



RESEARCH ARTICLE

Low renesting propensity and reproductive success make renesting unproductive for the threatened Piping Plover (*Charadrius melodus*)

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ABSTRACT

Upon reproductive failure, many bird species make a secondary attempt at nesting (hereafter, “renesting”). Renesting may be an effective strategy to maximize current and lifetime reproductive success, but individuals face uncertainty in the probability of success because reproductive attempts initiated later in the breeding season often have reduced nest, pre-fledging, and post-fledging brood survival. We evaluated renesting propensity, renesting intervals, and renest reproductive success of Piping Plovers (*Charadrius melodus*) by following 1,922 nests and 1,785 unique breeding adults from 2014 to 2016 in the Northern Great Plains of the United States. The apparent renesting rate for individuals was 25% for reproductive attempts that failed in the nest stage (egg laying and incubation) and only 1.2% for reproductive attempts when broods were lost. Renesting propensity declined if reproductive attempts failed during the brood-rearing stage, nests were depredated, reproductive failure occurred later in the breeding season, or individuals had previously renested that year. Additionally, plovers that nested on reservoirs were less likely to renest compared to other habitats. Renesting intervals declined when individuals had not already renested, were after-second-year adults without known prior breeding experience, and moved short distances between nest attempts. Renesting intervals also decreased if the attempt failed later in the season. Overall, reproductive success and daily nest survival were lower for renests than first nests throughout the breeding season. Furthermore, renests on reservoirs had reduced apparent reproductive success and daily nest survival unless the predicted amount of habitat on reservoirs increased within the breeding season. Our results provide important demographic measures for this threatened species and suggest that predation- and water-management strategies that maximize success of early nests would be more likely to increase productivity. Altogether, renesting appears to be an unproductive reproductive strategy to replace lost reproductive attempts for Piping Plovers breeding in the Northern Great Plains.

Keywords: fecundity, nest success, nest survival, renesting interval, replacement clutch, threatened species

La baja propensión a la anidación repetida y el bajo éxito reproductivo hacen que la anidación repetida sea improductiva para la especie amenazada *Charadrius melodus*

RESUMEN

Frente al fracaso reproductivo, muchas especies de aves hacen un segundo intento de anidación (en lo sucesivo, “anidación repetida”). La anidación repetida puede ser una estrategia efectiva para maximizar el éxito reproductivo actual y de por vida, pero los individuos se enfrentan a una incertidumbre en la probabilidad de éxito debido a que los intentos reproductivos iniciados más tarde en la estación reproductiva usualmente sufren una reducción en la supervivencia de las crías durante las etapas del nido, antes del emplumamiento y luego del emplumamiento. Evaluamos la propensión a la anidación repetida, los intervalos de anidación repetida y el éxito reproductivo de la anidación repetida en *Charadrius melodus* por medio del seguimiento de 1922 nidos y 1785 adultos reproductivos desde 2014 hasta 2016 en las Grandes Llanuras del Norte de Estados Unidos. La tasa aparente de anidación repetida de los individuos fue de 25% para los intentos reproductivos que fracasaron en la etapa de nido (puesta de huevos e incubación) y solo del 1.2% para los intentos reproductivos cuando se perdieron las crías. La propensión a la anidación repetida disminuyó si los intentos reproductivos fracasaron durante la etapa de cría de la nidada, si los nidos fueron depredados, si el fracaso reproductivo ocurrió más tarde en la estación reproductiva o si los individuos habían anidado repetidamente ese año. Adicionalmente, los individuos de *C. melodus* que anidaron en embalses tuvieron una menor probabilidad de anidar de nuevo en comparación a otros hábitats. Los intervalos de anidación repetida disminuyeron cuando los individuos no habían vuelto a anidar de nuevo, fueron adultos posteriores al segundo año sin experiencia reproductiva anterior conocida y se movieron cortas distancias entre los intentos de anidación. Los intervalos de anidación repetida también disminuyeron si el intento fracasó más tarde en la estación. En general, el éxito reproductivo y la supervivencia diaria del nido fueron menores para las anidaciones repetidas que para los primeros nidos a lo largo de la estación reproductiva. Más aún, las anidaciones repetidas en los embalses tuvieron un bajo éxito reproductivo aparente y una baja supervivencia diaria del

nido a no ser que la cantidad predicha de hábitat en los embalses aumente durante la estación reproductiva. Nuestros resultados brindan importantes medidas demográficas para esta especie amenazada y sugieren que las estrategias de manejo de la depredación y del agua que maximicen el éxito de los nidos tempranos probablemente aumentarían la productividad. En conjunto, la anidación repetida parece ser una estrategia reproductiva improductiva para reemplazar los intentos reproductivos perdidos para los individuos de *C. melodus* que crían en las Grandes Llanuras del Norte.

Palabras clave: *Charadrius melodus*, fecundidad, intervalo de anidación repetida, nidada de reemplazo, supervivencia del nido

INTRODUCTION

Although the benefit of successful renesting is obvious, the laying of replacement clutches may increase lifetime reproductive success only if this strategy does not inflict severe costs, such as a reduction in future fecundity or survival of breeders, as predicted by life history theory (Williams 1966, Stearns 2000). At best, renesting can only partially compensate for high rates of nest failure. Nest success declines seasonally in many species (Johnson and Walters 2008, Claassen et al. 2014, Weiser et al. 2018a), and renests are often less likely to hatch, in part because renests are necessarily produced later in the season than first nests (Arnold et al. 2010). Further, renests are inherently suboptimal as they occur after optimal timing for breeding (Nur 1986). Even if renests hatch at similar rates, young hatched later in the year often have lower pre- or post-fledging survival than earlier-hatched young (Daan et al. 1990, Dzus and Clark 1998, Brudney et al. 2013, Saunders et al. 2014). In some species, young hatched specifically from renesting attempts may have lower survival (Martin and Hannon 1987, De Neve et al. 2004, Becker and Zhang 2011). Therefore, offspring from renests are likely to be worth less than offspring from first nests as they are less likely to hatch and survive—potentially minimizing the benefit of replacing lost clutches without necessarily reducing the costs of egg production and parental care.

Individuals must weigh the potential cost of nesting late in the breeding season against the obvious benefit of producing young each year. However, environmental conditions are often dynamic and unpredictable, which complicates the ability to achieve a balance between current and future reproduction. Individuals can increase their current reproductive effort by replacing lost clutches but may do so only if environmental or physical conditions are favorable (Riechert et al. 2013, Blomberg et al. 2017). For instance, Greater Sage-Grouse (*Centrocercus urophasianus*) renesting was sensitive to drought conditions with individuals more likely to reneest in years with higher annual precipitation (Blomberg et al. 2017). While environmental conditions, which change annually, may affect habitat quality or quantity for nesting, conditions may deteriorate over the course of the breeding season as well (Yasué and Dearden 2006, 2008; Frey et al. 2016). Ultimately, the availability and quality of environmental

conditions, and therefore breeding habitat, may influence the decision to replace lost clutches and the success of renests for individuals.

Renesting propensity is affected by many factors including individual condition or quality, environmental factors, or time. Because reproduction and egg development are costly, parental quality is often cited as a potential factor. Increasing parental age or experience (Gregg et al. 2006, Devries et al. 2008), body condition (Devries et al. 2008, Blomberg et al. 2017), or quality (Gates et al. 2013, Riechert et al. 2013) all increase the likelihood of renesting. Food quality and availability (Preston and Rotenberry 2006, Schoech et al. 2008), drought (Blomberg et al. 2017), latitude, and weather (Martin and Wiebe 2004, Sandercock et al. 2005, Martin et al. 2011) also affect whether individuals reneest. The cause of reproductive failure may also influence renesting rates (Claassen et al. 2014, Pakanen et al. 2014). For instance, in Dunlin (*Calidris alpina*), renesting after nest predation was half as likely as after failures caused by other factors (Pakanen et al. 2014). However, overwhelmingly the main constraint to renesting is time—even in temperate latitudes. Renesting is more likely with earlier initiation dates (Arnold 1993, Grand and Flint 1996, Amat et al. 1999, Gregg et al. 2006, Arnold et al. 2010, Claassen et al. 2014), fewer prior nesting attempts (Fondell et al. 2006, Gregg et al. 2006, Arnold et al. 2010), with longer breeding seasons (Arnold 1993, Rooneem and Robertson 1997), and when nests are lost at early stages or earlier in incubation (Fondell et al. 2006, Claassen et al. 2014). Timing of a renesting attempt is influenced by date of previous nest failure and the amount of time it takes for an individual to initiate a replacement nest (i.e. the renesting interval). Short renesting intervals may improve reneest reproductive success because of seasonal declines in nest and brood survival (Roche et al. 2008, Claassen et al. 2014, Weiser et al. 2018a). The degree to which renesting serves as a productive strategy for individuals or the population is dependent on how successful renests are, particularly in terms of recruitment back into the breeding population (Martin and Hannon 1987, Martin et al. 2011). While parental quality, environmental factors, and the timing of the breeding season are important factors influencing renesting propensity, the degree to which each interacts with or supersedes others is still relatively unknown.

Renesting can make important contributions to an individual's annual fecundity and lifetime reproductive

success (Milonoff 1991, Murray 1991), and replacing lost clutches may be an important reproductive strategy especially for species with high rates of nest failure (Sandercock et al. 1999, Hipfner 2001, Arnold et al. 2010, Lishman et al. 2010). Clearly, quantifying renesting behavior is important for modeling population dynamics and for obtaining estimates of fecundity (Hoekman et al. 2002, Nagy and Holmes 2004, Grzybowski and Pease 2005, Pakanen et al. 2016). However, renesting propensity is poorly understood, and demographic models frequently lack accurate estimates of renesting rates, which can lead to underestimates of fecundity and overestimates of population size (Thompson et al. 2001, Sandercock et al. 2008, Arnold et al. 2010). For species of conservation concern, accurate demographic parameters are essential for ensuring conservation and management efforts are focused on processes that are most critical, particularly in dynamic and stochastic environments (Pakanen et al. 2016). Further, understanding the propensity to reneest and its productivity can be important for informing intensive conservation measures (i.e. predation management or water management). Population-level estimates of renesting propensity, renesting intervals, and reneest reproductive success can then be used to create more accurate demographic models and population size estimates. Understanding how changing environmental conditions or other potential factors may encourage or inhibit individuals from renesting can be an important component of demographic models of reproductive success at both the species and population levels.

The Piping Plover (*Charadrius melodus*; hereafter “plover”) is a small migratory shorebird endemic to North America with breeding populations in the Atlantic Coast, Great Plains, and Great Lakes regions. Federally listed primarily due to habitat loss and low reproductive output, plover breeding biology is studied throughout its range (USFWS 2003, 2009). Plovers in the Northern Great Plains rely on breeding habitat with little to no vegetative cover on riverine sandbars, reservoir shorelines, and wetlands in the Prairie Pothole Region commonly referred to as alkali lakes (Prindiville Gaines and Ryan 1988, Anteau et al. 2012a). Plovers nesting on reservoirs often face a novel threat of mid-season water level rise, which can flood nests and unfledged chicks and engulf nesting island habitats (Anteau et al. 2012a). Our understanding of the factors that may influence plovers to reneest following a flooding-related failure are thus unique to the Great Plains breeding population and have important implications for water management. Additionally, under current water management scenarios, reservoirs are a unique system to explore how changing the quantity of breeding habitat, rather than solely reducing habitat quality, may influence renesting. Current adaptive management plans do not explicitly account for replacing lost clutches, but rather focus on the

number of fledglings produced—as such understanding the role of renests in producing fledglings will aid conservation and management practitioners.

Plovers may reneest several times during the breeding season following the loss of a previous nest (Cairns 1982, Haig and Oring 1988, Claassen et al. 2014). In a study evaluating the factors influencing nest survival and renesting on individually marked plovers from the Great Lakes population, plovers showed a high propensity to reneest (49%), which declined over the breeding season and varied by cause of nest failure (Claassen et al. 2014). However, data on offspring survival were not included in that analysis, restricting our understanding to that of the nesting stage, and nearly all nests were protected by predator exclosures, which may have affected renesting propensity. From a conservation perspective, understanding the causes and consequences of renesting for each of the 3 breeding populations provides more detailed information for demographic models, which are unique to each breeding population (McGowan et al. 2014). Management actions, habitat types, and environmental factors differ among breeding populations, and adaptive management plans require accurate data unique to the breeding population.

Our objectives were 3-fold: to identify factors that (1) affected the likelihood of initiating a reneest (hereafter “renesting propensity”), (2) influenced the amount of time required to initiate a reneest (hereafter “renesting interval”), and (3) affected reneest reproductive success (failed during nest phase, hatched but failed during brood-rearing, or fledged at least one young). We investigated renesting performance in relation to environmental, individual, and temporal drivers (see Table 1 for specific a priori hypotheses). Lastly, we aimed to identify conservation and management actions that could improve the likelihood of successful breeding in light of renesting dynamics.

METHODS

Study Area and System

From 2014 to 2016, we monitored breeding Piping Plovers on alkaline lake, reservoir, and riverine nesting habitats from central South Dakota through North Dakota and into northeastern Montana, USA (Figure 1). In general, we studied the entire extent of the “U.S. Alkali Lakes” and the “Northern Rivers” portions of the Great Plains Piping Plover metapopulation as defined by McGowan et al. (2014). The alkali lakes study area consisted of ~150 basin (i.e. lake, pond, or slough) shorelines located on public and private lands in the Missouri Coteau ecoregion of North Dakota and Montana. Sites consisted of bare or sparsely vegetated sand and gravel shorelines and islands. The reservoir shoreline habitat was irregular, dissected,

TABLE 1. A priori hypotheses about variables affecting renesting propensity, renesting interval, and reneest reproductive success of Northern Great Plains Piping Plovers during 2014–2016.

Explanatory variable	A priori hypotheses
Failure date	Later failure dates for reproductive attempts will result in lower adult renesting propensity and longer renest intervals.
Age at failure	Older nests or broods will result in lower adult renesting propensity and longer renest intervals.
Cause of failure	Renesting propensity will be lower and renest intervals will be longer for brood failures and nest depredation events.
Index of change in available habitat from May to July	When less habitat is available later in the breeding season, renesting propensity will be reduced, renest intervals will be longer, and renest fate will be lower.
Habitat type	Failed nests on reservoirs will result in lower renesting propensity, longer renest intervals, and lower renest success.
Interaction between available habitat index and habitat type	Reservoirs with less available habitat in July will show more striking changes to renesting than rivers or alkali lakes.
Landform	On islands, renesting propensity will be reduced, renest intervals will be longer, and renest success will be lower.
Previously nested this year	Second/third nesting attempts will have lower renesting propensity, longer renest intervals, and reduced renest success.
Age and experience of pair	SY individuals and ASY individuals without previous breeding experience will have lower renesting propensity and longer renest intervals.
Renest clutch size	Individuals with smaller renest clutch sizes will decrease the renest interval.
Same mate	Changing mates between consecutive nesting attempts will increase the renest interval and reduce renest success.
Distance between nests	Farther distances between consecutive nesting attempts will increase the renest interval and reduce renest success.

and composed of a diversity of substrate types including sand, gravel, and shale (Anteau et al. 2012b). For our analyses, this habitat consisted primarily of mainland and island shorelines along Lake Oahe and Lake Sakakawea (2 mainstem reservoirs of the Missouri River) as well as several reservoir-like wetland basins with water management systems (e.g., Lake Audubon—Audubon National Wildlife Refuge [NWR], Medicine Lake—Medicine Lake NWR, Long Lake—Long Lake NWR, Jim Lake—Arrowwood NWR). The Lake Oahe reservoir extended from the headwaters of Lake Oahe, ~10 km south of Bismarck, North Dakota, to just north of Pierre, South Dakota. The Lake Sakakawea reservoir (from Garrison Dam near Riverdale, North Dakota, to White Tail Bay, North Dakota; see Anteau et al. 2014a, 2014b) was located ~80 km north of Bismarck, North Dakota. The riverine habitat consisted of the Missouri River's Garrison Reach, which extended from the Garrison Dam to the headwaters of Lake Oahe. Nesting habitat on the river reach primarily consisted of mid-channel low- to mid-elevation sandbars with some established woody vegetation (Sherfy et al. 2009, Anteau et al. 2019).

Data Collection

Each year, from late April to early August, crews searched appropriate habitat or used behavioral observations to locate plover nests and chicks. Sandbars and shorelines were grid-searched for nests generally until mid-July, but crews target-searched for new nests whenever adults were

present and exhibiting nesting behaviors. Once located, nests were monitored until completion (i.e. until all eggs either hatched or nests were determined to have failed). Nests were typically visited every 2–4 days, although some nests (~20%) were visited less regularly with intervals greater than 7 days. For each nest, data were collected about location, nest habitat, nest fate (success or failure), estimated date of hatch or failure, cause of nest failure, and adult identities. A small portion of nests included from the alkali lakes region had predator exclosures for some part of incubation (Appendix Table 6). The estimated date of hatch or failure was the midpoint date between the final 2 visits, except for known hatch dates when chicks were found in the nest bowl. We have banded plovers with a U.S. Geological Survey metal band and unique alphanumeric engraved flag since 2012 on the Garrison River Reach and Lake Sakakawea and beginning in 2014 on Lake Oahe and the alkali lakes. We trapped unbanded adult plovers on nests during incubation using either a modified remote-controlled walk-in trap or bow-net (Roche et al. 2014a). Individuals were attributed to nests by capturing of individuals on the nest, observing an identified individual return to incubate, or using high-definition video cameras set up near (45–60 cm away) nests for no more than 30 min at a time (Kodak PixPro spz1 video cameras; JK Imaging, Los Angeles, California, USA; Toy et al. 2017). We captured chicks by hand at the nest site, typically within a day of hatch. Following chick banding, we revisited each sandbar or shoreline site every 2–4 days and resighted chicks.

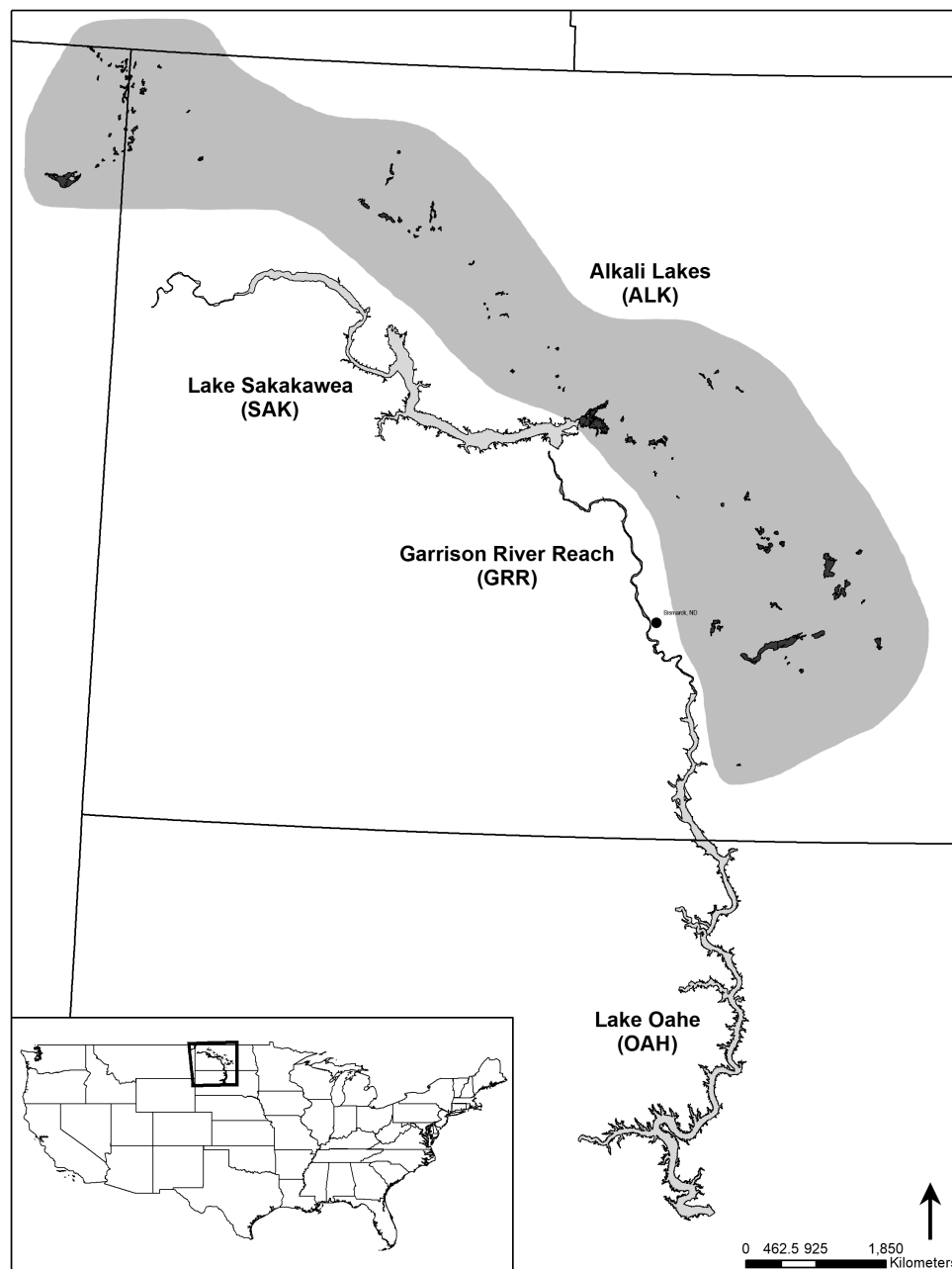


FIGURE 1. Piping Plover nesting areas in North Dakota, South Dakota, and Montana, USA, 2014–2016.

When appropriate, teams systematically worked through all areas in a grid formation, moving in one direction and in parallel, and typically resighted chicks with spotting scopes (Roche et al. 2014b).

Statistical Analyses

We investigated sources of variation in renesting propensity, length of the renesting interval, and renest reproductive success. A renest was defined as an additional reproductive attempt following a failure. We examined both the nesting

period (egg laying and incubation until hatching) as well as the brood-rearing period (hatching to 21 days old). A reproductive attempt was defined as “hatched” if at least one egg hatched and as “fledged” if at least one chick survived to 21 days post-hatch.

We defined apparent renesting propensity as the proportion of individuals that renested following a failed previous reproductive attempt (Arnold 1993, Claassen et al. 2014). Reproductive failure could occur during either nesting or brood-rearing stages. We calculated the renesting interval

as the number of days between failure of a previous reproductive attempt and initiation of the replacement nest; for example, if a nest failed on May 25 and the first replacement egg was laid on June 2, then the renesting interval was estimated as 8 days. As we likely missed some nests that were destroyed during early laying, renesting intervals may be shorter than estimated. We assumed that a renesting attempt was a continuation nest (i.e. replacement nests of birds that lost a nest during egg laying and renested soon after, with no interruption in laying) if nest loss occurred during egg laying and the replacement nest was initiated within 3 days of nest loss; these nests were excluded from analyses ($n = 3$). Nest initiation dates were estimated by backdating from hatch date, assuming a 2-day laying interval between eggs (Elliott-Smith and Haig 2004) plus a 28-day incubation period after the last egg was laid, or by egg flotation estimations if the nest failed (Liebezeit et al. 2007). Reproductive attempts were divided into 2 categories: first attempts and second/third attempts (see Results). Because individuals did not always reunite with their former mate for renesting, we analyzed renesting attempts separately for each individual and included a random effect of breeding pair. We defined renest reproductive success as a categorical response with reproductive attempts failing during nesting ("failed"), failing during the brood-rearing period ("hatched"), or successfully fledging one chick to at least 21 days old ("fledged"). Our categorization of "fledged" nests likely represents a minimum estimate due to imperfect detection of older chicks.

For each of the 3 response variables (renesting propensity, renesting interval, and renest reproductive success), we investigated variation in response to relevant covariates (Table 1). Nest initiation date and date of failure were correlated (Pearson's $r = 0.67$), so we only retained date of failure for analyses. For each analysis, we included only covariates for which we had formulated a priori hypotheses regarding how each covariate might explain variation in the specific parameter of interest (Table 1). We treated cause of reproductive attempt failure as a categorical factor with 5 levels. We were unable to determine cause of brood failures (i.e. predators, flooding), so all reproductive attempts that failed after hatching were treated as one category, distinct from the causes of nest failures: hatched, predation, flooding, severe weather, or abandoned/unknown. Flooding failures were caused by water level rise on the Missouri River system and were distinguishable from flooding due to storm events. Nests known to fail due to livestock ($n = 5$) or human trampling ($n = 4$) were included in depredated nests, and abandoned nests ($n = 22$) were included as unknown causes. However, a relatively large proportion of our nests (~43%) were conservatively placed into the unknown cause category due to a lack of evidence at the time of nest fating. Sandbars are dynamic with wind and water that can quickly scour away signs of predators. To avoid falsely attributing nests to alternative causes of failure, crews collected

multiple (2–4) pieces of evidence when fating nests, and if unclear, causes were left as unknown (Appendix Table 7). Habitat type was treated as a 3-level factor: reservoir, river, or alkali lake. Individuals were categorized into 1 of 4 age and experience levels: second-years without previous breeding experience, after-second-years with no documented previous breeding experience, after-second-years with known previous breeding experience, and individuals of unknown age and experience (newly banded adults; Appendix Table 8). Clutch size was defined as the maximum number of eggs seen during nest monitoring visits.

Lastly, we calculated a standardized index of the change in available nesting habitat from May to July. For wetland basins with water management systems, we used the maximum water elevation measures for each month at gauges monitored by the U.S. Fish and Wildlife Service. For all other alkaline lakes, we represented variation in climate with an index that was developed specifically for hydrological effects of climate on permanent and semi-permanent wetlands of the Prairie Pothole Region (Post van der Burg et al. 2016). This index is based on the Standard Precipitation–Evapotranspiration Index (SPEI; Beguería et al. 2014) but is calculated using a 72-mo average from monthly PRISM (Parameter-elevation Regressions on Independent Slopes Model) data from the PRISM Climate Group (Oregon State University, Corvallis, Oregon, USA) because that time frame has been demonstrated useful for predicting water level dynamics in wetlands of similar size and hydroperiod (Post van der Burg et al. 2016). We calculated a site-specific index of habitat change by subtracting SPEI values for May from those of July of each year. Negative values indicate dryer conditions and subsequent drawdown of water level and an increase in availability of nesting habitat (McCauley et al. 2016, Roche et al. 2016). For Garrison River Reach, we used the change in maximum monthly Garrison dam outflow ($1,000 \text{ ft}^3 \text{ s}^{-1}$) between May and July (data available from U.S. Army Corps of Engineers: <http://www.nwd-mr.usace.army.mil/rcc/projdata>). Positive values indicate that dam outflow increased during the breeding season, reducing available nesting habitat. For reservoirs, we used a predictive model on the amount of available plover habitat developed for Lake Sakakawea (Anteau et al. 2014b) and adapted for use on Lake Oahe, which takes into account elevation, vegetation growth, and ice scour. We calculated estimates of available habitat for May and July for each reservoir.

We investigated sources of variation in renesting propensity, renesting interval, and renest reproductive success using generalized linear mixed models (GLMM) using R statistical software (3.5.0; R Development Core Team 2018). For renesting propensity, we used a binomial distribution, and for renesting interval, we used a Poisson distribution (package *lme4*; Bates et al. 2015). We used an ordinal multinomial response for our categorical

renest reproductive success analysis (package *ordinal*; Christensen 2015). We first checked for correlations among the independent variables and reduced variables as needed (if $|r| > 0.6$; all remaining correlations were below $|r| = 0.3$). To ensure model convergence and interpretability of beta estimates, all covariates were standardized to a mean of 0 and a standard deviation of 1, except for the categorical covariates. We then calculated profile confidence intervals and evaluated the significance of each parameter of interest in the fitted global GLMM for each response variable. Because we assumed there was variation among years, and we wanted to account for this source of heterogeneity, we included year as an additional fixed effect. To account for multiple banded individuals at each nest, we included a random effect of breeding pair.

Lastly, we evaluated daily nest survival during the nesting period (egg laying and incubation) for first nests and renests using the nest survival module in program MARK 9.0 (White and Burnham 1999, Dinsmore et al. 2002) via R and the contributed R package *RMark* 2.2.5 (Laake 2013). The nest survival module in program MARK uses a generalized linear model with logit-link function and binomial errors to estimate daily nest survival probability as a linear function of the various combinations of the covariates described by the candidate models. We modeled all possible combinations of a linear time trend, attempt number of the nest (e.g., first attempt, renest), and habitat type of the nest and selected the model with the lowest AIC_c score (Burnham and Anderson 2002). We calculated cumulative nest survival to hatch using daily survival estimates from our top-supported model using an exposure period of 35 days. We used the delta method (*msm* package available in program R), daily survival rates generated at mean covariate values, and their associated variance-covariance matrices, to estimate cumulative survival rates and their associated 95% confidence envelopes.

RESULTS

We obtained data from 2,658 individual breeding attempts representing 1,785 unique individuals. We monitored 1,922 nests over 3 yr (2014–2016). Of those nests, we followed 643 broods from hatch to at least 21 days post-hatch. Most nests were found on the Garrison River Reach ($n = 741$) and Lake Oahe had the fewest nests ($n = 212$) over the 3 yr. Overall, most individuals only attempted one nest per year ($\bar{x} = 1.2$ nests, $SD = 0.46$, $n = 2,381$ of 2,685 individual breeding year attempts). Approximately 29% of individuals changed mates (divorced) between nesting attempts. The maximum number of breeding attempts within a year was 3; 10 individuals attempted 3 nests in one breeding season. We also noted 3 individuals that attempted second nests (i.e. multiple concurrent nest attempts or a second reproductive attempt following reproductive success). In 2 instances, separate individuals fledged young from an early breeding attempt and nested, unsuccessfully, a second time with a new mate. In the third case, one individual was captured incubating 2 simultaneous nests with different mates (initiated 4 days apart) ~34 m apart.

Renesting Propensity

Piping Plovers renested 247 times following 1,501 failed individual breeding attempts, a 16% apparent renesting propensity (Table 2). This differed based on the stage of reproductive failure, with individuals renesting following 240 of 960 (25%) attempts that failed in the nesting stage, but only 7 of 541 (1.2%) broods that failed. Nest losses were due to predation (18%), flooding (35%), severe weather (4%), and unknown causes (43%).

Reproductive failure date, cause of failure, habitat type, and nest attempt type (e.g., first reproductive attempt, second reproductive attempt) all significantly explained variation in renesting propensity. Renesting propensity decreased with later dates of reproductive failure ($\beta = -1.34$;

TABLE 2. Number of nests found, number of renests, apparent renesting propensity, apparent hatching success of renests, and apparent fledging success of renests of Northern Great Plains Piping Plovers during 2014–2016.

Year	Study area	Total number of nests	Number of renests	Percent of failed nests followed by a renest	Percent of renests that hatched	Percent of renests that fledged
2014	Alkali Lakes	106	4	21.1%	50.0%	0.0%
	Garrison River	235	35	29.2%	55.5%	18.5%
	Lake Oahe	72	4	15.6%	0.0%	–
	Lake Sakakawea	109	13	20.7%	7.8%	0.0%
2015	Alkali Lakes	159	20	30.2%	37.5%	12.5%
	Garrison River	254	36	31.8%	60.0%	0.0%
	Lake Oahe	67	3	17.2%	33.3%	0.0%
	Lake Sakakawea	204	27	25.7%	0.0%	–
2016	Alkali Lakes	150	17	29.7%	53.8%	30.8%
	Garrison River	252	51	43.3%	11.1%	5.6%
	Lake Oahe	73	8	29.2%	33.3%	0.0%
	Lake Sakakawea	241	17	17.6%	61.5%	0.0%

TABLE 3. Parameter estimates, standard errors (SE), and 95% confidence intervals (CI) from fitted models for renesting propensity, renest interval, and renest reproductive success of Piping Plovers in the Northern Great Plains region during 2014–2016. Significant variables are in bold.

	Renesting propensity			Renest interval			Renest reproductive success		
	β	SE	95% CI	β	SE	95% CI	β	SE	95% CI
(Intercept)	-4.53	1.01	(-6.64, -2.65)	0.84	0.65	(-0.41, 2.17)	-4.55	1.61	(-7.70, -1.40)
(Spacing)	-	-	-	-	-	-	9.33	0.88	(7.61, 11.05)
Failure date	-1.34	0.18	(-1.71, -0.99)	-0.18	0.07	(-0.32, -0.04)	-	-	-
Age at failure	0.20	0.24	(-0.27, 0.67)	0.10	0.09	(-0.10, 0.20)	-	-	-
Cause of failure: PREDATOR	1.98	0.74	(0.62, 3.61)	0.20	0.46	(-0.81, 1)	-	-	-
Cause of failure: UNK	2.82	0.70	(1.57, 4.39)	0.11	0.44	(-0.81, 0.91)	-	-	-
Cause of failure: WATER	3.01	0.73	(1.69, 4.62)	0.56	0.45	(-0.40, 1.37)	-	-	-
Cause of failure: WEATHER	2.61	0.86	(0.94, 4.41)	-0.71	0.56	(-1.93, 0.28)	-	-	-
Habitat type: RESERVOIR	-1.12	0.41	(-1.94, -0.31)	-0.27	0.25	(-0.79, 0.21)	-4.06	0.94	(-7.70, -1.40)
Habitat type: RIVER	-0.04	0.36	(-0.74, 0.67)	0.11	0.20	(-0.29, 0.49)	2.86	0.67	(1.54, 4.18)
Index of available habitat	-0.10	0.28	(-0.68, 0.43)	0.07	0.15	(-0.24, 0.37)	-0.06	0.41	(-0.87, 0.74)
Landform: ISLAND	0.21	0.21	(-0.21, 0.63)	0.02	0.12	(-0.20, 0.29)	-0.05	0.52	(-1.07, 0.98)
Previous attempt: yes	-1.13	0.54	(-2.18, -0.07)	0.69	0.34	(0.13, 1.43)	-	-	-
Mate 1—Age/exp: ASY/yes	0.46	0.29	(-0.10, 1.03)	-0.27	0.15	(-0.56, 0.02)	-	-	-
Mate 1—Age/exp: SY/no	0.70	0.51	(-0.30, 1.70)	-0.29	0.27	(-0.82, 0.23)	-	-	-
Mate 1—Age/exp: ASY/no	-0.09	0.52	(-1.11, 0.93)	-0.80	0.30	(-1.38, -0.22)	-	-	-
Mate 2—Age/exp: ASY/yes	-0.03	0.37	(-0.76, 0.70)	0.12	0.18	(-0.22, 0.47)	-	-	-
Mate 2—Age/exp: SY/no	-0.37	0.65	(-1.65, 0.90)	0.08	0.34	(-0.58, 0.74)	-	-	-
Mate 2—Age/exp: ASY/no	-0.17	0.59	(-1.34, 0.99)	-0.47	0.33	(-1.12, 0.18)	-	-	-
Renest clutch size	-	-	-	-0.08	0.08	(-0.24, 0.08)	-	-	-
Same mate: UNK	-	-	-	-0.32	0.18	(-0.67, 0.02)	0.19	1.08	(-1.93, 2.31)
Same mate: YES	-	-	-	-0.27	0.19	(-0.65, 0.10)	-0.05	1.19	(-2.38, 2.29)
Distance between nests	-	-	-	0.12	0.05	(0.01, 0.22)	0.02	0.47	(-0.89, 0.94)
Year: 2015	0.20	0.38	(-0.56, 0.95)	-0.08	0.24	(-0.52, 0.43)	-8.86	1.21	(-11.22, -6.49)
Year: 2016	0.05	0.35	(-0.63, 0.73)	0.21	0.20	(-0.14, 0.64)	-0.37	0.73	(-1.80, 1.05)
Habitat type—RESERVOIR: Available habitat	-0.06	0.36	(-0.76, 0.66)	-0.01	0.21	(-0.44, 0.38)	4.32	0.79	(2.78, 5.86)
Habitat type—RIVER: Available habitat	0.27	0.33	(-0.37, 0.94)	0.07	0.17	(-0.26, 0.43)	-4.25	0.67	(-5.56, -2.95)

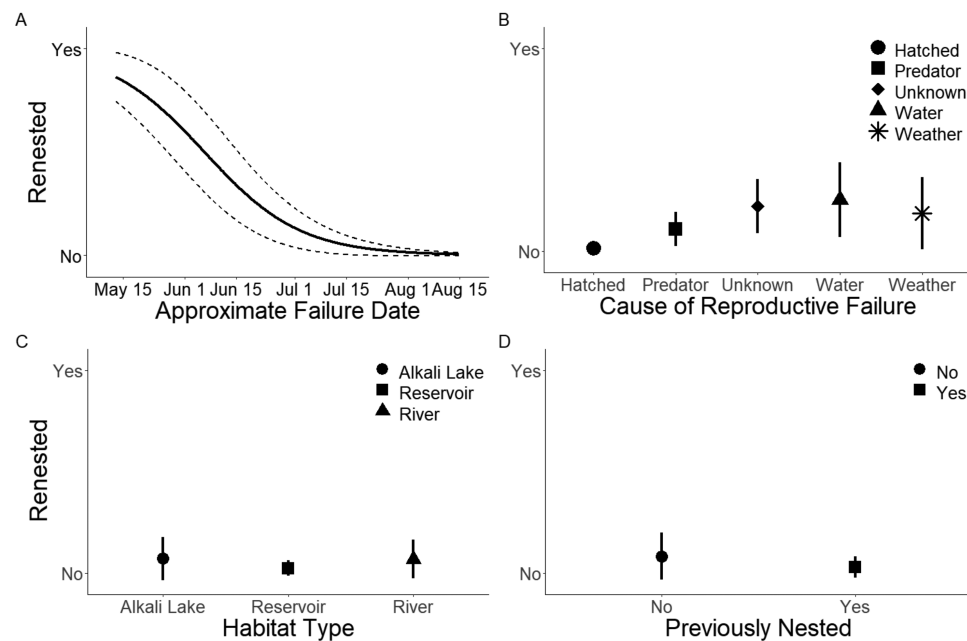


FIGURE 2. (A) Effects of failure date, (B) cause of reproductive failure, (C) habitat type, and (D) previous nests that year on renesting propensity of Northern Great Plains Piping Plovers during 2014–2016. Dotted lines and error bars indicate 95% confidence intervals.

95% CI $[-1.71, -0.99]$; Table 3, Figure 2A). Nests that hatched (but failed during the brood-rearing stage) were less likely to be replaced, followed by nests that were depredated (Table 3, Figure 2B). Additionally, renesting propensity was lower for birds that nested on reservoirs compared to alkali lakes or rivers (Table 3, Figure 2C). Lastly, individuals were less likely to renest following failure of their second nest attempt (Table 3, Figure 2D).

Renesting Interval

The mean observed renesting interval was 8.3 days (SD = 6.6; $n = 224$). Estimated renesting intervals were ~9 days when nest failure occurred but decreased to ~6 days when failure occurred during the brood-rearing stage. Renesting intervals were ~2 days longer for individuals that moved over a kilometer compared to individuals that did not, and of those that moved, 52% divorced their mate. The distance between nests varied (range: 4 m to 381 km; $\bar{x} = 12.9$ km; SD = 35.6 km), and 10% of individuals ($n = 29$ of 277) switched habitat types between nest attempts, 69% of which left reservoir habitats.

Renesting intervals were strongly affected by date of reproductive failure with intervals declining later in the breeding season ($\beta = -0.18$; CI $[-0.32, -0.04]$; Table 3, Figure 3A). First-to-second nest attempt intervals were shorter than second-to-third nest attempt intervals (Table 3, Figure 3C), and after-second-year adults without documented previous breeding experience also renested faster than other age/experience classes (Table 3, Figure 3B). Lastly, renesting intervals strongly increased

with increasing distances between nest locations ($\beta = 0.12$; CI $[0.01, 0.22]$; Table 3, Figure 3D).

Renest Reproductive Success

Renests generally were not as productive as first nests with only 21% of renests hatching (compared to 51% of first nests) and 5% fledging at least one chick (compared to 24% of first attempts). Individuals that moved farther than 150 m from their first nest had slightly lower hatching success (29.5% compared to 33.7%) and fledging success (23.8% compared to 24.1%). Renest reproductive success varied among years (2014: 57.5% nests failed, 8.0% fledged; 2015: 63.6% nests failed, 1.9% fledged; 2016: 42.9% nests failed, 7.1% fledged).

Renest reproductive success was lower on reservoirs than on alkali lakes or rivers (Table 3, Figure 4A). Renest reproductive success on reservoirs was lowest (hatching success: 21%, fledging success: 0%) compared to alkali lakes (hatching success: 27%, fledging success: 20%) and rivers (hatching success: 28%, fledging success: 9%). Reservoirs had a high probability that renest reproductive attempts would fail during the nesting stage, while rivers and alkali lakes had higher probabilities of fledging young. Additionally, renest fate on reservoirs interacted with the amount of available nesting habitat (Table 3). When relatively more habitat was available in July compared to May, renests on reservoirs had improved reproductive success with lower probabilities of nests failing and higher probabilities of nests hatching but failing during brood-rearing; however, if less habitat was available in July compared to

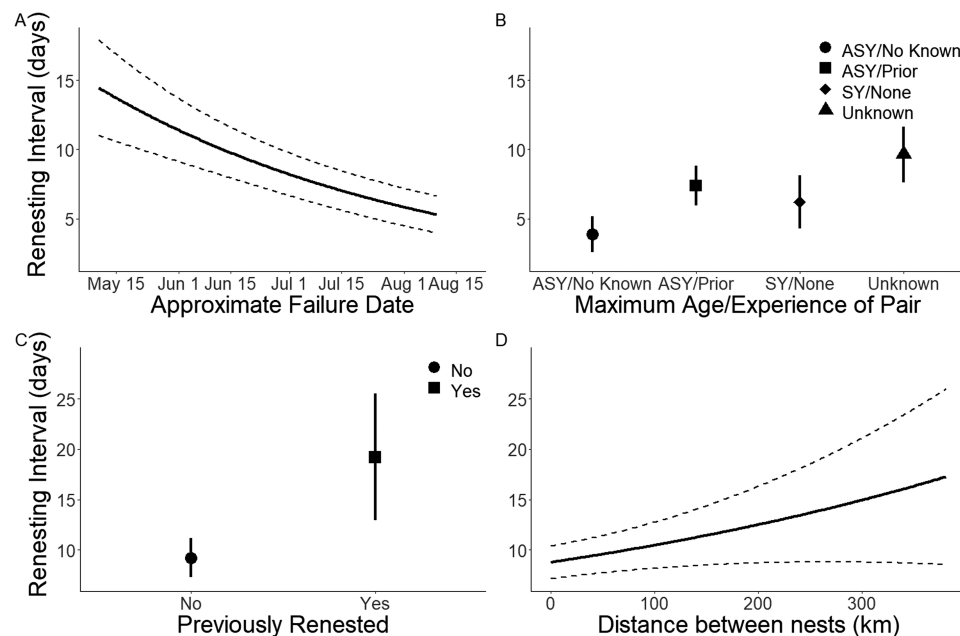


FIGURE 3. (A) Effects of failure date, (B) maximum age/experience of pair, (C) previous nests that year, and (D) distance between nests on renesting interval of Northern Great Plains Piping Plovers during 2014–2016. Dotted lines and error bars indicate 95% confidence intervals.

May, renests on reservoirs had low hatching success and high probabilities of nests failing (Table 3, Figure 4B, C).

We restricted our sample for daily nest survival to nests with known nest fates and short monitoring intervals (2–4 days). Our analysis included 1,703 nests (1,503 first nesting attempts and 200 renests). Renests showed significantly lower daily nest survival, even with a linear temporal trend included (Table 4, Figure 5A). Furthermore, reservoirs had lower daily nest survival than other habitat types (Table 4, Figure 5B). Cumulative nest survival averaged 0.46 (SE: 0.002) for first nests but only 0.27 (SE: 0.004) for renests (Table 5).

DISCUSSION

Renesting in Piping Plovers was influenced by temporal, environmental, and individual factors. Until a detailed population model is completed, we cannot quantitatively explore the benefits (increased productivity) of investing in current reproductive success against any potential costs (survival). However, it appears that the benefits of renesting are low for plovers nesting in the Northern Great Plains. In general, renesting propensity declined during the breeding season with individuals less likely to renest when nests or broods failed at later dates. Individuals nesting on reservoirs were less likely to renest and when they did so, had reduced success and lower daily nest survival compared to other habitat types, unless available nesting habitat increased within the breeding season. Renesting,

while a viable option for a small portion of the population, often has few benefits for most individuals. Thus, renesting is both an uncommon and unproductive reproductive strategy to replace lost reproductive attempts and increase fecundity for Northern Great Plains Piping Plovers.

Piping Plovers were less likely to renest later in the breeding season, but individuals that did renest later had shorter renesting intervals. Other studies of Piping Plovers have also found strong seasonal effects on reproductive success (Harris et al. 2005, Anteau et al. 2012a, Brudney et al. 2013, Claassen et al. 2014), and any factors that cause plovers to nest later are likely to lead to lower annual breeding productivity. The chance of renesting in early June (~June 6) was 50% but declined to 0% following a reproductive failure after July 10. Furthermore, the date of reproductive failure had a stronger influence for each of these aspects of renesting than the age of the reproductive attempt at the time of failure. Renesting intervals were highly variable (range: 0–35 days), but earlier failures and larger movements did result in longer renesting intervals. Individuals may have more nutritional/energetic flexibility later in the season or are likely constrained by a relatively short breeding season during which conditions are favorable for nesting leading to shorter renest intervals late in the breeding season (Verhulst and Nilsson 2008, Swift et al. 2018, Weiser et al. 2018b). Temporal constraints may be less severe compared to Holarctic breeders; however, the strong cutoff of reproduction in mid-July and shorter renesting intervals suggest some threshold for breeding

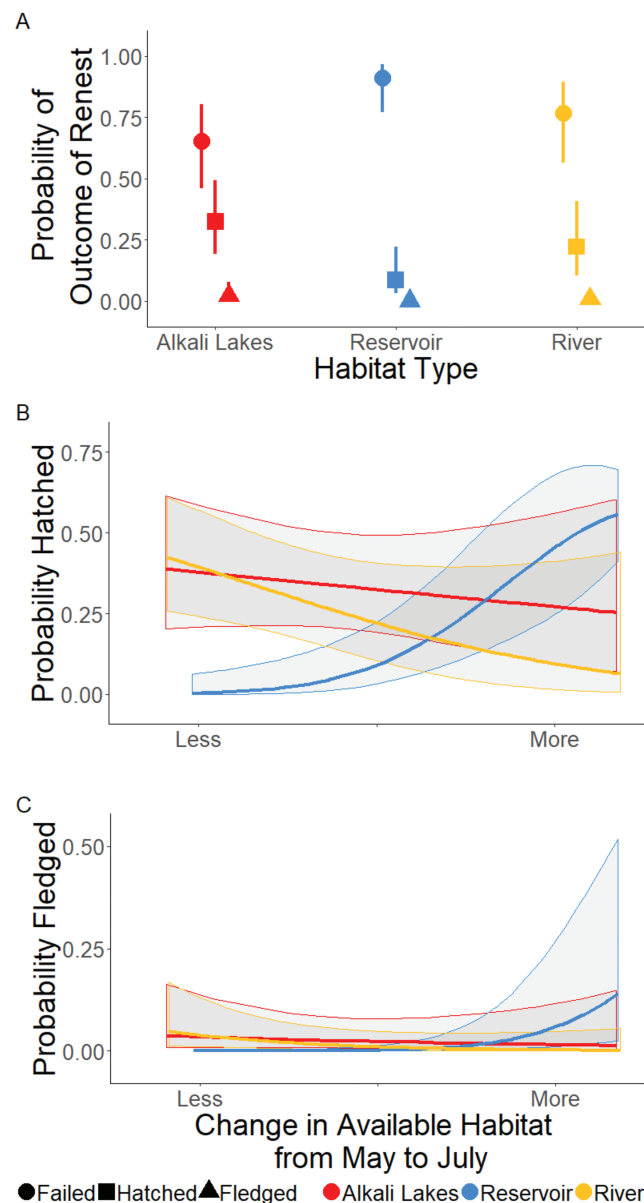


FIGURE 4. (A) Effects of habitat type and the interaction between habitat type and available habitat on the probabilities for renest reproductive success categories (nest failed, hatched but failed during brood-rearing, and successfully fledged one chick to at least 21 days post-hatch) of Piping Plovers during 2014–2016. Reservoirs (dark blue) had high probabilities of reproductive attempts failing (circles in A) during nesting and low probabilities of failing during brood-rearing (squares) or fledging chicks (triangles) unless relatively more habitat was available later compared to earlier in the breeding season (B, C). Shaded gray areas and error bars indicate 95% confidence intervals.

even in northern temperate latitudes. While individuals continued to initiate nests between June 6 and July 10, only 38% were successful at hatching and only 13% of those fledged at least one chick. Further, both first and renest attempts showed a significant linear decline with date in daily

TABLE 4. Model selection table for daily nest survival of Piping Plover nests during 2014–2016.

Model	ΔAIC_c	w_i	Dev
S(Renest + Habitat type + Time)	0.00	0.94	4808.95
S(Renest + Habitat type)	5.62	0.06	4816.57
S(Habitat type + Time)	19.53	<0.001	4830.47
S(Habitat type)	40.57	<0.001	4853.52
S(Renest + Time)	76.58	<0.001	4889.53
S(Renest)	80.65	<0.001	4895.60
S(Time)	94.68	<0.001	4909.63
S(Constant)	112.52	<0.001	4929.47

nest survival. Thus, reproductive attempts initiated later in the breeding season are worth less than earlier nests.

The cause of reproductive failure influenced renesting propensity. Reproductive attempts that failed during the brood-rearing stage were far less likely to be followed by a renest, regardless of age of brood at the time of failure, which may be a result of temporal or physiological constraints. The cost of egg laying after completing incubation (~32–36 days from nest initiation to hatch) may be too high for most individuals or may occur too late in the breeding season. Renesting may be an evolutionary adaptation to compensate for high rates of egg loss to predators and weather-related events (Sandercock et al. 1999, Lishman et al. 2010, Claassen et al. 2014). Interestingly, depredated nests were less likely to be followed by a renest than those that failed due to severe storms or flooding. Instead, plovers may be associating nest loss due to predators as a threat to their own survival or as a cue of higher probability that future attempts may also be at risk of nest predation because predators are likely to return to previous sites of predation (Martin et al. 2000, Pakanen et al. 2014). Water level rise that resulted in nests being flooded did not lower the rate of renesting nor did nest failure due to severe storms, but these threats to nests probably pose less of a threat to adult survival than predators and are less predictable. Plovers appear to adjust renesting decisions in relation to cues of predation risk based on their direct experience.

Nests on reservoirs had lower renesting propensity and renest reproductive success than nests on the river or alkali lake habitats. In fact, change in nesting habitat abundance was a significant predictor of renest reproductive success. Since the construction of dams on the Missouri River, plovers began nesting on shorelines and islands of reservoirs (Elliott-Smith and Haig 2004). As much as 60% of Missouri River plovers use mainstem reservoir habitats (Anteau et al. 2014b), and, in 2014–2016, 43% of nests were on mainstem reservoirs. However, reservoir use can vary among years (USFWS 2003, Anteau et al. 2014a), which is most likely correlated with water-surface elevation and thus available nesting habitat. In this study, mainstem reservoir elevations were similar

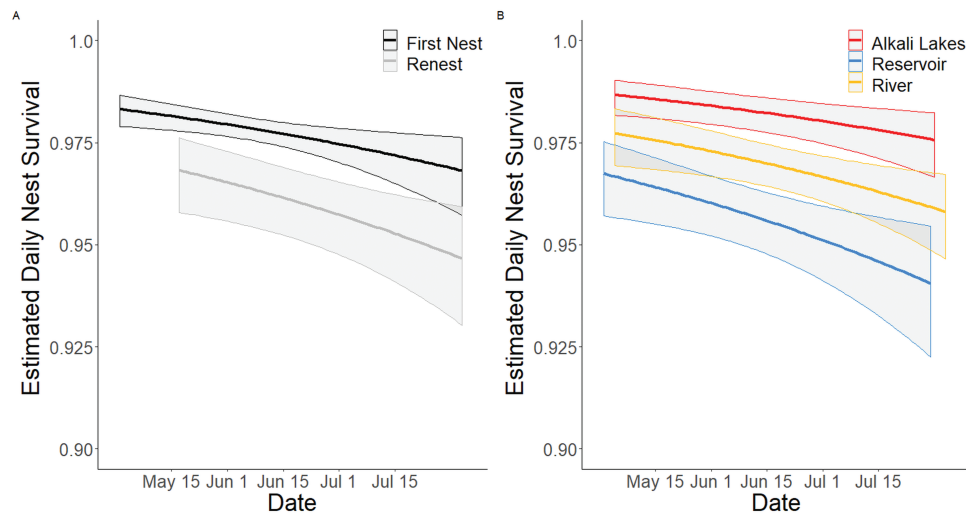


FIGURE 5. Daily nest survival of Northern Great Plains Piping Plovers during 2014–2016. **(A)** Renests (gray) had lower daily nest survival than first nests (black) throughout the breeding season. **(B)** Alkali lakes (red) had higher survival than reservoirs (dark blue) and rivers (yellow). Shaded gray areas indicate 95% confidence intervals.

TABLE 5. Cumulative nest survival estimates for first nests and renests in each of the 3 habitat types for Piping Plovers nests during 2014–2016.

		Cumulative survival	95% CI
Alkali Lakes	First nest	0.707	(0.705, 0.709)
	Renest	0.553	(0.547, 0.559)
Reservoir	First nest	0.415	(0.411, 0.419)
	Renest	0.224	(0.212, 0.236)
River	First nest	0.553	(0.550, 0.556)
	Renest	0.364	(0.355, 0.373)

across years with 1–2 m elevation water rise from May to July for Lakes Sakakawea and Oahe. Compared to average water elevations (from 1955 for Lake Sakakawea and 1967 for Lake Oahe to 2018), water levels were high for each year of our study (Appendix Table 9). However, our index of available habitat did vary considerably among the 3 yr. Compared to other habitat types, reservoir nesting individuals showed much lower apparent reneest reproductive success, unless available habitat increased during the breeding season from May to July. Reservoirs on the Upper Missouri River (upstream of Pierre, South Dakota) experience large interannual water level fluctuations in response to management and wet/dry climate periods (Anteau et al. 2014a, 2014b). Such interannual flooding and drawdown affects habitat abundance and availability among years, but within-year fluctuations in water elevations can dramatically influence individual nest success and reneesting propensity. Due to snowmelt in the Rocky Mountains and local precipitation, reservoirs on the Upper Missouri River often show mid-season water level rise (Anteau et al. 2012b). Upward elevation shifts of only a meter in height can

completely inundate nesting islands and shoreline habitats, flooding nests and drowning unfledged chicks. Mainstem reservoir nesting individuals thus face a more dynamic system both within and between years than individuals nesting on river or alkali lake habitats, which may cause the reduced reneesting propensity, apparent reneest reproductive success, and daily nest survival seen here. While individuals are capable of successfully hatching renests on reservoirs, we never documented a fledged reneest attempt on reservoir habitats. Thus, mid-season water level rise on mainstem reservoirs may be contributing to reduced reneesting and therefore lower reproductive success in plovers. Further, 69% of individuals that moved habitats between first and reneest attempts left reservoir habitats. Some individuals may respond to this dynamic system through breeding dispersal to riverine or alkali lake habitats.

In line with strong temporal and environmental constraints, individuals were more likely to reneest if they had not previously reneested that year. Only 10 individuals attempted a third nest, out of 2,658 individual breeding attempts recorded, and did so at longer intervals than between first and second nest attempts. High-quality individuals may be physiologically able to meet the costs of a second (or third) breeding attempt without being considerably stressed (Gates et al. 2013, Riechert et al. 2013). In our study, we lacked a direct measure of individual condition or quality to test this hypothesis. Instead, we relied upon individual age and previous years breeding experience, which were shown to be important for Great Lakes Piping Plovers (Claassen et al. 2014). While there was no age/experience effect on reneesting propensity or apparent reneest success, contrary to our predictions, after-second-year

adults without documented prior experience renested at shorter intervals than other age/experience classes. However, overall, age and experience were not strong determinants of renesting.

Estimates of apparent renesting propensity are biased low for several possible reasons common to field-based studies. Field crews may fail to detect a nest prior to failure (daily nest detection probabilities on the Garrison River Reach and Lake Sakakawea using the same nest searching protocols range from 0.5 to 0.65; [Shaffer et al. 2013](#)). Individuals may renest outside our study areas, which is unlikely given our current understanding of movements of individuals within our study area and the large area we searched for nests. Finally, we could have failed to associate an individual with a nest prior to failure. Similar issues may occur with longer renesting intervals, which may indicate additional attempts we failed to detect.

Replacing lost nests or broods through renesting may be an unproductive strategy for Piping Plovers in the Northern Great Plains. Renests had lower daily nest survival throughout the breeding season, and cumulative survival was lower for renests than first nests. Additionally, apparent renest reproductive success, which included post-hatch to fledge survival of broods, was low, particularly for individuals nesting on reservoirs. Renests may have lower daily nest survival due to some inherent quality of the individuals attempting those nests, suboptimal timing, or because individuals rush to nest in unsafe or unknown areas. Further, with seasonal declines in reproductive success, renesting may not increase current reproductive success, or at least may come at some long-term cost to annual survival ([Becker and Zhang 2011](#)). Lastly, renesting was fairly uncommon with only 25% of individuals that failed replacing reproductive attempts lost during the nesting stage. This differs considerably from the Great Lakes population of plovers, where 49% of failed pairs renested and one pair made five attempts in one year ([Claassen et al. 2014](#)). The dynamic and unstable environmental conditions that the Northern Great Plains population experiences likely contrast the conditions in the Great Lakes. If so, then these 2 populations may have settled on different bet-hedging strategies to cope with uncertainty and spatiotemporal variability in selective pressures, as has been demonstrated with variation in clutch size ([Boyce and Perrins 1987](#)), in order to maximize lifetime fecundity ([Olofsson et al. 2009](#), [Rees et al. 2010](#), [Chalfoun and Schmidt 2012](#)). Plovers in the Northern Great Plains may therefore be under different selective pressures than those in the Great Lakes, and thus, Northern Great Plains plovers may rely on relatively high annual survival ([Roche et al. 2010](#), [Anteau et al. 2019](#)) to maximize lifetime reproductive success. Further, the difference between the apparent renesting rate for the 2 populations and the overall lack of renest success in Northern

Great Plains plovers provide evidence that patterns from one population may not accurately inform the other. If managers use data from one population to inform intensive conservation and management strategies, the outcomes may not be similar across the 2 populations. Thus, unlike the Great Lakes population, the costs for Northern Great Plains plovers to renest likely do not outweigh the potential reproductive gains, which are modest at best.

Conservation Implications

A federally listed species, the Piping Plover is intensively managed throughout its range and in the Northern Great Plains management of water and predation (predator exclusions, predator removal) are common conservation strategies (USFWS 2016, 2018). Our results demonstrate that in the Northern Great Plains first nests are more valuable to individuals than renests, which occur less frequently and are less likely to be successful. Therefore, intensive management focused on the protection of first nest attempts would likely be more effective than strategies that assume equivalent productivity from renests. Predation management would be most beneficial early in the breeding season, protecting first nests, and potentially removing the need to renest by improving first nest reproductive success. Predator exclusions may be a useful strategy if nests are found and protected early in the breeding season (May/June). Alternatively, predator removal efforts that are successful at decreasing predator numbers early may reduce the number of first nests lost to predators. Predation management has the 2-fold benefit of protecting first nests and reducing the proportion of the population that may lose nests to predators, which had a low renesting propensity compared to other causes of nest failure.

Currently, the U.S. Army Corps of Engineers (USACE) utilizes some discretion with water management of the Missouri River to minimize the flooding of riverine nests and chicks due to spring and mid-summer rises (USFWS 2003). However, water management decisions are part of a complex balance of managing the Missouri River to mitigate downstream flooding, provide sufficient water supplies and flows for navigation, and support fisheries and endangered species (USFWS 2018). When making water management decisions the USACE is often faced with tradeoffs such as “sacrificing” nests or nesting habitat on upstream reservoirs to protect downstream riverine habitat. Generally, mid-summer rises are absorbed by the reservoirs of the Missouri River, particularly Lake Sakakawea, where increasing water levels are responsible for the greatest nest losses in most years ([Anteau et al. 2012a](#), [Shaffer et al. 2013](#)). Previously published renesting rates from the Great Lakes ([Claassen et al. 2014](#)) gave managers some hope that nest loss on the reservoirs due to mid-summer rise would be mitigated by renesting efforts in less vulnerable

habitats. However, our results show that nest losses on reservoirs likely result in total reproductive failure for the year because individuals nesting on reservoirs were less likely to reneest and when they did reneest, the secondary effort did not fledge chicks. Reservoirs could still contribute to population growth, particularly if managers can withhold mid-summer water level rise until nests hatch. In years with lower mid-summer water level rise, when habitat availability remains nearly constant or increases, nest survival was relatively high (Anteau et al. 2012a) and reneest reproductive success was higher. Incorporating nest initiation date, or ideally, nest attempt number, into adaptive management plans would have important consequences when deciding the relative reproductive costs of nest loss due to water management decisions. Areas with high numbers of reneests would be worth less to productivity estimates than areas with high numbers of first nests.

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Ethics statement: Our field protocols were approved by the USGS Northern Prairie Wildlife Research Center Animal Care and Use Committee.

Author contributions: MHS, MJA, and RJS developed the study objectives and designed the methods. MMR and DLT conducted the field work and collected the data. RJS analyzed the data and wrote the paper. All authors participated in editing the paper.

Data depository: Analyses reported in this article can be reproduced using the data provided by Swift et al. (2019).

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APPENDIX TABLE 6. Number of nests and percent of nests followed with predator exclosures used on alkali lakes for each year.

Year	Nests with exclosures	Percent of nests on alkali lakes exclosed
2014	33	31%
2015	28	18%
2016	27	18%

APPENDIX TABLE 7. Evidence used to determine cause of nest failure. We collected 2–4 pieces of evidence at the nest, and if we could not determine which category the nest fit into we left it as unknown. Some pieces of evidence (e.g., coagulated yolk) could occur for multiple causes of failure, which is why multiple lines of evidence were required. We did not determine cause of reproductive attempts that failed during the brood-rearing stage.

Cause of nest failure	Evidence
Hatched	Chicks in the nest bowl ^a Chick tracks in sand near the nest bowl Chicks (of appropriate age) observed near the nest bowl Chick droppings in or next to the nest bowl Pipping fragments or egg caps in the nest bowl
Predation	Predator marks on egg Predator tracks near nest bowl Eggs damaged or destroyed Yolk coagulated in bottom of nest bowl Predator feces at or near nest bowl Eggs crushed by humans (vehicle tracks or footprints) Eggs displaced from nest bowl Predator observed at the nest site Other predator sign: carcass or remains of adult, blood in nest bowl, or cached eggs found nearby
Flooding	Eggs/nest bowl under standing water or recently under water Eggs/nest bowl under sand or recently under sand Known water level rise inundated nest elevation Debris/wrack in or near the nest bowl Eggs displaced from nest bowl Habitat erosion
Severe weather	Eggs crushed, damaged, or destroyed Coagulated yolk or egg shells present Eggs displaced from nest bowl Hail damage to eggs (from known storm) Eggs/nest bowl under standing water or recently under water—no known water level rise Wet substrate, nest not inundated—rain damage Sand drifted over eggs
Abandoned ^b	Eggs suspended in sand Cold eggs Nest bowl not maintained Sand stuck to eggs Eggs not rotated Condensation on eggs

^a Only evidence that did not require additional support. If chicks were found in the nest bowl, then the nest was categorized as hatched.

^b Abandoned nests were included in the unknown category and required 3 visits to the nests with evidence of abandonment.

APPENDIX TABLE 8. Number of individuals in each age and experience class for each year. After-second-year (ASY) adults could have been banded as adults or as chicks in a prior year. Second-year (SY) birds were banded as chicks in the year prior. Unknown-age birds were newly captured as an adult.

Year	Age	Experience	<i>n</i>
2014	ASY	No known	42
	ASY	Known	150
	SY	No known	44
	Unknown	Unknown	481
2015	ASY	No known	47
	ASY	Known	389
	SY	No known	63
	Unknown	Unknown	420
2016	ASY	No known	76
	ASY	Known	565
	SY	No known	64
	Unknown	Unknown	317

APPENDIX TABLE 9. Mean mainstem reservoir elevations for May–July for Lake Sakakawea (SAK) and Lake Oahe (OAH) in 2014–2016 as well as since dam creation.

Reservoir	Year	Mean elevation (m.a.s.l.)
SAK	1955–2018	557.8
	2014	560.6
	2015	561.3
	2016	561.0
OAH	1967–2018	488.5
	2014	490.7
	2015	491.0
	2016	491.2