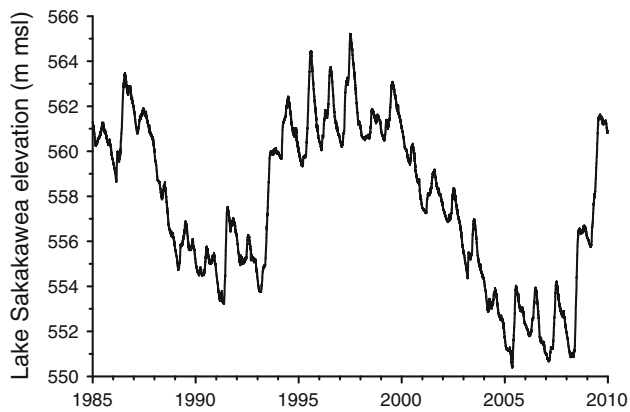
The Federally (United States) threatened population of plovers in the Northern Great Plains used breeding habitats on alkali wetlands and sandbars of major rivers of the United States and Canada, but in the 1950s, shorelines of managed reservoirs became a novel alternative breeding habitat for this population. By 2006, 29 % of this

population used reservoir habitat (Elliott-Smith et al. 2009). However, nesting habitats on reservoirs have a more diverse array of substrate sizes, elevations, and slopes and a larger range of water level fluctuations than those where plovers evolved (Anteau et al. 2012). Accordingly, it is possible that nest-site selection behaviors evolved by plovers at their historic breeding habitat will not lead to successful reproduction for plovers breeding at reservoirs.

Lake Sakakawea (hereafter SAK) is a large (163,800 ha) reservoir of the Missouri River (Fig. 1). SAK became an important breeding area for plovers with 43 % of Missouri River adult plovers recorded there in 2005 [US Army Corps of Engineers (USACE), unpublished data]. Water levels on SAK fluctuate widely in response to climate variability and management actions (Fig. 2). Declines in water levels provide an abundance of newly exposed unvegetated shoreline that is used extensively by nesting plovers; coinciding with water declines from 1998 to 2005 was a >500 % increase in breeding adults (USACE, unpublished data). Water levels also vary intra-annually (Fig. 2); generally increasing in early summer resulting from Rocky Mountain snow melt and local precipitation. Intra-annual increases in water level at SAK typically occur between the time plovers initiate and hatch nests (Wiltermuth et al. 2009), which potentially puts nests at



**Fig. 1** Map of North Dakota, USA depicting our study area (shaded in gray) at Lake Sakakawea and an example of our study area segmentation



**Fig. 2** Water level at Lake Sakakawea during 1985–2009. Adapted from USACE (2010)

risk of inundation, depending upon where and when nests are initiated. Indeed, plovers at SAK preferred sites that were lower, relative to water level at initiation date, than were unused sites (Anteau et al. 2012), clearly exposing nests on reservoirs to risk of inundation if water level increases during the nesting period.

Reservoirs are prime examples of human controlled and manipulated systems, so understanding habitat characteristics that influence nest survival of plovers on SAK is a logical step toward understanding productivity responses of animals to novel and highly modified environments.

Furthermore, this understanding would have relevance to management of this species because reservoirs are used heavily by plovers and provide a diverse and dynamic system with opportunities for enhancing plover productivity through management of habitat or water level. Accordingly, we evaluated characteristics that influence daily survival rates (DSR) of 346 plover nests from summers 2006–2009. Specifically, we examined several mechanistic hypotheses that may influence nest survival (Table 1). Then we used our best model to predict nest success for 1985–2009. Lastly, we examined observed and predicted nest success in relation to habitat preference data (Anteau et al. 2012) and all available nest survival data for plovers to evaluate if habitat preferences optimize nest survival in this novel habitat.

## Materials and methods

### Study area

Our study area included all shoreline and island habitats at SAK (Fig. 1). Each year our study area was bounded between the shoreline elevation and the maximum flood level of the reservoir (565 m msl). Detailed description of our study area and processes influencing habitat dynamics are available in Wiltermuth et al. (2009), Anteau and Sherfy (2010), and Anteau et al. (2012).

**Table 1** Model suites, variable names and descriptions, and hypothesized relationships with daily nest survival of piping plovers at Lake Sakakawea during summers 2006–2009

Suite	Variable name	Variable description	Hypothesis
INUNDATION	Relative elevation	Interval-specific relative elevation above water (transformed by hyperbolic tangent)	Nests with low relative elevations are at risk of failure by inundation
ISOLATION	Island distance	Distance of Island to shoreline (ln)	Islands farther from shore have fewer land predators and less nest predation than mainland shorelines
	Habitat index	Proportion of unvegetated habitat within 75 m of nest	Larger patches of habitat are less likely to attract predators
	Distance to shoreline	Distance between the nest and the shoreline at initiation date	Nests farther from the shoreline are safer from predators that may forage along the shoreline
CRYPSIS	Vegetation cover	Percent coverage of vegetation and litter at the nest site	Vegetation at the nest site increases nest crypsis and decreases nest predation by visual foragers
	Cobble	Presence or absence of a cobble at the nest site	Cobble at the nest site increases crypsis of adult during incubation and decreases nest predation by visual foragers
	Gravel	Percent coverage of gravel at the nest site	Gravel at the nest site increases egg/nest crypsis and decreases nest predation by visual foragers
VISIBILITY	Slope at 10 m	Maximum slope of four measurements radiating out 10 m from nest	Greater slopes decrease visibility from the nest and decrease effectiveness of nest defense behaviors
	Vegetation cover at 10 m	Mean percent coverage of vegetation and litter of four quadrats 10 m from the nest	Greater vegetation cover decreases visibility from the nest and decreases effectiveness of nest defense behaviors

**Table 2** Numbers of 2-km segments and sampling percentages (%) of shoreline surveyed within high ( $n = 53$ ), medium ( $n = 88$ ), and low ( $n = 403$ ) historical piping plover nest abundance strata on Lake Sakakawea, North Dakota

Years	Total	High	Medium	Low
2006	17 (3.1)	7 (13.2)	5 (5.7)	5 (1.2)
2007	30 (5.5)	18 (34.0)	7 (8.0)	5 (1.2)
2008	30 (5.5)	18 (34.0)	7 (8.0)	5 (1.2)
2009	35 (6.4)	24 (45.2)	6 (6.8)	5 (1.2)

### Sampling design and allocation

We used a stratified-random sampling design based on historic plover nest densities (USACE, unpublished data) to allocate our survey effort. We used 2004 National Agricultural Imagery Program photos to delineate the shoreline of SAK. We divided the shoreline into 544 segments  $\sim 2$  km in length (Fig. 1). We classified each segment into one of three strata based on counts of nests from 1998 to 2005; the strata were defined as: low use ( $<2$  nests), medium use (2–9 nests), and high use ( $>9$  nests). We used Neyman allocation (Thompson et al. 1998) to guide sampling intensity for each stratum, and all segments were selected randomly from strata. We selected 18 segments for inclusion in all years, we added 12 segments during 2007–2009, and we selected seven additional high use segments for 2009 because increased water level had inundated two segments and markedly reduced available habitat on other segments (Table 2).

### Nest searching and monitoring

We systematically searched study segments for nests every 2–3 days throughout the nesting season (April–July) in 2006–2009. We searched for nests (scrape containing  $\geq 1$  egg) and also used adult behavior consistent with nest defense to aid in searching for nests. Upon discovery of a nest, we recorded a GPS location (post-processed differential correction; Trimble® model GeoXT, Trimble Navigation Limited, Sunnyvale, CA) and floated eggs to estimate incubation stage (Hays and LeCroy 1971). We estimated nest initiation date with the following equation: initiation date = discovery date – days incubated –  $2 \times (\text{clutch size} - 1)$ . Examination of the incubation period for plovers at SAK and other Missouri River breeding areas indicated that the incubation period for plovers averaged 25 days (B. Skone, US Geological Survey, unpublished data). Accordingly, we estimated hatch date by adding 25 days to the date when incubation began, as determined by flotation or laying sequence. We revisited nests on our search interval, except we visited nests

daily beginning one day prior to expected hatch or if we observed pipped eggs. Frequent nest visits improved our ability to accurately determine nest fate.

We classified nests as successful if we observed any of the following evidence in or within 0.3 m of the nest bowl: appropriate-aged chicks, pipping fragments (eggshell fragments 1–4 mm without membranes attached), shells from hatched eggs (Mabee 1997), chick droppings, or chick tracks. We classified nests that did not meet any of the above criteria as failed if all eggs were inundated (displaced from the nest bowl and missing due to wave action), crushed by hail or an animal, drifted under sand, abandoned, or if nest/eggs were missing and could not have hatched based on the previously estimated hatch date. We classified nests as unknown fate if (1) we had no evidence of what had happened, (2) the only evidence we had was appropriately aged chicks in the vicinity of a nest ( $>0.3$  m), or (3) the nest/eggs were missing and it was possible that the nest could have hatched based on the estimated hatch date.

### Nest-site characteristics

We measured habitat characteristics at the nest site ( $1\text{-m}^2$  quadrat centered on the nest) and at 3- and 10-m radii from the nest (hereafter nest areas). Nest areas consisted of four habitat measurements using the  $1\text{-m}^2$  quadrat in each cardinal direction ( $n = 4$  for each distance). We took nest site and area measurements upon nest discovery or on the next visit. We also measured shortest distance from the nest to the shoreline of SAK using a laser range finder (Bushnell Elite 1500, Overland Park, KS, and Opti-Logic 800XL, Tullahoma, TN). We collected position and elevation data at the center of each quadrat. We measured elevation using a (1) rotating laser level (LaserMark™ LMH-GR, CST/Berger, Watseka, IL) relative to a nearby temporary elevation benchmark or (2) real-time kinematic survey (Trimble GPS model 5800 and 5700). We measured benchmark elevations annually with survey-grade GPS equipment (Trimble® GPS model 5800 and 5700) using fast-static data collection  $>120$  min, National Geodetic Survey OPUS-static processing (National Oceanic and Atmospheric Administration, Washington, DC).

Within each quadrat we collected a suite of habitat variables describing vegetation cover, substrate composition, and debris cover. We used a modified Daubenmire (1959) classification for visual coverage estimations of vegetation, substrate and debris variables. The classification was as follows: 0, 0–5, 6–15, 16–30, 31–45, 46–70,  $>70$  % (Sherfy et al. 2009). Within all quadrats, we noted the presence or absence of a cobble and estimated coverage of gravel, small debris ( $<2$ -cm diameter objects) and leaf litter (Sherfy et al. 2009). We converted all visual cover classifications to the mid-point of their class (Sherfy et al. 2009).

We calculated the amount of bare-substrate obstruction by summing the percentages of (1) vegetation cover, (2) leaf litter, and (3) small debris. We calculated means for bare-substrate obstruction at 3 and 10 m from the nest ( $n = 4$  for each). Slope 3 and 10 m from the nest was calculated using the maximum slope measured among the nest and each of the four nest-area measurements at each distance. We calculated the percent of unvegetated habitat within 75 m of each nest, using a supervised habitat classification ( $<15\%$  vegetation cover = unvegetated) that was derived using remote sensing of pan-sharpened SPOT 5 satellite imagery (Spot Image Corporation, Chantilly, VA; M.J. Anteau, US Geological Survey, unpublished data).

### Statistical analyses

We used logistic exposure models (Shaffer 2004) to examine factors that influenced daily survival of nests throughout laying and incubation periods. We calculated interval length (days) as the visit date minus the previous visit date; however, if the nest hatched or failed during the interval and the estimated hatch date was greater than the previous visit date then we assigned interval length as the minimum of (1) visit date minus the previous visit date, or (2) estimated hatch date minus the previous visit date. For each nest-visit interval, we calculated the relative elevation above the water level of SAK by subtracting maximum reservoir pool elevation (USACE 2010) for the interval from the elevation of the nest site (hereafter relative elevation). We calculated the maximum temperature and wind speed for each interval using weather data from the weather station nearest to each nest (National Climatic Data Center, National Oceanic and Atmospheric Administration, <http://www.ncdc.noaa.gov/oa/ncdc.html>). We calculated nest age by adding  $2 \times$  (clutch size  $- 1$ ) to the number of days incubated, and mid-interval age was the nest age at the midpoint between present and previous visits. For all models the effective sample size was calculated as the number of days nests were known to survive  $+ \text{total number of intervals in which a failure occurred}$  (Rotella et al. 2004).

We examined four suites of variables that represent different hypotheses (Table 1). We also included year, mid-interval age, mid-interval date, and maximum temperature and wind speed as covariates in all models. We predicted these covariates may be important for explaining variation in nest survival, but were not relevant to our hypotheses. Unlike other breeding habitats for plovers, managers did not install predator exclosures around plover nests at SAK, so we did not incorporate an exclosure effect in our models.

Prior to model selection we competed VISIBILITY variables measured at 3 and 10 m. The full model with the VISIBILITY variables measured at 10 m (deviance

1,235.79,  $k = 17$ ,  $AIC_c = 1,269.91$ ,  $w_i = 0.92$ ) fit the data better than that with the 3 m scale (deviance 1,240.55,  $k = 17$ ,  $AIC_c = 1,274.67$ ,  $w_i = 0.08$ ). Accordingly, for subsequent models we used only the VISIBILITY suite with variables measured at 10 m to avoid potential multicollinearity issues. Then we examined correlations among all variables. The absolute values of correlation coefficients were below 0.2 and 0.1 in 87 and 58 % of the covariate pairs, respectively. Four pairs of covariates had correlation coefficients  $>0.4$  (mid-interval date-by-maximum temperature: 0.44, mid-interval age-by-mid-interval date: 0.46, island distance-by-habitat index: 0.51, and vegetation cover at nest-by-vegetation cover at 10 m: 0.58).

We also examined whether nest survival varied among strata to determine if survival estimates would need to be weighted in accordance to strata to produce a SAK-wide estimate. No nests were observed in the low-use stratum, so examination of strata only encompassed medium and high use areas. We evaluated strata in our full model. We concluded the effect of strata ( $\beta = -0.1065 \pm 0.2064$  SE; 85 % CL:  $-0.4037, 0.1907$ ; Wald  $\chi^2 = 0.27$ ) was not an important influence on nest survival, and we did not include strata in subsequent models.

We examined the null model, each suite individually, and all possible combinations of model suites (16 models). We ranked models by Akaike's information criterion corrected for small sample size ( $AIC_c$ ) and selected the most parsimonious model based on  $AIC_c$  and model weights ( $w_i$ ) for all models (Burnham and Anderson 2002). We plotted and interpreted covariates for which the 85 % confidence limit of the estimate did not overlap zero (Arnold 2010).

Catastrophic nest failures due to a single mortality agent can violate the assumption that nests fail independently of one another (Johnson and Shaffer 1990). However, if catastrophic failure is predictable on the basis of a measured covariate, then it is still reasonable to assume that nest fates are independent, conditional on that covariate being in the model (Shaffer 2004). In our case, elevated rates of nest failure resulting from rising lake levels were predictable from occasion-specific knowledge of the relative elevation of each nest above the water level, justifying the assumption of conditionally independent nest fates.

### Data visualization

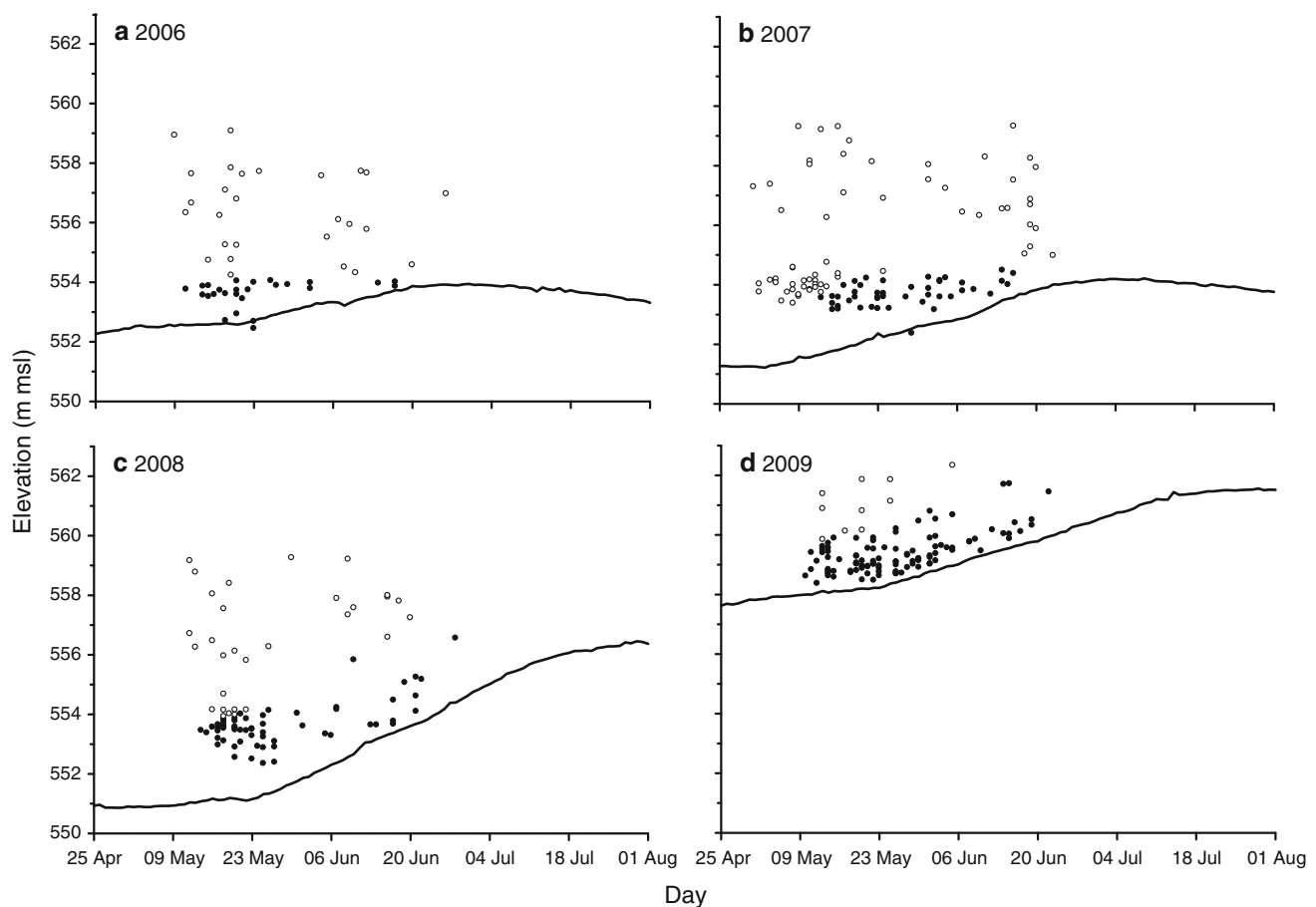
We estimated DSRs ( $\pm 85\%$  CL) in relation to important covariates using procedures outlined in Shaffer and Thompson (2007). For each covariate, we estimated DSR ( $\pm 85\%$  CL) at  $>20$  levels that were systematically allocated throughout the covariate range. We plotted spline curves for estimates ( $\pm 85\%$  CL) of covariates in our most parsimonious model using SigmaPlot (version 10.0, Systat Software Inc., San Jose, CA).



We constructed a series of plots that characterized potential nest site inundation in relation to the timing and amplitude of water level increases in summers 2006–2009 (Fig. 3). We classified nest sites as either (1) locations where the relative elevation of the nest site was  $<0.36$  m prior to the estimated hatch date (hereafter inundated nest sites), or (2) locations where relative elevation was  $>0.36$  m above the lake elevation until the estimated hatch day (hereafter dry nest sites). We used 0.36 m above the lake as a threshold because below this elevation (1) DSR declined precipitously from 0.90 (see below; Fig. 4) and (2) nests with relative elevation  $<0.36$  generally were in danger of inundation through wave action. We assumed that the clutch size of nests that failed during laying would have been four eggs thus requiring 31 days to hatch. We plotted inundated and dry nest sites in relation to their elevation, the nest initiation date, and the changing elevation of the water surface at SAK (Fig. 3).

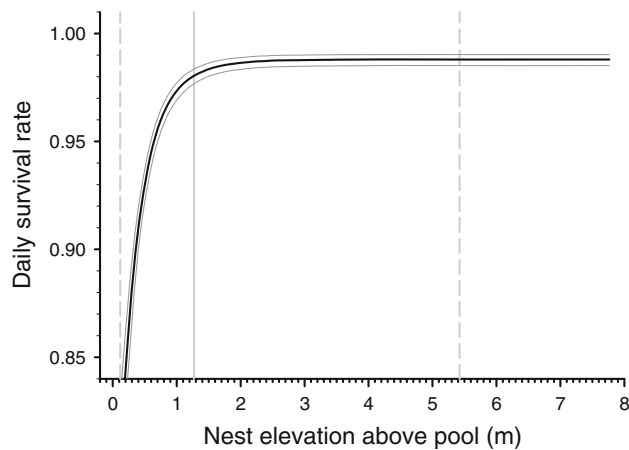
#### Estimating nest success

Choosing a method for estimating nest success is not straightforward when DSRs are low and not temporally consistent (Shaffer and Thompson 2007). We caution against computing cumulative nest survival from our daily estimates without accounting for trends in DSRs by mid-interval date (Fig. 5) and relative elevation (a date-varying covariate). Similarly, we believe Horvitz–Thompson estimators would be problematic because of the low survival rates we observed (Shaffer and Thompson 2007). We reported apparent nest success rates because our intensive monitoring techniques should have led to minimal bias resulting from nests failing prior to our crews being able to find them (Johnson and Shaffer 1990; Shaffer 2004). However, we acknowledge that our apparent nest success estimates could be slightly high, especially for 2006 because in that year the average age of nests upon discovery was 7 days.



**Fig. 3** Elevation (m msl) at initiation date for nests that were above the water level ( $>0.36$  m) until their expected hatch date (31 days after nest initiation; *unshaded circles*) and those that were below water level ( $<0.36$  m) before their expected hatch date (*shaded*

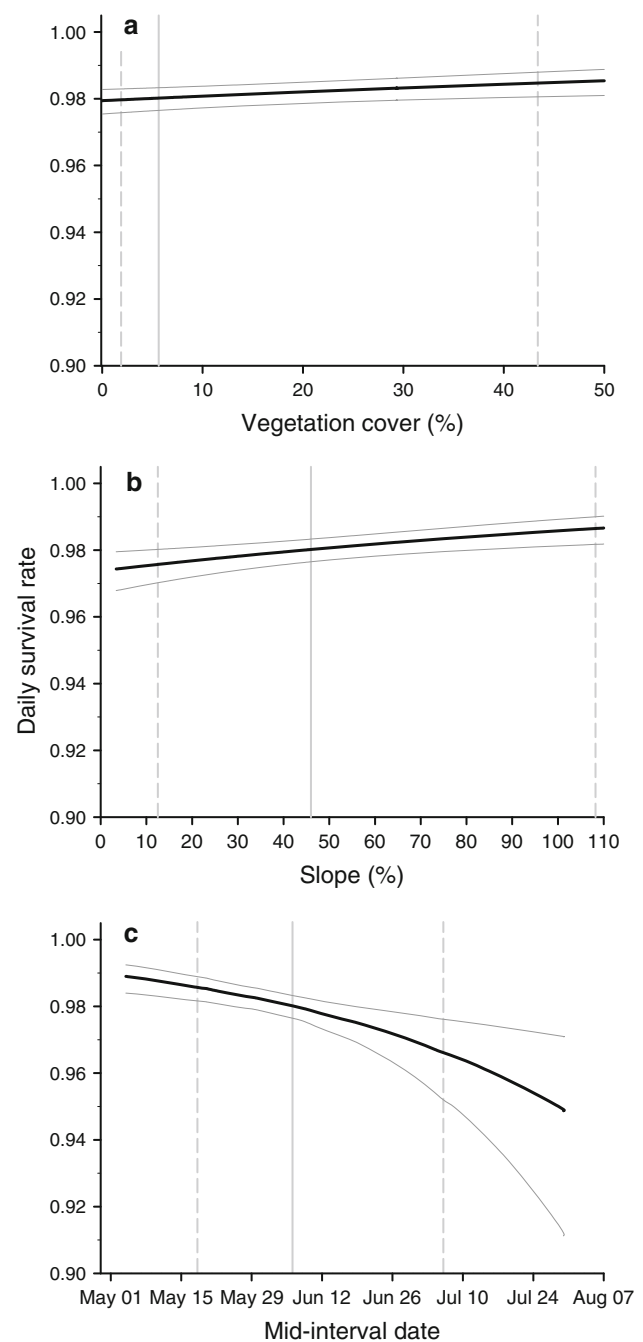
*circles*), including surface water level (m msl; *black line*) during summers 2006–2009 at Lake Sakakawea. Water level data adapted from USACE (2010)



**Fig. 4** Relationship of relative elevation above pool level (m) to daily survival rate ( $\pm 85\%$  CL) for piping plover nests at Lake Sakakawea during summers 2006–2009. *Solid vertical line* indicates the median relative elevation, and *dashed vertical lines* indicate 5th and 95th percentiles

#### Hindcasting virtual nest success

Our estimates of nest success were influenced by the water level changes that occurred in the years of our study. However, since plovers were listed in 1985, water-level increases on SAK have varied in timing and amplitude annually. Accordingly, it is important to understand how nest success may respond to those past water level histories. Given that the relative elevation of the nest was the most important and influential variable in our most parsimonious model (see “Results”), we used our model to predict nest success under water level regimes that occurred on SAK during summers 1985–2009. For each year, we derived a sample of virtual nests ( $n = 346$ ) with identical initiation dates and relative elevations (at initiation date) to our observed nest data from 2006 to 2009. We then estimated daily relative elevation of each virtual nest based on the recorded reservoir water elevations for each day the nest could have been active (31 days past initiation day). We used our entire sample of virtual nests for years (1985–2009) when water level was  $<556$  m ( $n = 10$ ) and only those derived from 2009 for years when water level was  $>556$  m ( $n = 15$ ). Limiting virtual nests for high water years minimized the number of nests that had to be excluded from the analysis because their estimated nest elevation was above our study area boundary (only 1 % of virtual nests excluded). For each year, virtual nest, and day we created a nest-survival prediction using time-varying estimates for relative elevation (calculated from daily water level) and mid-interval day. We set values for other covariates at their medians observed during 2006–2009. We used our nest initiation dates in past years because there was no trend in the timing of initiations for plover



**Fig. 5** Relationships of **a** percent vegetation cover 10 m from the nest, **b** percent slope 10 m from the nest, and **c** mid-interval date to daily survival rate ( $\pm 85\%$  CL) for piping plover nests at Lake Sakakawea during summers 2006–2009. *Solid vertical line* indicates the median of the independent variable, and *dashed vertical lines* indicate fifth and 95th percentiles

nests at SAK since 1998, when monitoring began (USACE, unpublished data). Our approach assumed that other sources of mortality (e.g., predation) and nest-site characteristics were constant and that our sample of nests approximated them. For each virtual nest, we calculated the

cumulative survival probability (hereafter nest success) and 85 % confidence limits by multiplying all daily survival estimates and estimates of upper and lower 85 % confidence limits. We calculated annual means for virtual nest success. Lastly, we plotted virtual nest success for 1985–2009 in relation to water level rise (May 15–June 30) and initial water level (May 15) using a contour plot (SigmaPlot).

## Results

We measured habitat characteristics at 52, 101, 83, and 110 nest sites in 2006–2009, respectively. Nest searches were conducted on segments at an average interval of 4.7, 2.9, 2.9, and 3.1 days in 2006–2009, respectively. Return visits to check nest status occurred more frequently (4.4, 2.6, 2.3, and 2.7 days in 2006–2009, respectively). The average number of days between discovery of the nest and estimated nest initiation were 7.0, 3.8, 3.3, and 2.7 days in 2006–2009, respectively.

Apparent nest success ( $\pm$ SE) was 24 ( $\pm$ 6), 28 ( $\pm$ 4), 24 ( $\pm$ 5), and 3 ( $\pm$ 2) % in 2006–2009, respectively. Regardless of eventual fate of nests, 42–91 % of nest sites were inundated prior to the date the nest was expected to hatch (Fig. 3).

We modeled 2,022 intervals representing an effective sample size of 4,981. The model containing the INUNDATION and VISIBILITY suites (Table 1) was the most parsimonious; it accounted for >71 % of the model weight among our set of 16 models (Table 3). Within this model, the hyperbolic tangent of relative elevation was the most influential variable (Wald  $\chi^2 = 217.53$ ) and had a strong positive relationship with DSR ( $\beta = 3.3851 \pm 0.2295$  SE; Fig. 4). DSR also was positively correlated with vegetation cover (Wald  $\chi^2 = 3.64$ ,  $\beta = 0.0070 \pm 0.0037$  SE; Fig. 5) and slope at 10 m from the nest (Wald  $\chi^2 = 5.43$ ,  $\beta = 0.0062 \pm 0.0027$  SE; Fig. 5). DSR was 2.4, 0.7, and 1.7 % greater in 2006, 2007, and 2008 than it was in 2009,

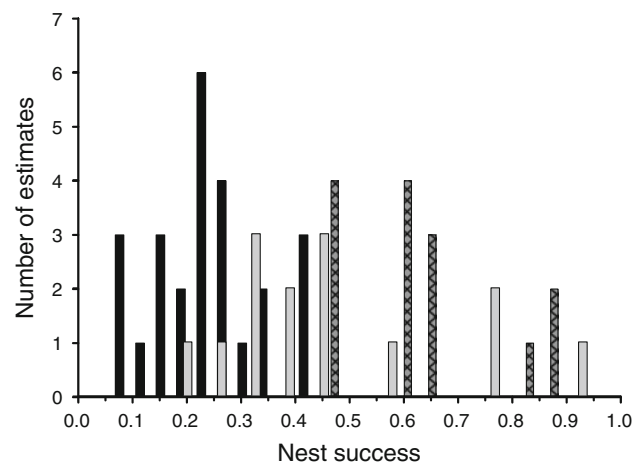
while holding all other covariate values at their medians. DSR was negatively correlated with mid-interval date (Wald  $\chi^2 = 6.39$ ,  $\beta = -0.0181 \pm 0.0071$  SE; Fig. 5).

Predicted virtual nest success (upper and lower 85 % CL) was 35 (30, 40), 28 (24, 31), 21 (18, 23), and 8 (6, 9) % for nests in 2006–2009, respectively. Model predicted virtual nest success had good correspondence with observed apparent nest success ( $R^2 = 0.72$ ), despite our assumption that non-inundation mortality was constant. From 1985 to 2009, 33 % of years had predicted nest success <19 % and 67 % of years had predicted nest success <25 % (Fig. 6). Increases in water level during the breeding season had a greater negative influence on predicted annual nest success when water level was higher on May 15 (Fig. 7).

## Discussion

### Observed and predicted nest success estimates

Distributions of our observed and model-predicted nest success estimates for SAK are markedly lower than those observed at other breeding areas (Fig. 6). We assume that

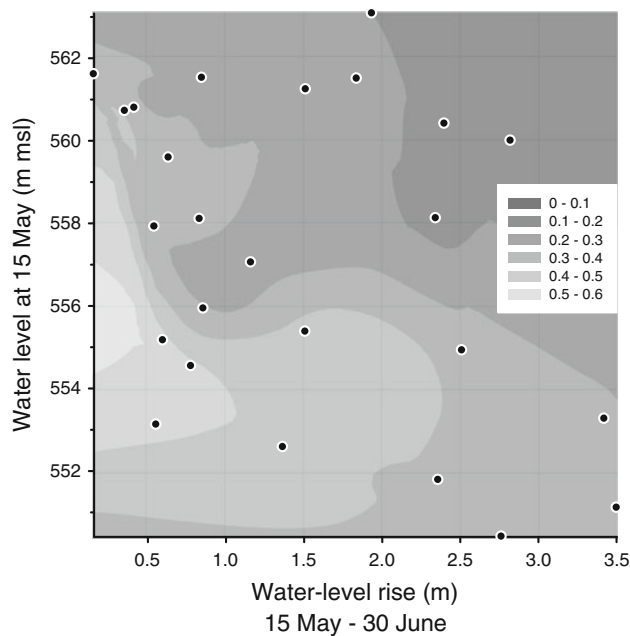


**Fig. 6** Histograms of nest success estimates for piping plovers throughout their breeding range. *Black bars* are annual mean predicted nest success of virtual piping plover nests at Lake Sakakawea during summers 1985–2009 ( $n = 25$ ); *light-grey bars* are nest success estimates from published literature where nests were not protected by predator exclosures or fencing ( $n = 14$ ) (Haig and Oring 1988; Prindiville Gaines and Ryan 1988; Rimmer and Deblinger 1990; Mayer and Ryan 1991; Patterson et al. 1991; Melvin et al. 1992; Powell and Cuthbert 1992; Espie et al. 1996; Mabee and Estelle 2000; Kruse et al. 2001; Harris et al. 2005; Ivan and Murphy 2005; Cohen et al. 2009); *dark-grey bars (with cross hashing)* are nest success estimates from published literature where nests were protected by predator exclosures or fencing ( $n = 14$ ) (Rimmer and Deblinger 1990; Mayer and Ryan 1991; Patterson et al. 1991; Melvin et al. 1992; Espie et al. 1996; Jones 1997; Mabee and Estelle 2000; Kruse et al. 2001; Ivan and Murphy 2005; Cohen et al. 2009; Catlin et al. 2011; J.H. Stucker and F.J. Cuthbert, unpublished data)

**Table 3** Model suites, number of parameters (K), Akaike's information criterion for small sample size ( $AIC_c$ ), increase over the lowest  $AIC_c$  ( $\Delta AIC_c$ ), and Akaike model weight ( $w_i$ ) of models ( $w_i > 0.01$ ) used to examine factors influencing daily nest survival of piping plovers at Lake Sakakawea

SUITES	K	$AIC_c$	$\Delta AIC_c$	$w_i$
INUNDATION, VISIBILITY	11	1,261.7	0.0	0.71
INUNDATION, VISIBILITY, ISOLATION	14	1,264.3	2.6	0.19
INUNDATION, VISIBILITY, CRYPSIS	14	1,267.4	5.7	0.04
INUNDATION	9	1,268.1	6.3	0.03





**Fig. 7** Success of virtual piping plover nests in relation to initial water level and water level rise. Circles represent annual nest success estimates (1985–2009) used to build the response surface. Lighter shades represent higher nest success

the array of published nest success estimates for plovers from studies conducted throughout their breeding range are representative of conditions that contribute to the population of plovers being in continued jeopardy of extinction (Elliott-Smith and Haig 2004). Thus, our estimates suggest that when SAK is used heavily by plovers it represents a potential threat to the persistence of the plover population because of the potential for marked decreases in recruitment. Nest success is just one component of recruitment, higher chick survival rates could compensate for high nest losses. However, without strong density-dependent chick survival, fewer nests hatching would translate to fewer chicks fledging and recruiting into this population. Furthermore, as water level increases the amount of brood-rearing habitat decreases. For another study at SAK, we recorded the ratio of fledglings to the minimum number of adult pairs as 0.46, 0.30, and 0.04 for 2007, 2008, and 2009, respectively (M.J. Anteau, US Geological Survey, unpublished data). Our estimates of fledge ratios were well below the estimated 1.10 that is required to maintain a stable population (Larson et al. 2002). Regardless of chick survival rates, nest survival was so low that potential compensatory relationships with chick survival did not cause fledging rates to increase to a level that even approaches that required for a stable population.

According to the 2001 international census of plovers, SAK accounted for 40, 11, and 7 % of the Missouri River, Northern Great Plains, and world plover populations,

respectively, and 29 % of Northern Great Plains plovers used reservoirs during summer 2006 (Elliott-Smith and Haig 2004; Elliott-Smith et al. 2009). However, the detection rate of plovers from previous monitoring may be lower on SAK and perhaps other reservoirs than other reaches of the Missouri River (T.L. Shaffer, US Geological Survey, unpublished data); thus, the international census and monitoring data likely underestimate the proportion of the plover population using SAK and other reservoirs for breeding. SAK and other reservoirs were used heavily by plovers including during drought years (e.g., 2006, 2007), years when their natural wetland habitats should be readily available in adjacent areas (Anteau 2012). This suggests that reservoir habitat is not just selected when all other available habitat is used or otherwise unavailable. Based on monitoring data from 2010, only 6 % of plovers using the Missouri River were observed on SAK (USACE, unpublished data) suggesting that number of plovers breeding at SAK varies with water level fluctuations and requires further study. All told, we argue that SAK and perhaps other reservoirs are variably important areas for plovers with respect to their potential to influence population-wide recruitment. Moreover, reservoirs have great potential for catastrophic reproductive failure, but provide opportunities for conservation through water level management and habitat manipulation because lands within the flood stage are publically owned and managed.

### Ecological trap

When faced with an array of options at SAK, plovers preferred nest locations that were lower in elevation, than those available (Anteau et al. 2012); however, lower-elevation nest sites clearly are more vulnerable to inundation. Accordingly, nest-site selection features lead to nest failures for plovers nesting at SAK, except in fairly rare years when water level begins low and increases little or late during the nesting season. Similarly, our hindcasting results indicate that success of virtual plover nests at SAK was markedly low, relative to other breeding areas, during most years since the listing of the species in 1985. We found that slope and vegetation 10 m from nests positively influenced DSR of nests. However, vegetation and slope 10 m from nests were not important for nest-site selection by plovers, but vegetation and slope 3 m from nests negatively influenced nest-site selection (Anteau et al. 2012). Incongruence between nest-site selection results and those for nest survival suggest a spatial mismatch exists between cues plovers use for selection of habitat and features that influence breeding success. Lastly, island habitats on reservoirs attract adult plovers for nesting (M.J. Anteau, US Geological Survey, unpublished data), but do not provide a detectable increase in DSR of nests. Altogether, habitat-

selection behaviors at the landscape-, territory-, and nest-scale led plovers to nest in areas where they experienced low nest success in most years since the species was federally listed in 1985 and fits the definition of an ecological trap (see Schlaepfer et al. 2002; Robertson and Hutto 2006).

The lack of evidence in support of ecological traps in avian literature is largely due to the difficulty of measuring habitat preference and individual fitness in quantitative studies (Robertson and Hutto 2006; Part et al. 2007). Furthermore, for an ecological trap to impact a population it must (1) have long-term effects relative to the generation time of the species and (2) be spatially widespread so that a significant proportion of the population is exposed to the habitat conditions that lead to the trap (Robertson and Hutto 2006). In our example of plovers at SAK, (1) habitat preference and nest success were quantitatively assessed in randomized studies (here and Anteau et al. 2012); (2) the conditions leading to the traps were long term, as demonstrated by virtual nest success estimates from 1985 to 2009; and (3) habitat conditions leading to the ecological trap likely influenced a significant proportion of the Northern Great Plains population. To our knowledge, our study provides the first quantitative evidence that strongly suggests a sustained ecological trap scenario for a substantial proportion of a bird population.

### Inundation

Although inundation is not a widespread risk to avian nest success in many other habitats, there are a number of examples in which management of reservoirs (Brown and Johnson 1985) or climate changes and global sea-level rise present clear threats of nest inundation for avian species (Whitehead and Tschirner 1990; Bayard and Elphick 2011). It is evident from our data that, at this managed reservoir, inundation is the greatest threat to nest success for plovers. Furthermore, we believe that nest inundation is likely to be an increasing threat to some avian species globally as climate changes, there are increasing frequencies of extreme weather events, sea-level rise increases inundation of coastal nesting areas during high-tide cycles, and an increasing human population demands water management practices that may run counter to conservation of avian species (Vorosmarty et al. 2000; Goswami et al. 2006; Bayard and Elphick 2011).

Water level at SAK generally increases during the summer, corresponding to the period when plovers nest. The timing and height that water level rises in the summer varies annually at SAK and is an important determinant of DSR of nests. For example, in years when the summer rise was relatively low and late or when plovers initiated nests

early (e.g., 2007; Fig. 3), nest sites were less likely to be inundated because some nests were initiated above the elevation of the eventual rise and others were initiated early enough that eggs could hatch prior to inundation of the nest site. However, in 2009 a rapid increase in water level that began in early spring resulted in nearly all plover nest sites being inundated prior to the date when eggs could have hatched.

Nest mortality from factors other than inundation was relatively low for plovers at SAK. Our model predicted that nest success of plovers would be >65 % if relative elevation remains >2 m throughout laying and incubation which is similar to findings of other studies of plovers when nests were not protected from predation by exclosures (Fig. 6). However, in the past 25 years a low and stable water level has not occurred at SAK (Fig. 7; USACE 2010). These results suggest a potential for SAK to contribute positively to the Northern Great Plains population, if intra-annual water level fluctuations can be managed and predation rates do not increase.

### Visibility and nest defense

During nesting and brood rearing plovers use a broken wing display to lure potential predators away from their nest or chicks (Elliott-Smith and Haig 2004), but this defensive behavior is only effective if the plover can detect approaching predators and have adequate time to react. Indeed, Anteau et al. (2012) reported that plovers selected nest sites with consistently low slopes and low vegetation cover within 3 m of the nest, which improved outward visibility. Herein, we predicted that less vegetation and slope within a certain distance from the nest would increase DSRs by improving visibility and effectiveness of nest defense behavior if those habitats were limiting on SAK (Gotmark et al. 1995; Koivula and Ronka 1998; Amat and Masero 2004). Contrary to our prediction, vegetation cover and slope at 10 m had weak-positive correlations with DSR, suggesting that somewhere between 3 and 10 m of outward visibility is adequate for plovers to see approaching predators and effectively use their nest defense behavior. Heterogeneity of vegetation has been linked with site selection and survival of plover nests at alkali wetlands in North Dakota (Prindiville Gaines and Ryan 1988). Vegetation on SAK generally grows in clumps or patches, so increased vegetation cover at 10 m is indicative of increased vegetation heterogeneity. We speculate that increased topographic complexity and vegetation heterogeneity 10 m from the nest increases the effectiveness of the broken-wing behavior because it provides screening that increases the distance plovers can move from their nest, undetected, before starting their broken-wing behavior.

## Nest crypsis

Plovers prefer nest sites with cobble and high percentages of gravel, apparently because these habitats increase nest (gravel) and adult (cobble) crypsis (Prindiville Gaines and Ryan 1988; Colwell et al. 2011; Anteau et al. 2012). There are two possible reasons that the CRYPSIS suite had little support in explaining variation in DSR. First, the predator community affecting nest success of plovers could be largely comprised of mammals that rely on scent to detect prey. Second, nearly all nests at SAK may have been adequately cryptic to reduce the probability of being discovered by visual predators because gravel and cobble are abundant. Our data indicated that 54 nests failed with evidence of destroyed eggs in the bowl, 23 of these nests (42.6 %) had yolk coagulated in the bottom of the nest bowl, suggesting predation by birds (Sargeant et al. 1998), which are visual nest predators. Thus, we assume that the CRYPSIS suite was not supported because gravel, cobble, and vegetation are not limited at SAK and most nests had enough gravel, cobble, or vegetation nearby to enhance nest crypsis. Accordingly, our results do not negate the importance of nest crypsis for plovers, rather its importance is demonstrated through effective nest-site selection because abundant gravel habitats were available (Anteau et al. 2012). However, our assumption about the importance of nest crypsis could be tested in a situation where plovers experience relatively high nest predation by visual predators and cobble, gravel, or vegetation are rare enough that they do not occur at many nest sites. Indeed, on alkali wetlands in North Dakota where gravel likely is less common, it was positively correlated with nest success (Prindiville Gaines and Ryan 1988). Similarly, gravel was nearly twice as abundant at successful than at failed least tern (*Sternula antillarum*) nests on Missouri River sandbars in South Dakota (Sherfy et al. 2012).

## Isolation from predators

We assumed that the distance of a nest from the shoreline and the proportion of unvegetated habitat 75 m around a nest would be positively correlated with DSR because predators often travel and forage along shorelines and they more closely examine small patches of habitat that are different from the surroundings if there is a history of rewards in those habitats (Sovada et al. 2000). However, these variables were not important in explaining variation in DSR. Plover nests are relatively rare and occur in habitats that only few other ground-nesting species use [i.e., killdeer (*Charadrius vociferus*) and least tern] so there may be little benefit for would-be nest predators to target and search patches of unvegetated shoreline, regardless of their size.

We also predicted that plovers nesting on islands farther from the mainland shoreline would be isolated from some sources of predation because we assumed mammals would not typically swim across wide spans of open water to islands at SAK. However, our data suggest avian predators were responsible for nearly half of depredated nests. Furthermore, we observed at least three occurrences of coyotes (*Canis latrans*) apparently stranded on islands after ice out and remained on those islands during the nesting season. Coyotes likely were responsible for predation of plover and other bird nests. Accordingly, nests on mainland and island shorelines had similar DSRs regardless of island distance from the mainland; thus, selection for islands by plovers did not effectively isolate nests from predators on SAK.

## Implications for conservation

Understanding habitat affinities and requirements is an important prerequisite to effective management of a species and their habitats. Our results demonstrate the importance of evaluating habitat selection parameters and their potential influences on breeding success in cases where habitats are highly manipulated, more diverse, or more dynamic than conditions in which animals evolved and developed habitat-selection behaviors. For example, lower-elevation-nesting habitat was found to have a greater likelihood of being used by plovers than higher habitat (Anteau et al. 2012), suggesting that plovers use lower elevation sites as a cue for an optimal nest location. While lower elevation sites might be optimal in systems without great dynamics in water levels, our results indicate nests at those sites have a high likelihood of nest failure on a reservoir with dynamic water levels.

Availability and quality of breeding habitats within the Northern Great Plains are critical to the conservation of this plover population (Elliott-Smith and Haig 2004). An additional challenge for managers of plovers is that there can be shifts in availability and quality of habitats among reservoirs, river sand bars, and wetlands in response to local weather, system-wide Missouri River water conditions, or water management. On all three landforms, unvegetated breeding areas are maintained by fluctuations in water level, but on reservoirs water level fluctuations generally are much greater than those on riverine or wetland habitats. Due to competing interests among stakeholders, major changes in water management practices may not be an available tool for generating habitat for plovers, so managers are interested in creating or enhancing habitat in alternative ways (c.f., Sherfy et al. 2009). Our results suggest that efforts to create nesting habitats on this dynamic reservoir would be mostly unsuccessful in years with high summer inflows (see Fig. 7), unless (1) plovers nest early enough for nests to hatch before the summer rise

or the summer rise is later in the year, (2) plovers could be enticed to nest at higher elevations through habitat manipulations, or (3) impacts of the summer rise on nests can be alleviated through targeted water management. However, any water level management to minimize the effect of a mid-summer rise upon nest success needs to be conducted in such a way that it does not appreciably minimize the inter-annual fluctuations in water level that create and maintain habitat on reservoir systems or jeopardize recruitment of plovers downstream.

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