

Direct and indirect effects of nesting density on survival and breeding propensity of an endangered shorebird

DANIEL H. CATLIN , † DANIEL GIBSON , KELSIE L. HUNT, MERYL J. FRIEDRICH, CHELSEA E. WEITHMAN, SARAH M. KARPANTY, AND JAMES D. FRASER

Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, Virginia 24061 USA

Citation: Catlin, D. H., D. Gibson, K. L. Hunt, M. J. Friedrich, C. E. Weithman, S. M. Karpanty, and J. D. Fraser. 2019. Direct and indirect effects of nesting density on survival and breeding propensity of an endangered shorebird. *Ecosphere* 10(6):e02740. 10.1002/ecs2.2740

Abstract. Density-dependent regulation is a fundamental part of ecological theory and a significant driver of animal demography often through complex feedback loops. We investigated the relationship between flood- and demographically induced fluctuations in density and the breeding propensity and survival of a pioneer species, the piping plover (plover, *Charadrius melodus*). We captured and marked adult and hatchling plovers on the Gavins Point Reach of the Missouri River in South Dakota and Nebraska, USA, from 2005 to 2014. In 2010 and 2011, historically high water levels and flooding inundated much of the plover's sandbar nesting habitat on the Missouri River. We developed a Bayesian formulation of a multievent model, or a multistate survival model with state uncertainty to estimate breeding propensity simultaneously with survival. Although plovers are conspicuous, their breeding status can be difficult to establish with certainty, which necessitated the use of uncertain states. With this model, we investigated the effect of sex, habitat availability, river flow, and density (birds/ha nesting habitat) on survival of hatch year and breeding and non-breeding adult plovers. In addition, we estimated the transition rates for these age classes between breeding and non-breeding states. Non-breeding adults ($\bar{\phi}_{\text{AHY, n}} = 0.58 \pm 0.06$) had lower survival rates than breeding adults ($\bar{\phi}_{\text{AHY, b}} = 0.80 \pm 0.04$), and both breeding survival and breeding propensity decreased with increasing nesting density. Not only did survival and breeding propensity decrease directly at higher nest densities, but survival also was indirectly impacted by increasing the proportion of non-breeding birds with relatively low survival. Thus, plovers were regulated through a complex set of feedback loops, acting as densities increased. Our findings underscore the intricacy of density-dependent regulation and suggest that detailed demographic studies are needed to fully understand these effects.

Key words: breeding propensity; density dependence; Missouri River; piping plover.

Received 3 January 2019; revised 15 March 2019; accepted 8 April 2019. Corresponding Editor: Brooke Maslo.

Copyright: © 2019 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** dcatlin@vt.edu

INTRODUCTION

Population regulation through density dependence is a fundamental concept in ecology and underpins many of the fluctuations in animal abundance that we observe (Newton 1994, 1998). Density-dependent population change often is a function of limited habitat negatively impacting one or more vital rate in a population, sometimes through complex negative feedback loops (Gill

et al. 2001). Although density-dependent regulation is common (Gibbons et al. 1993, Newton 2004, Norris et al. 2004), the specific effect on each vital rate often is not known (Newton 1998, 2004). Density can affect any of the demographic parameters that drive populations (e.g., Ferrer and Donazar 1996, Both 1998, Paradis et al. 2002, Matthysen 2005), such that studies focused on understanding density-dependent population regulation should endeavor to look broadly to

detect potentially complicated interactions between habitat, density, and demography (Gill et al. 2001).

Piping plovers (*Charadrius melodus*, hereafter plovers) are migratory, territorial shorebirds that nest on sparsely vegetated beaches on the Atlantic coast, Great Lakes, and Great Plains in the United States and Canada (Elliot-Smith and Haig 2004). Across their range, disturbances (e.g., high-water events on rivers, reservoirs, and alkali lakes; coastal storms) are essential for maintaining early successional habitat. However, these environmental disturbances often impact human safety and infrastructure (Morton 1976, Pielke et al. 2008, USFWS 2009). Consequently, numerous structures and habitat modifications (e.g., dams, jetties, dunes, etc.) have been built to protect human interests (Gittman et al. 2015), which often influence habitat succession or the stable state of the system (Schupp et al. 2013, Gittman et al. 2016). Ultimately, plovers were listed under the U.S. Endangered Species Act in 1986, as a result of habitat loss and low reproductive output (U.S. Fish and Wildlife Service 2009). While significant gains have been made toward recovery (USFWS 2009), habitat limitation and resulting density-dependent regulation continue to plague the species.

A key plover nesting area is on the Missouri River in North Dakota, South Dakota, and Nebraska, USA, where they nest on river sandbars (Catlin et al. 2015). In June 2010, relatively high water submerged nearly all sandbar habitat, severely impinging on reproductive output of plovers and other ground-nesting birds at several locations on the river. In 2011, increased mountain snowpack and spring precipitation resulted in historically high water in the Missouri River, and water again covered almost all nesting habitat. As a result, few nests were initiated, fewer hatched, and reproductive output was essentially 0 in that year. Although some areas were less affected by the high flows, these sandbars experienced extremely high rates of predation during the 2011 flood, and reproductive output at these sites was very low (Catlin et al. 2015). Despite the immediate negative impacts of the flood on reproductive effort and success, the two high-water years subsequently created an abundance of nesting habitat throughout the system by redistributing sand

and scouring existing sandbars of vegetation (Hunt et al. 2018).

Previous studies have indicated that plover reproduction (Hunt et al. 2018), immigration, and emigration (Catlin et al. 2015) are density dependent, but key aspects of demography such as adult survival and breeding propensity (Weithman et al. 2017) are relatively unstudied with respect to density. The objectives of this study were to evaluate the effect of nesting density on the breeding propensity and survival of second year (one year post-hatch) and adult plovers, and to compare survival rates for breeding and non-breeding birds. We used data from a 10-yr study of plover demography to address these objectives. Plovers on the Missouri River are habitat limited (Catlin et al. 2015, Hunt et al. 2018), so we hypothesized that nesting density would be negatively correlated with breeding propensity. The implicit assumption is that territoriality will limit population sizes either directly or indirectly (Brown 1969). As the size of breeding populations increases, individuals can compress territories (Severinghaus 1996), move to subpar habitat where survival and reproduction are relatively low (Gill et al. 2001), or skip breeding (e.g., Sedinger et al. 2001, Reed et al. 2004, Hoy et al. 2016, Blomberg et al. 2017). We hypothesized that severe flooding in 2010 and 2011 would lead to higher than average proportions of non-breeding birds because large swaths of habitat were inundated during those events. And finally, because plovers have high levels of breeding philopatry, which presumably benefits their survival through familiarity with their habitat (Temeles 1994, Yoder et al. 2004), we hypothesized that non-breeding birds would have lower survival than breeding birds; thus, survival would be indirectly impacted by nesting density.

MATERIALS AND METHODS

Study area

We studied piping plovers nesting on sandbars in the Missouri National Recreational River on the Gavins Point Reach (GVP), a 95-km stretch of river between the Gavins Point Dam (42°51' N, 97°29' W) and Ponca State Park (42°36' N, 96°42' W) in 2005–2014 (Fig. 1). Additionally, in 2007–2014, we studied plovers nesting on engineered

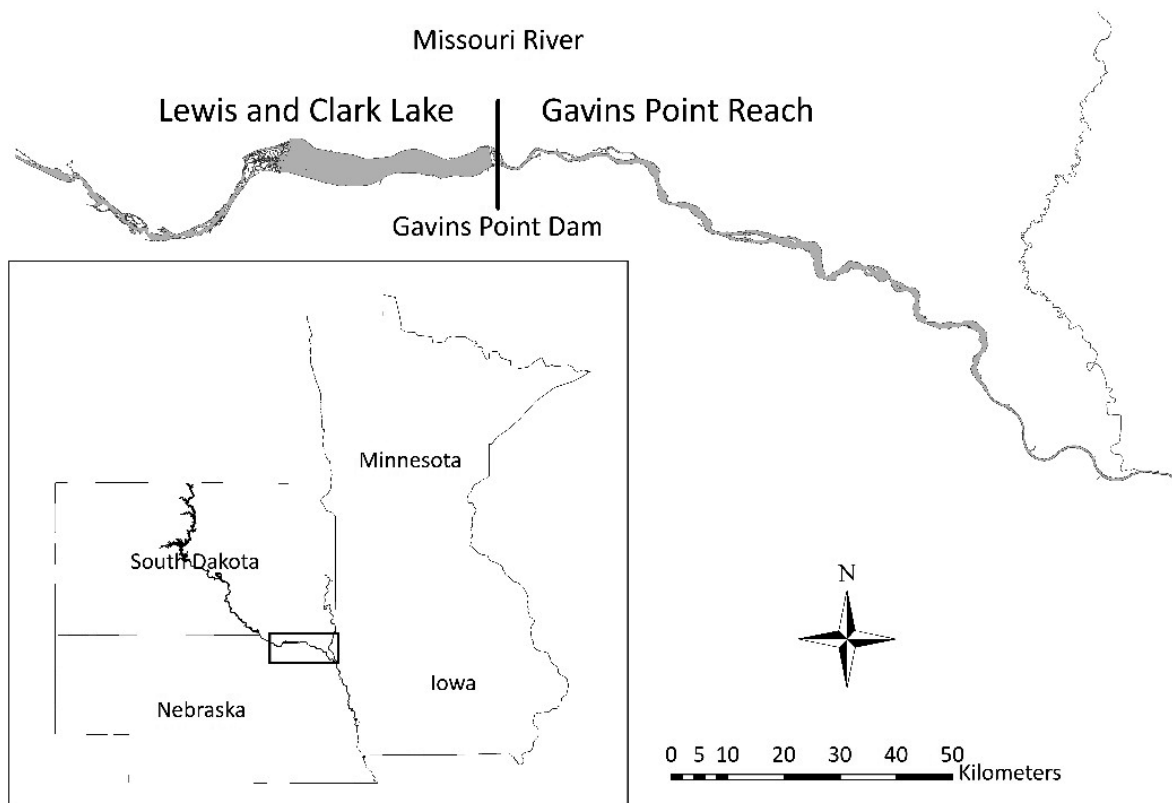


Fig. 1. Study area map showing piping plover breeding locations on Lewis and Clark Lake and the Gavins Point Reach of the Missouri River.

sandbars in Lewis and Clark Lake (LCL, 42°51' N, 97°47' W; Fig. 1). The GVP is one of the last unchannelized portions of the Missouri River (USFWS 2003, Catlin et al. 2011, 2015).

Field methods

We searched plover habitat (i.e., unvegetated and sparsely vegetated wet and dry sand habitat) during the plover breeding season (April–August) from 2005 to 2014. At all sites, we visually scanned the area for both banded and unbanded adults and chicks, watched for behavior suggestive of nesting or breeding, and searched for nests by walking through all potential nesting habitat. We captured incubating after hatch year (AHY, ≥ 1 yr post-hatch) plovers using drop door traps placed over their nests (cf. Weller 1957, but often manually triggered), and hatch year (HY, hatch to following breeding season) birds were caught by hand as soon as possible after hatching (usually within the first 3 d

after hatch). Birds were banded using a unique color band combination. We determined the sex of adult birds based on plumage, behavior (Gratto-Trevor 2011), or nesting with a known sex bird. We attempted to resight all banded birds every 2 d throughout the breeding season. In addition to resighting, we attempted to determine whether banded individuals were nesting in a given year. We associated adults with nests if the bird was captured on a specific nest or if we observed it incubating eggs or brooding chicks.

Model development

Basic model.—We developed a multievent model to estimate apparent survival (ϕ) and transition (ψ) between breeding and non-breeding states. The multievent model is a modified multi-state model that allows for uncertain state assignment (Pradel 2005). In this study, for example,

we were able to directly observe breeding (e.g., a bird captured incubating a nest), but birds that were seen, but not seen breeding, could be either non-breeders or breeders we failed to detect breeding. We based our parameterization of the multievent model after Pradel (2005) and a hierarchical Bayesian multistate model (Kéry and Schaub 2012; Appendix S1). There were three underlying states, among which birds could transition in this model: (1) alive and breeding (b), (2) alive and not breeding (n), and (3) dead (d; Table 1).

To account for uncertainty in state assignment, we divided the observation process (p) into three categories: (1) seen but not seen breeding, (2) seen breeding, and (3) not seen (Table 2). The state and observation matrices were the same for both AHY and HY birds except that HY birds cannot be in the breeding state, and therefore, the probability that a breeding bird is not seen breeding (π) given that it was seen was set to 0 for those birds. We modeled π as a constant for the remaining birds. Model priors and full likelihood can be found in the supplemental material (Appendix S2). Exploratory modeling indicated that the probability of resighting a breeder (p_b) was 1, so we modeled this parameter as constant (sex and time invariant) for all analyses. We assumed that the resighting rate for

non-breeding individuals (p_n) was sex-specific but similar for both hatch year and after hatch year birds because of prior modeling, and our resighting efforts throughout the study were consistent and intensive (Catlin et al. 2015, 2016, Hunt et al. 2018). We estimated separate survival and transition rates for AHY and HY non-breeders and sex-specific survival and transition rates for both breeders and non-breeders. For birds of unknown sex, we built a mixture model into the likelihood that assigned individuals to one or the other sex as a Bernoulli trial with a uniform (0,1) prior on the probability. We modeled random temporal variation in survival of breeders and non-breeders and in the transition rates among these states (see Appendix S2 for model code).

Covariate models.—We used covariates for average flow in June (peak of breeding season), the amount of nesting habitat available, and population density to examine plover population regulation. These factors have been shown to affect plover reproduction (Catlin et al. 2013, Hunt et al. 2015, 2018) and movement (Catlin et al. 2015), and each is a potential index to habitat limitation and thus population regulation. In general, as flows increase, the area of sandbar available to plovers decreases, which leads to increased nesting densities, but the relationship between flow and habitat is not necessarily linear (Catlin et al. 2010). Although peak flows would be associated with the lowest amount of habitat, we chose to use average flow in June because plovers can readily reneest after flooding, such that daily peaks may be less representative of the flow (and therefore habitat) available during the bulk of the season when birds are choosing to breed. Thus, we used multiple measures of habitat availability to understand the drivers in this system.

We developed three additional models, adding each covariate separately to the basic model described above to test their individual effects on demography. Each covariate was added to the state- and age-specific survival and transition parameters, in place of the parameter-specific random temporal variation, such that the covariate had an independent effect on each of the parameters (Appendix S2). We used the average daily outflow from the Gavins Point Dam in June as an index to flows during the plover breeding season (USACE 2014). The amount of nesting habitat (defined as open or sparsely vegetated

Table 1. State transition (ψ) matrix for a multievent survival (ϕ) model for breeding (b) and non-breeding (n) piping plovers on the Missouri River (2005–2014).

State	Non-breeder _{t+1}	Breeder _{t+1}	Dead _{t+1}
Non-breeder _t	$\phi_n \times \psi_{n \rightarrow n}$	$\phi_n \times \psi_{n \rightarrow b}$	$1 - \phi_n$
Breeder _t	$\phi_b \times \psi_{b \rightarrow n}$	$\phi_b \times \psi_{b \rightarrow b}$	$1 - \phi_b$
Dead _t	0	0	1

Table 2. Multievent survival model observation probabilities (p) for non-breeding (n) and breeding (b) piping plovers on the Missouri River (2005–2014).

Observation	Non-breeder	Breeder	Dead
Seen not breeding	p_n	$p_b \times \pi$	0
Seen breeding	0	$p_b \times (1 - \pi)$	0
Not seen	$1 - p_n$	$1 - p_b$	1

Note: Pi (π) represents the probability that a breeding bird is not seen breeding given that it was seen (p_b).

dry or wet sand, <30% ground cover) was estimated from Pan-sharpened multispectral Quick-Bird (satellite) imagery (1 m resolution) that was classified using Definiens Developer Software (C. Huber, USACE, unpublished data). We used estimates of population size from a robust design Barker survival model (Kendall et al. 2013, Weithman et al. 2017) to calculate population density (adult birds/ha nesting habitat). All covariates were standardized (mean = 0, SD = 1) prior to analysis, allowing for comparison of relative effect sizes across models. All estimated annual vital rates were produced from the basic model, representing the mean rates over all covariates. The tests of the effect of covariates were from their respective covariate models. Posterior means are presented as mean \pm 1 SD unless otherwise indicated.

Model specification.—We specified models within R (R Core Team 2012) using the package jagsUI to call JAGS (Plummer 2003) and export model results back to R. After assessing the performance of a series of exploratory model runs, we ran four chains of 40,000 with an adaptive phase of 15,000 runs and a burn-in period of 100 for each analysis. We determined parameter convergence using the Brooks-Gelman-Rubin criterion (\hat{R}) (Brooks and Gelman 1998), and we considered models that had $\hat{R} < 1.1$ at each parameter node to have reached convergence.

Goodness of fit.—There is no goodness-of-fit test specifically for multievent models (Pradel 2005). Therefore, we assessed the fit of the data to a simple multistate model (i.e., no state uncertainty) using the median \hat{c} test in Program MARK (White and Burnham 1999), which would result in a conservative goodness-of-fit estimate. We used a model with full time and state variability in all parameters and age-specific (hatch year vs. after hatch year) variability in the non-breeding state parameters.

RESULTS

We captured and banded 3533 individuals; 2702 were banded as chicks and 831 were banded as adults. Of these birds, 1276 were resighted as adults, of which 453 (35.5%) were known females, and 506 (39.7%) were known males. Of the 3214 resightings of adult birds, 2340 (73%) were seen breeding. Mean June flow was

$1008.39 \pm 1109.47 \text{ m}^3/\text{s}$, peaking at $3936.04 \text{ m}^3/\text{s}$ in 2011 during the flood. The mean amount of plover habitat available was $881.34 \pm 974.08 \text{ ha}$, with the lowest amount (47.63 ha) occurring during the 2011 flood and the highest (2944.38 ha) in 2012. Mean density was $1.40 \pm 1.80 \text{ adults/ha}$ and ranged from 0.07 adults/ha in 2012 and 5.74 adults/ha in 2011. Flow was highly correlated with density ($r = 0.91$, $P < 0.001$) but less with habitat ($r = -0.27$, $P = 0.49$). Density and habitat were negatively correlated ($r = -0.59$, $P = 0.09$).

Goodness of fit

The median \hat{c} indicated that the general multistate model fit our plover data well, showing no indication of lack of fit ($\hat{c} = 1.03 \pm 0.16$).

Resighting

Resighting rates for non-breeding individuals ($\bar{p}_n = 0.64 \pm 0.06$, $\sigma_n = 0.53 \pm 0.23$) were lower than rates for breeding birds ($\bar{p}_b = 1.00 \pm 0.001$), and females had lower resight rates than males as non-breeders ($\beta = -0.67 \pm 0.22$). The rate at which breeding birds were resighted but not identified as breeders (π) was 0.14 ± 0.02 . The probability that birds of unknown sex were assigned as female was 0.48 ± 0.02 , which was similar to the observed proportion of females among birds of known sex (0.47).

Survival

Average hatch year survival ($\bar{\phi}_{\text{HY}} = 0.25 \pm 0.04$) was lower than both non-breeding adults ($\bar{\phi}_{\text{AHY}, n} = 0.58 \pm 0.06$) and breeding adults ($\bar{\phi}_{\text{AHY}, b} = 0.80 \pm 0.04$), and it increased substantially following the 2011 flood (Fig. 2A). Both breeding adults and non-breeding birds (AHY and HY) had similar levels of temporal variability in survival ($\sigma_b = 0.50 \pm 0.20$, $\sigma_n = 0.52 \pm 0.13$) despite generally lower survival of non-breeding birds (Fig. 2B, C). There was some indication that female plovers had higher breeding survival than males ($\beta = 0.18 \pm 0.19$, Fig. 2B), but sex did not appear to affect either hatch year ($\beta = -0.11 \pm 0.23$) or after hatch year non-breeding survival ($\beta = 0.09 \pm 0.21$).

Breeding propensity and transitions among breeding states

Breeding propensity of returning hatch year birds averaged 0.31 ± 0.06 , showing two distinct

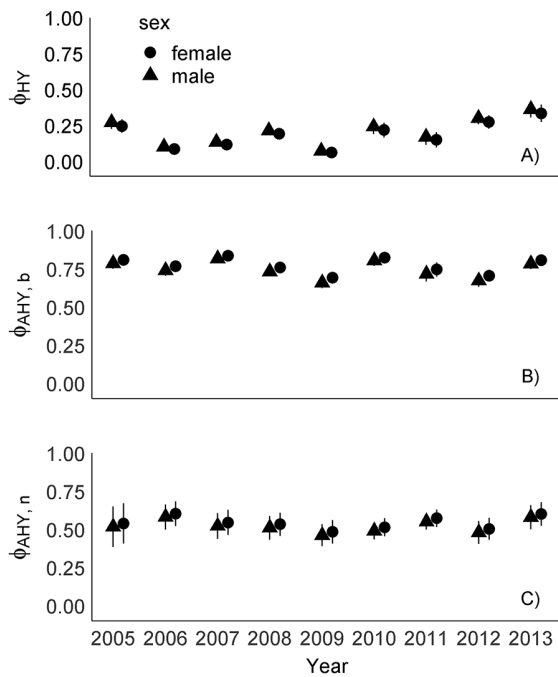


Fig. 2. Annual apparent survival rates (ϕ) of (A) hatch year (HY), (B) breeding (b), and (C) non-breeding (n) after hatch year (AHY) female and male plovers on the Missouri River. High-water events occurred in the 2010 and 2011 breeding seasons. Error bars represent 1 SD.

peaks in 2008–2009 and 2013–2014 (Fig. 3). Female birds tended to breed in their second year at a higher rate than males ($\beta = 0.27 \pm 0.29$), but there was substantial overlap in the estimates (Fig. 3). The probability that a breeding bird transitioned to a non-breeding bird averaged 0.25 ± 0.08 , but showed a relatively high level of temporal variation ($\sigma_{b \rightarrow n} = 1.10 \pm 0.41$). Annual estimates ranged from 0.10 to 0.56 and were steady and relatively low before the flood and two to three years after the flood, peaking during the flooding in 2010 and 2011 and in the year following the flood (Fig. 4A). The average probability of an adult bird transitioning from a non-breeding to breeding state was 0.47 ± 0.07 with moderate temporal variation ($\sigma_{n \rightarrow b} = 0.56 \pm 0.17$; Fig. 4B). The rate of transitioning from non-breeding to breeding was highest in 2012, but there were relative peaks in 2009 and in 2014 as well (Fig. 4B).

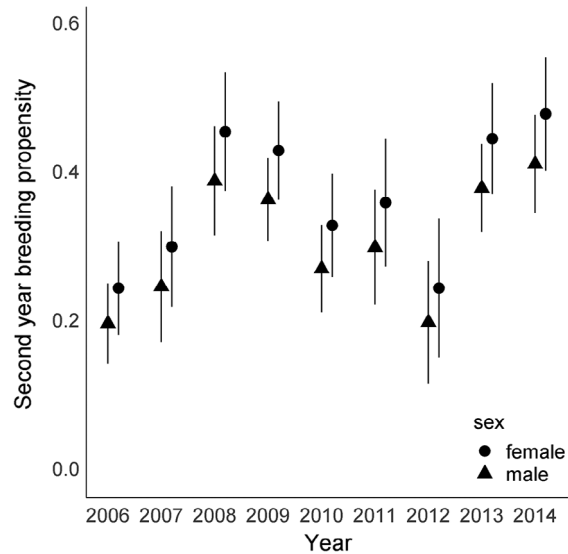


Fig. 3. Annual breeding propensity of second-year plovers into the breeding population on the Missouri River by sex. High-water events occurred in the 2010 and 2011 breeding seasons. Error bars represent 1 SD.

Covariate effects

Breeding survival was positively correlated with average flow in June ($\beta = 0.20 \pm 0.11$), but non-breeding adult survival was negatively correlated with it ($\beta = -0.28 \pm 0.10$). Hatch year survival was positively correlated with the amount of available habitat ($\beta = 0.54 \pm 0.09$), and both breeding survival ($\beta = -0.21 \pm 0.08$) and hatch year survival ($\beta = -0.65 \pm 0.12$) were negatively related to density.

The transition of adult plovers from the non-breeding state to the breeding state was negatively related to both flow ($\beta = -0.31 \pm 0.13$; Fig. 5) and density ($\beta = -0.41 \pm 0.12$; Fig. 6). Similarly, the transition of adults from the non-breeding to breeding state was positively correlated with the amount of habitat present in the study area ($\beta = 0.33 \pm 0.12$; Fig. 7). The transition of breeders into the non-breeding state was positively related to both flow ($\beta = 0.53 \pm 0.07$; Fig. 5) and density ($\beta = 0.52 \pm 0.08$; Fig. 6) and negatively related to habitat, but the effect was not significant ($\beta = -0.24 \pm 0.18$; Fig. 6). In terms of relative effect size, density appeared to have the greatest effect on plover demography (Fig. 8).

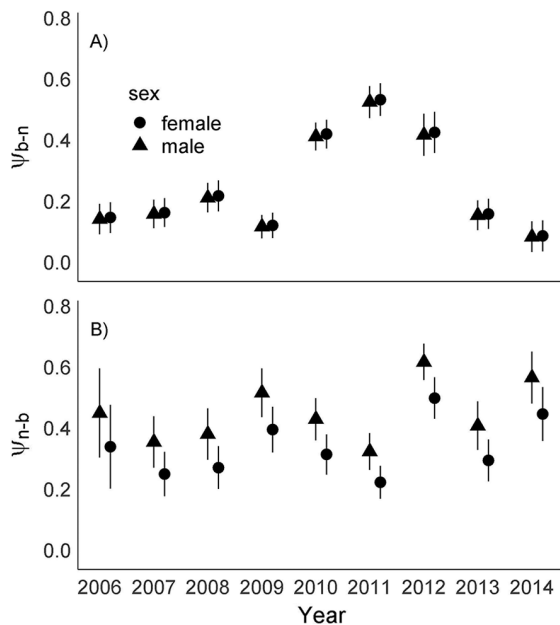


Fig. 4. Annual transitions (ψ) between (A) breeding (b) and non-breeding (n) states and (B) the reverse for adult female and male piping plovers on the Missouri River. High-water events occurred in the 2010 and 2011 breeding seasons. Error bars represent 1 SD.

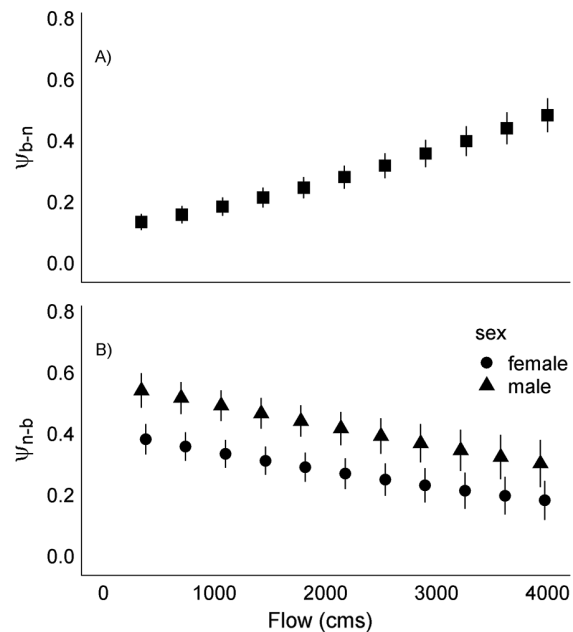


Fig. 5. Predicted relationship between average flow in June on the transition between (A) breeding (b) and non-breeding (n) states (invariant by sex) and (B) the reverse on adult female and male piping plovers on the Missouri River. Error bars represent 1 SD.

DISCUSSION

Our results indicate that plover populations on the Missouri River were regulated through direct density-dependent impacts on adult survival, hatch year survival, and breeding propensity. Moreover, these birds were indirectly affected by density because at higher nest densities, fewer plovers bred, and non-breeding plovers had lower survival. Previous studies have indicated that reproductive output (chick survival), site fidelity, and immigration rates are also density dependent in this population (Catlin et al. 2015, Hunt et al. 2015, 2018). Thus, piping plovers experienced a complex interaction of negative feedback loops that regulated their populations as density fluctuated. A key factor in the decline of plovers throughout their range is the loss of habitat through development and disturbance (USFWS 2009); thus, it is not surprising to detect correlations with habitat, density, survival, and the transition between breeding and non-breeding states in adults. Plovers are territorial (Elliot-Smith and Haig 2004), and increasing

density should constrain the number of breeding pairs through negative density-dependent demographic impacts, as the population approaches carrying capacity (Newton 1998). As densities of wintering Black-tailed godwits (*Limosa limosa*) increased in Britain, their populations exhibited a similarly complex suite of interactions, with feeding rates, survival, and arrival at breeding locations all negatively impacted by density (Gill et al. 2001). Gill et al. (2001) attributed these changes to the buffer effect, where increases in numbers were primarily at poor quality sites, such that population averages of demographic rates decline. In the case of the floods in 2010 and 2011, so little habitat was available throughout the range that a small number of birds made presumably poor breeding decisions, such as breeding on gravel roads in farm fields and parking lots adjacent to the flooded river (D. Catlin, *unpublished data*), similar to the buffer effect observed in godwits (Gill et al. 2001). Moreover, the few birds that did breed suffered extremely high depredation rates of their nests (Catlin et al. 2015), suggesting

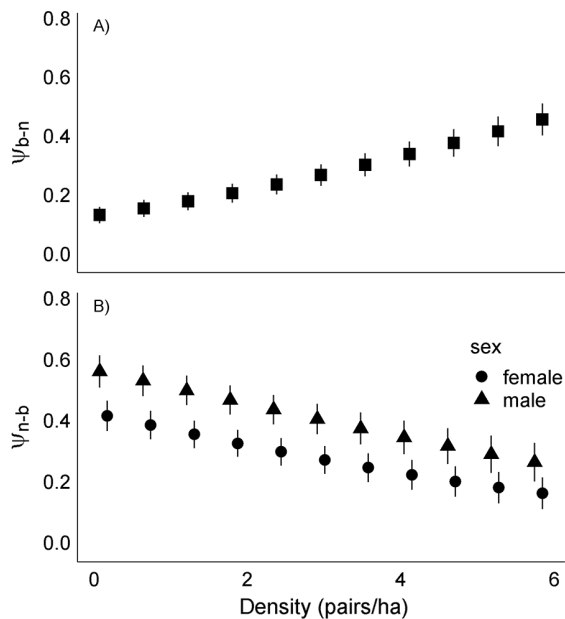


Fig. 6. Predicted relationship between nesting density (pairs per hectare of nesting habitat) and the transition between (A) breeding (b) and non-breeding (n) states (invariant by sex) and (B) the reverse on adult female and male piping plovers on the Missouri River. Error bars represent 1 SD.

that they were using subpar habitat, and the return from breeding was minimal that year.

Non-breeding birds had lower survival than breeding birds, regardless of age. Since first-year survival included the pre-fledge period in our study, lower survival in that group is to be expected, but the estimate of survival for non-breeding adult piping plovers was also considerably lower than that of breeding adults in this system and throughout the species range (see review in Catlin et al. 2015). Breeding propensity is one of the least well-understood reproductive parameters because non-breeders often are absent from or less detectable on the breeding grounds (Etterson et al. 2011). In these situations, breeding propensity often is estimated using a variant of the robust design model (Kendall and Bjorkland 2001, Kendall and Nichols 2002). However, these models assume that (1) non-breeders and breeders have identical survival probabilities; and (2) presence is equivalent to breeding. In this study, we demonstrated that both of these assumptions would have been violated in this system, as

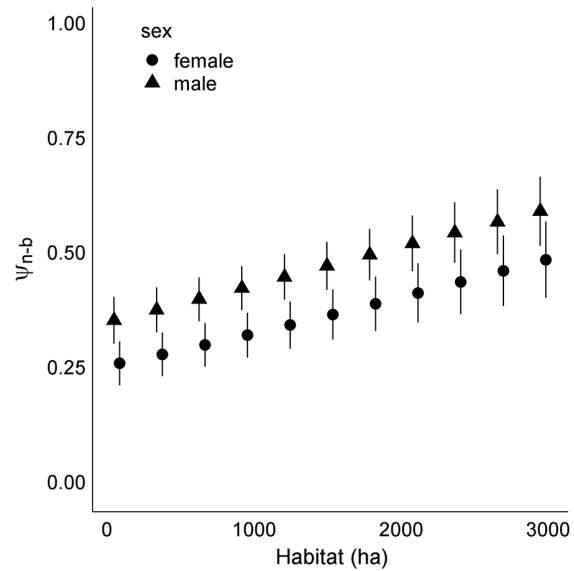


Fig. 7. Predicted relationship between the amount of nesting habitat available on the transition of female and male adult piping plovers between the non-breeding (n) and breeding (b) states on the Missouri River. Error bars represent 1 SD.

survival differed between breeders and non-breeders, and birds were imperfectly classified to breeding state. As meeting these assumptions is difficult, unbiased estimates of survival from non-breeding individuals are rare. No difference in survival was observed between breeding and non-breeding greater snow geese (*Chen caerulescens*, Souchay et al. 2014), but non-breeding wandering albatrosses (*Diomedea exulans*) had slightly higher rates of survival than breeding birds, presumably because of the cost of reproduction in the species (Barbraud and Weimerskirch 2012).

Here, the difference between breeding and non-breeding survival suggests that either breeding or the behaviors and activities associated with it confer some survival benefit to piping plovers (at least when breeding densities are relatively low), or breeding propensity is an indicator of individual quality and therefore inherently linked with survival (Sedinger et al. 2008, Aubry et al. 2011). Although plovers of both sexes have generally high breeding propensity, there appears to be more impetus for males to breed in any given year (Weithman et al. 2017). Unmated males that are attempting to breed may be at greater risk of predation because of their

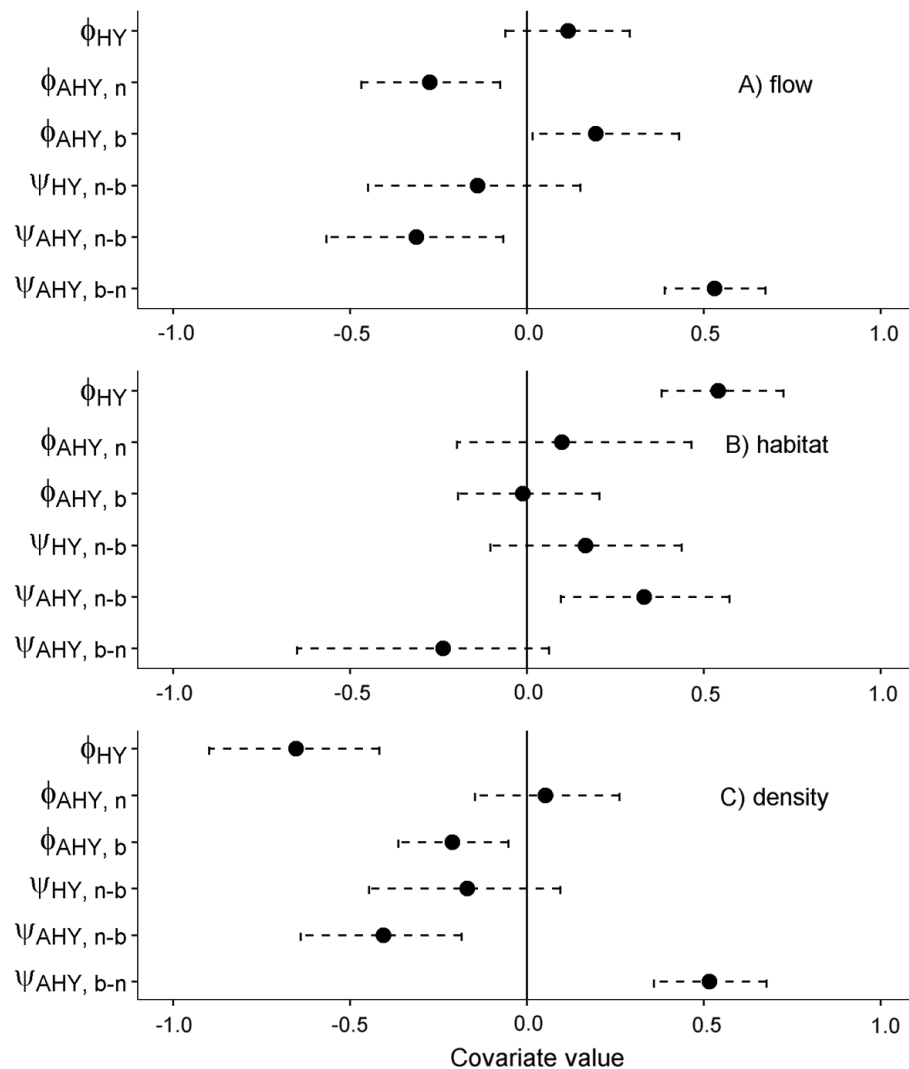


Fig. 8. Beta covariate estimates for the effect of (A) average flow in June, (B) the amount of habitat available, and (C) density on piping plover survival (ϕ) and transition between breeding states (ψ , b—breeder, n—non-breeder) on the Missouri River. Error bars represent 1 SD.

conspicuous displays and aggressive territorial interactions (Elliot-Smith and Haig 2004). At least some unpaired male plovers will continue to sing well into the breeding season before abandoning the attempt if they remain unpaired (D. Catlin, *personal observation*), with the last nests laid typically around the end of June and beginning of July (Catlin et al. 2015). Non-breeding female plovers, however, would presumably not have a territory and thus would be more mobile. Our data indicated that both male and female plovers that were not breeding were less likely to

be detected, and that females were less likely than males, which may be further evidence that non-breeding birds tended to be more mobile. Many studies have affirmed the fidelity of plovers to locations across the annual cycle; fidelity of breeding birds to their populations (variously defined) across several studies was $\geq 83\%$ and $\geq 46\%$ for returning hatch year birds (Catlin et al. 2015) and appears to be relatively high for wintering birds as well (Gratto-Trevor et al. 2016, Gibson et al. 2018). Moreover, when plovers move, they do not disperse far; the median

distance traveled between consecutive years and nests for plovers in this population was 153 m (Friedrich et al. 2015). Familiarity with a site then may confer a survival benefit through reduced territorial interactions (Temeles 1994) or through a reduction in predation associated with site familiarity (Yoder et al. 2004). There is evidence that female piping plovers in the Great Lakes have higher fledging success when they have experience at a breeding site (Saunders et al. 2012), but there is little known about the benefits of fidelity to survival. If birds that have relatively high site fidelity are more likely to breed, then lower survival of non-breeding birds could act to reinforce high site fidelity.

As predicted, large proportions of the breeding population transitioned to the non-breeding state during the high-water events in 2010 and 2011, but we did not anticipate that value remaining high the following year (Fig. 4). There also was, however, a large proportion of non-breeding adults from the flood years that returned to the breeding state in 2012 (Fig. 4). We speculate that the relatively high level of transitions (i.e., breeding to non-breeding and vice versa) observed in the year following the flood may have resulted from a breakdown in their typical social structure. Despite their high site fidelity, flooding in 2011 precluded most territorial establishment on the Gavins Point Reach that year, and only small pockets of nesting habitat remained throughout the Great Plains (D. Catlin, *personal observation*). Moreover, the flooding dramatically changed the landscape of sandbars within the river, increasing the amount of habitat 10-fold and reorienting it as well (Hunt et al. 2018). As further evidence of a change in the social structure following the flood, double brooding (i.e., the production of a second clutch after fledging a first brood) is rare in plovers, but the rate increased substantially in 2012 when nesting densities were very low (Hunt et al. 2015). Because of relatively high survival and fidelity for piping plovers in this study, we speculate that a level of familiarity among breeding birds was lost temporarily when the flood rearranged habitat and birds.

When plover populations have experienced large-scale habitat increases, populations have generally increased as well, but there typically is a lag between habitat creation and rapid population growth, despite relatively high reproductive

output immediately following the disruption (Wilcox 1959, Cohen et al. 2009, Hunt et al. 2018). In the case of the Missouri River after the 2011 flood, we now have evidence from this study that fewer birds bred than we would have expected, which could explain the lag in population growth despite high average reproductive output for the birds that did breed (Hunt et al. 2018).

Non-breeding birds in our study also were more difficult to detect than their breeding counterparts. A previous study indicated that some non-breeders did not return to the study area (Weithman et al. 2017) and thus were not observable, but not all non-breeding plovers were absent from the study area. The difficulty in accurately detecting and counting non-breeding individuals complicates the use of standard measures of reproductive output (e.g., chicks fledged per pair) to predict population growth. There are examples of a mismatch between the expectation based on estimated reproductive output and the reality of population growth for piping plovers (Hecht and Melvin 2009). While some mismatches could be due to unmeasured immigration (Cohen et al. 2009), our results suggest that variable breeding propensity could also affect these predictions. Similarly, detection can affect estimates of first-year breeding propensity. Our estimates of first-year breeding propensity are much lower than those in Saskatchewan (females 68%, males 41%), but those rates did not account for imperfect detection (Gratto-Trevor et al. 2010). In a study of Great Lakes plovers that did control for imperfect detection, Saunders et al. (2014) found that 35% of male birds breed in their first year and 56% of females do, which is comparable to the rates for males we noted in our study but was still far lower for females.

Multievent models are an extremely flexible, albeit under-utilized, tool for accounting for imperfectly observable heterogeneity among individuals (Gimenez et al. 2018). Developing multievent models in a Bayesian framework requires only slight changes to the model likelihood and initial latent state information relative to standard multistate models (Kéry and Schaub 2012). Although multievent models require a larger number of estimated parameters relative to similarly parameterized multistate or robust design models, depending on the magnitude of state misclassification and variation in demographic

rates or detection among individuals across states, the use of multievent models may violate fewer assumptions, resulting in less biased and more informative parameter estimates. In this study, the use of multievent models allowed us to detect the complexities of density-dependent feedback loops in plovers, particularly the effects of density on breeding propensity and the effects of density on different breeding states.

ACKNOWLEDGMENTS

Funding was provided by the U.S. Army Corps of Engineers, the U.S. Fish and Wildlife Service, and Virginia Tech. Funding for publication was provided by the Virginia Tech Open Access Subvention Fund. We thank cooperators, the National Park Service, U.S. Fish and Wildlife Service, South Dakota Department of Game, Fish, and Parks, Nebraska Game and Parks Commission, and the Missouri River Institute for support throughout the project. We acknowledge the tireless efforts of our many technicians throughout the project and the numerous individuals providing us with off-site resights. This work was conducted under Institutional Animal Care and Use Committee permits 11-027 and 14-003 and U.S. Fish and Wildlife Service Threatened and Endangered Species permit TE103272-3.

LITERATURE CITED

- Aubry, L. M., E. Cam, D. N. Koons, J. Y. Monnat, and S. Pavard. 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. *Journal of Animal Ecology* 80:375–383.
- Barbraud, C., and H. Weimerskirch. 2012. Estimating survival and reproduction in a quasi-biennially breeding seabird with uncertain and unobservable states. *Journal of Ornithology* 152:S605–S615.
- Blomberg, E., D. Gibson, M. Atamian, and J. S. Sedinger. 2017. Variable drivers of primary versus secondary nesting; density-dependence and drought effects on greater sage-grouse. *Journal of Avian Biology* 48:827–836.
- Both, C. 1998. Experimental evidence for density dependence of reproduction in great tits. *Journal of Animal Ecology* 67:667–674.
- Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7:434–455.
- Brown, J. L. 1969. Territorial behavior and population regulation in birds: a review and re-evaluation. *Wilson Bulletin* 81:293–329.
- Catlin, D. H., J. H. Felio, and J. D. Fraser. 2013. Effects of water discharge on fledging time, growth, and survival of piping plovers on the Missouri River. *Journal of Wildlife Management* 77:525–533.
- Catlin, D. H., J. D. Fraser, and J. H. Felio. 2015. Demographic responses of piping plovers to habitat creation on the Missouri River. *Wildlife Monographs* 192:1–42.
- Catlin, D. H., J. D. Fraser, J. H. Felio, and J. B. Cohen. 2011. Piping plover habitat selection and nest success on natural, managed, and engineered sandbars. *Journal of Wildlife Management* 75:305–310.
- Catlin, D. H., R. B. Jacobson, M. H. Sherfy, M. J. Anteau, J. H. Felio, J. D. Fraser, C. Lott, T. L. Shaffer, and J. H. Stucker. 2010. Discussion of “Natural hydrograph of the Missouri River near Sioux City and the least tern and piping plover” by Donald Jorgensen. *Journal of Hydrological Engineering* 15:1076–1078.
- Catlin, D. H., S. L. Zeigler, M. B. Brown, L. R. Dinan, J. D. Fraser, K. L. Hunt, and J. G. Jorgensen. 2016. Metapopulation viability of an endangered shorebird depends on dispersal and human-created habitats: piping plovers (*Charadrius melodus*) and Prairie Rivers. *Movement Ecology* 4:6.
- Cohen, J., L. Houghton, and J. Fraser. 2009. Nesting density and reproductive success of piping plovers in response to storm- and human-created habitat changes. *Wildlife Monographs* 173:1–24.
- Elliot-Smith, E., and S. Haig. 2004. Piping plover (*Charadrius melodus*), version 2.0. In A. F. Poole, editor. *The Birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Etterson, M. A., et al. 2011. Modeling fecundity in birds: conceptual overview, current models, and considerations for future developments. *Ecological Modelling* 222:2178–2190.
- Ferrer, M., and J. A. Donazar. 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles. *Ecology* 77:69–74.
- Friedrich, M. J., K. L. Hunt, D. H. Catlin, and J. D. Fraser. 2015. The importance of site to mate choice: mate and site fidelity in Piping Plovers. *Auk* 132:265–276.
- Gibbons, D. W., J. B. Reid, and R. A. Chapman. 1993. *Atlas of breeding birds in Britain and Ireland: 1988–91*. Poyser, London, UK.
- Gibson, D., et al. 2018. Impacts of anthropogenic disturbance on non-breeding body condition, survival, and population growth of a shorebird. *Condor* 120:566–580.
- Gill, J. A., K. Norris, P. M. Potts, T. G. Gunnarsson, P. W. Atkinson, and W. J. Sutherland. 2001. The buffer

- effect and large-scale population regulation in migratory birds. *Nature* 412:436–438.
- Gimenez, O., E. Cam, and J. M. Gaillard. 2018. Individual heterogeneity and capture-recapture models: What, why and how? *Oikos* 127:664–686.
- Gittman, R. K., F. J. Fodrie, A. M. Popowich, D. A. Keller, J. F. Bruno, C. A. Currin, C. H. Peterson, and M. F. Piehler. 2015. Engineering away our natural defenses: an analysis of shoreline hardening in the US. *Frontiers in Ecology and the Environment* 13:301–307.
- Gittman, R. K., S. B. Scyphers, C. S. Smith, I. P. Neylan, and J. H. Grabowski. 2016. Ecological consequences of shoreline hardening: a meta-analysis. *BioScience* 66:763–773.
- Gratto-Trevor, C. L. 2011. Ageing and sexing the piping plover *Charadrius melodus*. *Wader Study Group Bulletin* 118:118–122.
- Gratto-Trevor, C. L., J. P. Goosen, and S. M. Westworth. 2010. Identification and breeding of yearling piping plovers. *Journal of Field Ornithology* 81:383–391.
- Gratto-Trevor, C., S. M. Haig, M. P. Miller, T. D. Mullins, S. Maddock, E. Roche, and P. Moore. 2016. Breeding sites and winter site fidelity of Piping Plovers wintering in The Bahamas, a previously unknown major wintering area. *Journal of Field Ornithology* 87:29–41.
- Hecht, A., and S. M. Melvin. 2009. Population trends of Atlantic Coast Piping Plovers, 1986–2006. *Waterbirds* 32:64–72.
- Hoy, S. R., A. Millon, S. J. Petty, D. P. Whitfield, and X. Lambin. 2016. Food availability and predation risk, rather than intrinsic attributes, are the main factors shaping the reproductive decisions of a long-lived predator. *Journal of Animal Ecology* 85:892–902.
- Hunt, K. L., L. R. Dinan, M. J. Friedrich, M. Bomberger Brown, J. G. Jorgensen, D. H. Catlin, and J. D. Fraser. 2015. Density dependent double brooding in piping plovers (*Charadrius melodus*) in the northern Great Plains, USA. *Waterbirds* 38:321–329.
- Hunt, K. L., J. D. Fraser, M. J. Friedrich, S. M. Karpanty, and D. H. Catlin. 2018. Demographic response of an imperiled shorebird suggests that engineered habitat restoration is no match for natural riverine processes. *Condor: Ornithological Applications* 120:149–165.
- Kendall, W. L., R. J. Barker, G. C. White, M. S. Lindberg, C. A. Langtimm, and C. L. Penalzoa. 2013. Combining dead recovery, auxiliary observations and robust design data to estimate demographic parameters from marked individuals. *Methods in Ecology and Evolution* 4:828–835.
- Kendall, W. L., and R. Bjorkland. 2001. Using open robust design models to estimate temporary emigration from capture-recapture data. *Biometrics* 57:1113–1122.
- Kendall, W. L., and J. D. Nichols. 2002. Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. *Ecology* 83:3276–3284.
- Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Elsevier, New York, New York, USA.
- Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. *Ecography* 28:403–416.
- Morton, R. 1976. Effects of Hurricane Eloise on beach and coastal structures, Florida panhandle. *Geology* 4:277–280.
- Newton, I. 1994. Experiments on the limitation of bird breeding densities: a review. *Ibis* 136:397–411.
- Newton, I. 1998. Population limitation in birds. Academic Press, New York, New York, USA.
- Newton, I. 2004. Population limitation in migrants. *Ibis* 146:197–226.
- Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences* 271:59–64.
- Paradis, E., S. R. Baillie, W. J. Southerland, and R. D. Gregory. 2002. Exploring density dependent relationships in demographic parameters in populations of birds at a large spatial scale. *Oikos* 97:293–307.
- Pielke Jr., R., J. Gratz, C. Landsea, D. Collins, M. Saunders, and R. Musulin. 2008. Normalized hurricane damage in the United States: 1900–2005. *Natural Hazards Review* 9:29–42.
- Plummer, M. 2003. A program for analysis of Bayesian graphical models using Gibbs sampling. In 3rd International Workshop on Distributed Statistical Computing (DCS2003), Vienna, Austria.
- Pradel, R. 2005. Multievent: an extension of multistate capture-recapture models to uncertain states. *Biometrics* 61:442–447.
- R Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reed, E. T., G. Gauthier, and J. F. Giroux. 2004. Effects of spring conditions on breeding propensity of greater snow geese. *Animal Biodiversity and Conservation* 27:35–46.
- Saunders, S. P., T. W. Arnold, E. A. Roche, and F. J. Cuthbert. 2014. Age-specific survival and recruitment of piping plovers *Charadrius melodus* in the Great Lakes region. *Journal of Avian Biology* 45:1–13.

- Saunders, S. P., E. A. Roche, T. W. Arnold, and F. J. Cuthbert. 2012. Female site familiarity increases fledging success in piping plovers (*Charadrius melodus*). *Auk* 129:329–337.
- Schupp, C. A., N. T. Winn, T. L. Pearl, J. P. Kumer, T. J. B. Carruthers, and C. S. Zimmerman. 2013. Restoration of overwash processes creates piping plover (*Charadrius melodus*) habitat on a barrier island (Assateague Island, Maryland). *Estuarine Coastal and Shelf Science* 116:11–20.
- Sedinger, J. S., N. D. Chelgren, D. H. Ward, and M. S. Lindberg. 2008. Fidelity and breeding probability related to population density and individual quality in black brent geese *Branta bernicla nigricans*. *Journal of Animal Ecology* 77:702–712.
- Sedinger, J. S., M. S. Lindberg, and N. D. Chelgren. 2001. Age-specific breeding probability in black brant: effects of population density. *Journal of Animal Ecology* 70:798–807.
- Severinghaus, L. L. 1996. Territory strategy of the migratory Brown Shrike *Lanius cristatus*. *Ibis* 138:460–465.
- Souchay, G., G. Gauthier, and R. Pradel. 2014. To breed or not: a novel approach to estimate breeding propensity and potential trade-offs in an Arctic-nesting species. *Ecology* 95:2745–2756.
- Temeles, E. J. 1994. The role of neighbors in territorial systems – when are they dear enemies. *Animal Behaviour* 47:339–350.
- USACE [U.S. Army Corps of Engineers]. 2014. Missouri River flow data. <http://www.nwd-mr.usace.army.mil/rcc/projdata/gapt.pdf>
- USFWS. 2009. Piping plover (*Charadrius melodus*) 5-year review: summary and evaluation. USFWS, Hadley, Massachusetts, USA.
- USFWS [U.S. Fish and Wildlife Service]. 2003. Amendment to the 2000 biological opinion on the operation of the Missouri River main stem reservoir system, operation and maintenance of the Missouri River bank stabilization and navigation project, and operation of the Kansas River reservoir system. USFWS, Lakewood, Colorado, USA.
- USFWS [U.S. Fish and Wildlife Service]. 2009. Piping Plover (*Charadrius melodus*) 5-year review. USFWS, Hadley, Massachusetts, USA.
- Weithman, C. E., D. Gibson, K. L. Hunt, M. J. Friedrich, D. F. Fraser, S. M. Karpanty, and D. H. Catlin. 2017. Senescence and carryover effects of reproductive performance influence migration, condition, and breeding propensity in a small shorebird. *Ecology and Evolution* 7:11044–11056.
- Weller, M. W. 1957. An automatic nest-trap for waterfowl. *Journal of Wildlife Management* 21:456–458.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(Supplement):120–138.
- Wilcox, L. 1959. A twenty year banding study of the piping plover. *Auk* 76:129–152.
- Yoder, J. M., E. A. Marschall, and D. A. Swanson. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology* 15:469–476.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2740/full>