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RESEARCH ARTICLE

Environmental and ecological conditions at Arctic breeding sites have limited effects on true survival rates of adult shorebirds

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ABSTRACT

Many Arctic shorebird populations are declining, and quantifying adult survival and the effects of anthropogenic factors is a crucial step toward a better understanding of population dynamics. We used a recently developed, spatially explicit Cormack–Jolly–Seber model in a Bayesian framework to obtain broad-scale estimates of true annual survival rates for 6 species of shorebirds at 9 breeding sites across the North American Arctic in 2010–2014. We tested for effects of environmental and ecological variables, study site, nest fate, and sex on annual survival rates of each species in the spatially explicit framework, which allowed us to distinguish between effects of variables on site fidelity versus true survival. Our spatially explicit analysis produced estimates of true survival rates that were substantially higher than previously published estimates of apparent survival for most species, ranging from $S = 0.72$ to 0.98 across 5 species. However, survival was lower for the *arcticola* subspecies of Dunlin (*Calidris alpina arcticola*; $S = 0.54$), our only study taxon that migrates through the East Asian–Australasian Flyway. Like other species that use that flyway, *arcticola* Dunlin could be experiencing unsustainably low survival rates as a result of loss of migratory stopover habitat. Survival rates of our study species were not affected by timing of snowmelt or summer temperature, and only 2 species showed minor variation among study sites. Furthermore, although previous reproductive success, predator abundance, and the availability of alternative prey each affected survival of one species, no factors broadly affected survival across species. Overall, our findings of few effects of environmental or ecological variables suggest that annual survival rates of adult shorebirds are generally robust to conditions at Arctic breeding sites. Instead, conditions at migratory stopovers or overwintering sites might be driving adult survival rates and should be the focus of future studies.

Keywords: true survival, spatially explicit Cormack–Jolly–Seber models, Bayesian survival analysis, breeding dispersal, alternative prey hypothesis, waders

Las condiciones ambientales y ecológicas de los sitios reproductivos del Ártico tienen efectos limitados en las tasas de supervivencia verdadera de las aves playeras adultas

RESUMEN

Muchas poblaciones de aves playeras del Ártico están disminuyendo, por lo que es crucial cuantificar la supervivencia de los adultos y los efectos de los factos antrópicos para avanzar en un mejor entendimiento de las dinámicas de sus poblaciones. Usamos el modelo Cormack-Jolly-Seber espacialmente explícito recientemente desarrollado en un contexto bayesiano para obtener estimaciones a gran escala de las tasas de supervivencia anual verdadera para 6 especies de aves playeras en 9 sitios reproductivos a través del Ártico de América del Norte entre 2010 y 2014. Evaluamos los efectos de variables ambientales y ecológicas, del sitio de estudio, del destino del nido y del sexo en las tasas de supervivencia anual para cada especie en un contexto espacialmente explícito, lo que nos permitió distinguir entre los efectos de las variables en la fidelidad al sitio versus la supervivencia verdadera. Nuestro análisis espacialmente explícito generó estimaciones de tasas de supervivencia verdadera que fueron sustancialmente más altas que las estimaciones previamente publicadas de la supervivencia aparente para la mayoría de las especies, en un rango entre $S = 0.72$ a 0.98 para 5 especies. Sin embargo, la supervivencia fue más baja para la subespecie *Calidris alpina arcticola* ($S = 0.54$), nuestro único taxón estudiado que migra a través del Corredor de Vuelo del este de Asia-Australasia. Como otras especies que usan el corredor de vuelo, *C. a. arcticola* podría estar experimentando tasas de supervivencia insosteniblemente bajas como resultado de la pérdida de hábitat migratorio de parada. Las tasas de supervivencia de nuestras especies de estudio no fueron afectadas por la fecha de derretimiento de la nieve o la temperatura de verano, y solo dos especies mostraron una variación menor entre los sitios de estudio. Más aún, aunque el éxito reproductivo previo, la abundancia de depredadores y la disponibilidad de presas alternativas cada una afectaron la supervivencia de una especie, ningún factor afectó de modo global la supervivencia de las especies. En general, nuestros hallazgos de pocos efectos de las variables ambientales o ecológicas sugieren que las tasas de supervivencia anual de las aves playeras adultas son generalmente robustas a las condiciones en los sitios reproductivos del Ártico. En cambio, las condiciones en los sitios de parada migratoria o en los sitios de invernada podrían estar determinando las tasas de supervivencia de los adultos y deberían ser el foco de fututos estudios.

Palabras clave: análisis bayesianos de supervivencia, aves limícolas, dispersión reproductiva, hipótesis de presa alternativa, modelos Cormack-Jolly-Seber espacialmente explícitos, supervivencia verdadera

INTRODUCTION

Anthropogenic effects of climate change, habitat loss, and invasive species are the primary threats to biodiversity (Hoffmann et al. 2010). Climate change is occurring rapidly in the Arctic, where annual temperatures are expected to warm by 4–7°C by the end of the 21st century and snowmelt is expected to progressively occur earlier in the spring (IPCC 2013). Birds that breed at high latitudes currently benefit from a seasonal pulse of invertebrate prey and low abundance of predators, parasites, and pathogens, but environmental change could lead to changes in seasonal phenology or exposure to novel threats (Bradley et al. 2005, Tulp and Schekkerman 2008, Nolet et al. 2013). Climate change has already altered resource phenology and habitats to the extent that some Arctic birds have experienced range shifts or population declines (Gilchrist and Mallory 2005, Ballantyne and Nol 2015).

Another major change in Arctic ecosystems is the dampening of cyclic population dynamics of arvicoline (formerly microtine) rodents, including lemmings and voles (Nolet et al. 2013). The alternative prey hypothesis predicts that population cycles of rodents play a key role in sustaining populations of other vertebrates at a similar trophic level. Specifically, in years of high abundance of arvicoline rodents, generalist predators switch to a diet composed mainly of arvicolines, allowing high rates of successful reproduction for Arctic birds (Angelstam et al. 1984, Summers et al. 1998, Blomqvist et al. 2002). However, climate change has reduced the amplitude and periodicity of population cycles of arvicolines in some areas of the Arctic (Kausrud et al. 2008, Gilg et al. 2009, Schmidt et al. 2012). Arctic-breeding birds might now be subject to more constant rates of predation, resulting in reduced reproductive success and declining populations (Fraser et al. 2012, Nolet et al. 2013). However, most evidence for the alternative prey hypothesis is from the Palearctic, while evidence from the Nearctic is mixed (summarized by McKinnon et al. 2014). The implications of the alternative prey hypothesis for adult survival of Arctic birds have not been well studied. In addition, it is unclear whether the alternative prey hypothesis would apply to adult survival, such that survival rates should be higher in years with higher abundance of alternative prey, as well as to reproductive success.

Predator communities in the Arctic are also changing as a result of climate change and human activities. Range expansion of the red fox (*Vulpes vulpes*) into the Arctic has been attributed to climate-driven changes at lower trophic levels (Killengreen et al. 2007), and wide-ranging generalist predators such as foxes, gulls, and ravens benefit from anthropogenic food subsidies (NAS 2003, Weiser and Powell 2010, Julien et al. 2014). Subsidized predators often continue to take natural prey as well, potentially increasing predation pressure on other Arctic species. Higher numbers of generalist predators could become particularly problematic in the context of loss of population cycles in Arctic rodents.

A combination of climate change and increased predation pressure could exacerbate population declines for Arctic-breeding birds. Many shorebirds are long-lived, migratory, and dependent on breeding areas in the Arctic, and thus might be especially vulnerable to global change (Myers et al. 1987, Piersma and Lindström 2004, Thomas et al. 2006). Nearly half of shorebird populations worldwide, including 61% of populations in North America and 88% of species in the East Asian–Australasian Flyway, have shown long-term population declines associated with anthropogenic change (International Wader Study Group 2003, Andres et al. 2012, Hua et al. 2015). Declines have been attributed to loss of habitat at key migratory stopover and nonbreeding sites, which can have strong effects on population trends (Baker et al. 2004, MacKinnon et al. 2012). However, if environmental or ecological changes in the Arctic pose additional threats, quantifying the corresponding responses of demographic rates would help to inform conservation management.

Annual survival of adults is the main driver of population dynamics in long-lived vertebrates, including many birds (Sæther and Bakke 2000). Annual survival rates of Arctic-breeding shorebirds are not well known, and previous estimates have usually been from field studies at a single site (Sandercock and Gratto-Trevor 1997, Warnock et al. 1997, Sandercock et al. 2000, Johnson et al. 2001, Fernández et al. 2003, Rice et al. 2007, Almeida 2009), or rarely across a flyway (Piersma et al. 2005). Many Arctic-breeding shorebirds have broad geographical ranges, and information from single sites might not be generalizable to the entire distribution of a species (Senner et al. 2017). Range-wide estimates of survival from multisite studies are therefore crucial for understanding the demography of Arctic birds. Moreover, disentangling true survival from site fidelity is difficult or impossible in most mark–recapture survival analyses without the addition of supplementary data (Sandercock 2006), and only one ad hoc method to correct for local dispersal has been tested in Arctic shorebirds (Taylor et al. 2015). A newly developed spatially explicit survival model dramatically improves the ability to estimate true survival by explicitly incorporating a dispersal kernel to account for permanent emigration (Schaub and Royle 2014). The model is ideally suited to free-ranging animals that could be resighted anywhere within a study area, but the practical applications of this method remain broadly unexplored, with only 2 empirical applications thus far (Mumme 2015, Honeycutt et al. 2016).

Drivers of adult survival in Arctic-breeding shorebirds are also not well understood. Individual traits such as age or time-since-marking, sex, and reproductive success can affect apparent survival of adult shorebirds through losses to mortality or permanent emigration (Reed and Oring 1993, Warnock et al. 1997, Flynn et al. 1999, Sandercock et al. 2000). Extrinsic factors that affect adult survival of some species of Arctic shorebirds include severe weather events, climatic conditions, and predation (Evans and Pienkowski 1984, Xu et al. 2015). Given the anthropogenic changes expected in Arctic ecosystems, a broad-scale investigation of the effects of climate and ecological communities on shorebird survival is needed to inform conservation strategies.

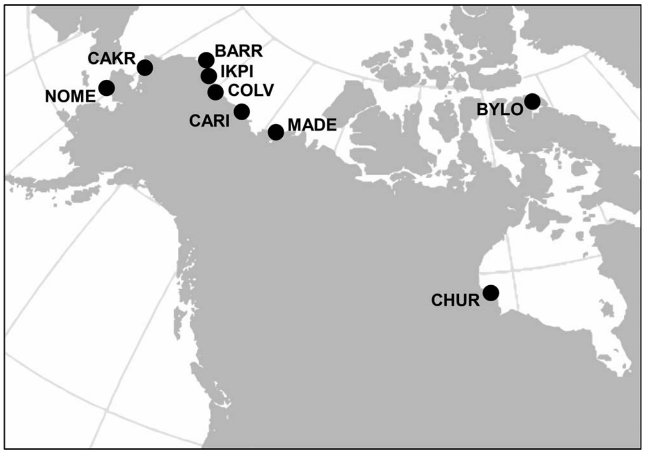

FIGURE 1. Study sites in Alaska and Canada where adult shorebirds were marked and resighted by the Arctic Shorebird Demographics Network. See Supplemental Material Table S1 for complete names and geographic coordinates of the study sites.

To quantify the demography of migratory shorebirds during the breeding season, we monitored individually marked shorebirds at 9 Arctic sites that were part of the Arctic Shorebird Demographics Network (ASDN; Brown et al. 2014). Our study included 6 species with diverse breeding systems: 1 plover, 3 sandpipers, and 2 phalaropes. We implemented spatially explicit Cormack–Jolly–Seber (sCJS) models in a Bayesian framework (Schaub and Royle 2014) to (1) produce the first broad-scale estimates of true survival for 6 species of shorebirds, and (2) evaluate effects of environmental and ecological conditions on annual survival rates. Based on the assumption that anthropogenic change is pushing the Arctic beyond the natural range of variation in which Arctic birds evolved, we predicted that survival rates of adult shorebirds would be lower with earlier spring snowmelt, warmer summer temperatures, higher abundance of predators, and lower abundance of arvicoline rodents. Our broad-scale estimates of survival and effects of environmental and ecological variables will provide key information for identifying how conditions in breeding areas contribute to population regulation of migratory shorebirds in the Nearctic.

METHODS

We monitored shorebird populations, and environmental and ecological conditions, at 9 study sites in Arctic and Subarctic Alaska and northern Canada in 2010–2014 (Figure 1, Supplemental Material Table S1). Field seasons spanned the shorebird nesting period from late May through July. All study sites followed standardized field protocols developed by the ASDN, but study plot

TABLE 1. Six species of Arctic-breeding shorebirds marked and resighted at 9 sites in Alaska and Canada, 2010–2014. Site-specific sample sizes are given in Supplemental Material Table S3.

Common name	Scientific name	Species code	Population trend [a]	Number marked	Proportion resighted
American Golden-Plover	*Pluvialis dominica*	AMGP	2	45	0.13
pacifica Dunlin [b]	*Calidris alpina pacifica*	DUNLpac	1	28	0.57
arcticola Dunlin [c]	*C. a. arcticola*	DUNLarc	3	204	0.38
hudsonia Dunlin [d]	*C. a. hudsonia*	DUNLhud	1	97	0.43
Semipalmated Sandpiper	*C. pusilla*	SESA	2	687	0.44
Western Sandpiper	*C. mauri*	WESA	2	335	0.38
Red-necked Phalarope	*Phalaropus lobatus*	RNPH	3	302	0.26
Red Phalarope	*Ph. fulicarius*	REPH	2	269	0.10

[a] From long-term estimates (Andres et al. 2012); 1 = stable, 2 = apparent decline, 3 = significant decline.
[b] Marked at one site: CAKR.
[c] Marked at 4 sites: BARR, IKPI, COLV, CARI.
[d] Marked at one site: CHUR.

configuration varied among sites depending on habitat type and nest density of shorebirds (Brown et al. 2014). We summarize relevant field methods here; see Brown et al. (2014) for a complete description of our protocols.

Arctic-breeding Shorebirds

At each study site, we live-captured and individually marked adult shorebirds for 3 or more years in designated study plots (2010–2013). The total area of study plots averaged 422 ha across all sites (Supplemental Material Table S1). For initial marking, we trapped adult shorebirds on the nest during incubation. We marked each bird with a unique combination of field-readable leg bands, usually a colored flag with an alphanumeric code and 2–4 color bands. We used plumage, morphometrics, and behavioral cues to determine the sex of marked individuals when possible (Sandercock 1998, Gates et al. 2013, Brown et al. 2014). We monitored each nest through the expected hatch date to determine nest fate as hatched, failed, or unknown. In subsequent years, we resighted or recaptured banded birds in our study plots during systematic surveys or during nest searching and monitoring. We recorded a bird as alive and encountered in a given year if it was physically recaptured once or resighted at least twice. We recorded the capture, resighting, and nesting locations of each individual that was observed, using hand-held GPS units, in decimal degrees to the nearest 0.00001 degree, with an accuracy of ±5 m. If a nest was found for an individual, we used the nest as the individual's location for a given year; otherwise, we averaged the points where the bird was resighted to use as the location.

We marked a total of 5489 adults of 27 species of shorebirds at participating sites in the ASDN (Lanctot et al. 2015). We restricted our analysis to a subset of 6 species with $\geq$50 adults marked, with at least 10% resighted in one or more years during our study, including all subspecies where applicable (Table 1). Of our 6 study species, 4 (American Golden-Plover [*Pluvialis dominica*] and calidridine sandpipers) show moderate to strong fidelity to breeding territories (Johnson et al. 1997, Sandercock et al. 2000), while the 2 phalaropes defend mates rather than territories and are expected to show more opportunistic settlement strategies (Saalfeld and Lanctot 2015).

Environmental Variables

To estimate the annual timing of snowmelt at each study site, we used daily satellite data with a resolution of 4 km (National Ice Center 2008). We recorded the timing of snowmelt at each site as the first date when the grid cell containing the field camp was categorized as "land" based on a combination of visible imagery, spectrometry, and microwave data (National Ice Center 2008). Estimates from satellite imagery were positively correlated with field observations for 7 sites where field crews arrived before snowmelt was complete ($r > 0.65$; 1–5 years per site).

To characterize ambient temperature during the breeding season, we used hourly data from permanent weather stations near our study sites (Government of Canada 2015, National Centers for Environmental Information 2015, CEN 2016). If no permanent station was near a study site, we collected weather data with an automated portable weather station deployed at the field camp (Onset Hobo Weather Station, U30 Series; Pocasset, Massachusetts, USA). For 2 field sites where both sources of data were available, temperatures from permanent and portable weather stations were highly correlated ($r > 0.95$, slope ≈ 1.0; 1–5 years for each site).

We summarized temperature data across the nest initiation period, when most individuals were present at the breeding site (Colwell 2010). For each site, we calculated the distribution of nest initiation dates for each species, pooled across years. To eliminate outliers, we censored the earliest and latest 2.5% of nests and used the remaining dates to define the nest initiation period. We averaged daily temperatures across the species-specific nest initiation period to obtain site- and year-specific mean temperatures for each species. Our study period included a leap year, so we used ordinal dates for all calculations and analyses; but we present our results as calendar dates for ease of interpretation.

Ecological Variables

We recorded the numbers of arvicoline rodents and predators observed per person-hour as an index of current local abundance during the shorebird nesting season (Hochachka et al. 2000). Observations were recorded either as part of dedicated surveys or incidentally over the course of field work during each day of the shorebird breeding season. Observations for the BYLO field site (Bylot Island; Supplemental Material Table S1) were collected as part of a concurrent study (G. Gauthier, personal communication). We categorized potential predators of shorebirds as either avian (diurnal raptors, gulls, and jaegers) or mammalian (foxes; Supplemental Material Table S2). We did not include other potential predators that rarely prey on shorebirds or their eggs (Liebezeit and Zack 2008, McKinnon and Bêty 2009). At each study site, we categorized each year as low, moderate, or high arvicoline abundance relative to other years at that site. We centered indices of abundance of avian and mammalian predators to site-specific means to account for differences among sites in survey methods and evaluate effects of deviations from the local mean.

Survival Model

We modeled each shorebird species separately, and did not share information among models because our study species varied with respect to migratory strategies and other life-history traits that could influence survival. We also separated 3 subspecies of Dunlin (*Calidris alpina*) that had disparate breeding ranges, migratory strategies, and wintering regions (Table 1; Warnock and Gill 1996), for a total of 8 study taxa.

We used a spatially explicit Cormack–Jolly–Seber (sCJS) model in a Bayesian framework to estimate annual survival (S), probability of encounter (p), dispersal distances among years (D), and effects of environmental and ecological variables on S and p for each study species (Schaub and Royle 2014). The spatially explicit Bayesian framework provided the hierarchical model structure necessary to estimate S while simultaneously accounting for imperfect detection or temporary emigration ($p < 1$) as well as permanent emigration from the study area (Schaub and Royle 2014). By explicitly incorporating dispersal, the sCJS model eliminates a major problem of traditional CJS models, which cannot differentiate between permanent emigration and mortality and thus produce negatively biased estimates of apparent survival (Schaub and Royle 2014). Our estimates of S therefore approximate the true survival rates of our study species, rather than unquantified combinations of true survival and site fidelity.

The sCJS model estimates S and p in the same way as previously described CJS models (Sandercock 2006, Kéry and Schaub 2012), with the simultaneous estimation of dispersal distance (Schaub and Royle 2014). To model dispersal, the sCJS model estimates variance among years in the locations at which each individual was observed, for latitude and longitude separately (Schaub and Royle 2014). The resulting dispersal kernel for each species is used to predict the individual's location on occasions when the individual was not observed. If the expected location is within a study plot, the individual is estimated to be either dead or not detected, depending on p. If the expected location is outside the study plot, the probability that the individual was alive vs. dead depends on S. Jointly, the estimation of dispersal and p correct the estimate of S for both permanent and temporary emigration, thus arriving at an estimate of true survival that would not be possible without a spatially explicit model. Long-distance dispersal events may not be observed within the study area, but the model assumes that dispersal distances follow a distribution (normal, in our models) that is centered on the individual's previous location, so the probability of long-distance movements can still be inferred from records of shorter-distance dispersal, especially for species that show moderate to high site fidelity.

In our models, dispersal information for each species was shared across sites. Based on previous information about within-species variation in dispersal distances (Taylor et al. 2015, Lanctot et al. 2016), we allowed dispersal to vary by sex in male-territorial species (i.e. not phalaropes) because females tend to disperse farther than males, and by nest fate in all species because individuals that failed to hatch a nest tend to disperse farther than successful birds.

We modeled S and p with a logit link. We converted locations from decimal degrees to UTMs so that dispersal distances would be modeled in meters. The probabilities of S and p for each site i and time t depended on a set of v variables, $\mathrm{X}_1 \ldots \mathrm{X}_v$, and their corresponding effect sizes, $\beta_1 \ldots \beta_v$ on the logit scale:

$$\mathrm{logit}(S_{i,t}) = \beta_{S_1} \cdot \mathrm{X}_{1_{i,t}} + \ldots \beta_{S_v} \cdot \mathrm{X}_{v_{i,t}}$$

$$\mathrm{logit}(p_{i,t}) = \beta_{p_1} \cdot \mathrm{X}_{1_{i,t}} + \ldots \beta_{p_v} \cdot \mathrm{X}_{v_{i,t}}$$

The full model for each shorebird species included time-since-marking, study site, sex, nest fate, 2 environmental variables, and 3 ecological variables as potential predictors of S, and site and sex as potential predictors of p (Table 2). We standardized each continuous variable across all sites with a z-transformation by subtracting the global mean and dividing by one standard deviation. We also tested for a relationship between each pair of explanatory variables with

TABLE 2. Variables considered for effects on annual survival (*S*), probability of encounter (*p*), and breeding dispersal (*D*) of Arctic-breeding shorebirds. Continuous variables were standardized to the global mean and one standard deviation before incorporation in the survival model.

Type	Variable	Levels or units	Processes for which effect was tested
Random on intercept	Individual		*S*, *p*
Fixed	Study site	9 sites	*S*, *p*
	Time-since-marking	First yr, >1 yr	*S*
	Sex	Female, male, unsexed	*S*, *p*, *D*
	Nest fate, by sex	Hatched, failed, unknown	*S*, *D*
Environmental	Mean temperature[b]	Difference from site mean in °C	*S*
	Snow-free date	Difference from site mean in days	*S*
Ecological[a]	Avian predator abundance	Number observed per person-hour	*S*
	Fox abundance	Number observed per person-hour	*S*
	Arvicoline rodent abundance	Low, moderate, high	*S*

[a] Not tested for *pacifica* or *hudsonia* Dunlin (small samples).
[b] Across the observed nest-initiation period for a given species at each site.

function lmer in package lme4 (Bates et al. 2014) in R 3.3.1 (R Core Team 2017), including random effects of site and year, to assess whether multicollinearity would result from including all variables in the same model. We tested for effects of variables measured in year t on survival (S) from year t to year $t+1$, but we did not test for lag effects given the relatively short duration of our study. We included random effects of individual on S and p to facilitate estimation of effects of individual variables such as sex and nest fate (Cam et al. 2013). To prevent non-identifiability of parameters in the sCJS framework, we excluded temporal effects, specifically a random effect of year, from our sCJS models (Schaub and Royle 2014).

We binned time-since-marking into 2 categories and compared the first year after capture versus all subsequent intervals to account for potential transient individuals (Sandercock 2006). We included 3 categories for sex (female, male, or unsexed) in case there was a bias in terms of which birds were unsexed. For Western Sandpipers (*Calidris mauri*), all but 19 individuals (4%) were sexed by culmen length, so we excluded unsexed individuals from the model and tested only for a difference between males and females. We captured few female phalaropes because males provide sole parental care in these species, so we excluded females for both phalarope species. We tested for effects of nest fate, categorized as hatched, failed, or unknown (uncertain or not observed) on survival of all taxa, and allowed the effect of nest fate on S to vary by sex when sex was also included in the model. We had adequate samples of marked and resighted birds to test environmental and ecological variables for 6 taxa, including the *arcticola* subspecies of Dunlin. The *pacifica* and *hudsonia* subspecies of Dunlin occurred at only one site each, for which we had only 3 years of ecological data, so we did not test for effects of ecological variables for those 2 subspecies.

Our aim was to make inference from only variables that helped to explain variation in S or p. We used stochastic search variable selection (SSVS) to test our full model and determine which variables should be retained in the final model (George and McCulloch 1993, O'Hara and Sillanpää 2009). SSVS explicitly integrates variable selection into the main analysis. In each iteration, the model determines whether the variance of β_ν is best described as small (near zero), in which case β_ν is restricted to values near the prior mean of zero; or large, in which case β_ν is freely estimated. An indicator variable, θ_ν, indicates the proportion of iterations in which β_ν is freely estimated and thus inclusion of variable ν in the model is supported. If θ_ν is close to one, the effect of the variable is nonzero and should be retained in the model. The literature provides little guidance as to what threshold should be used to retain a variable in the model, so we used $\theta_\nu \geq 0.70$ to indicate that a variable likely had an effect and should be retained. We first ran the full model for each species, then dropped variables with $\theta_\nu < 0.70$ and ran the model with only the remaining variables. If necessary, we repeated the process until all $\theta_\nu \geq 0.70$ for each species.

Few previous estimates of S, p, or effects of explanatory variables were available for most Arctic-breeding shorebirds, so we used uninformative priors on the logit scale for all parameters in our model. We used uniform priors (range: 0–10) for variances, which must have a nonnegative value, and wide normal priors (mean = 0, variance = 100, restricted to range from −10 to 10 to improve computational efficiency) for effect sizes. We implemented our Bayesian sCJS model in JAGS 4.2.0 (Plummer 2003) using the runjags package

(Denwood 2016) in R 3.3.1 on the Beocat high-performance computing cluster at Kansas State University. We provide example JAGS code (Supplemental Material Appendix) that was developed from published examples (Kéry and Schaub [2012] for the basic CJS model, Schaub and Royle [2014] for the sCJS model, and Almaraz et al. [2012] for SSVS). We discarded an adaptation period of 5,000 iterations and a burn-in period with a further 10,000 iterations, which consistently produced good mixing across 6 chains. We then ran each model for 30,000 iterations and saved the output from every third iteration to avoid autocorrelation, resulting in 10,000 saved iterations used to generate posterior distributions of parameters, which achieved convergence as indicated by Gelman–Rubin statistics of <1.10 for all parameters (Brooks and Gelman 2012). We used the final model for each species to estimate the mean and 95% Bayesian credible interval (BCI) for each demographic parameter (S and p) and dispersal variance, by sex and nest fate where indicated, back-transformed to the natural scale. Values of θ are presented in the Results as mean ± SD, while values of demographic parameters are presented as mean (95% BCI) to fully portray parameter uncertainty.

RESULTS

Shorebird Data

We marked 28–687 individuals per species or subspecies during the first 4 years of our study (2010–2013), and resighted 6–304 individuals (2011–2014; Table 1, Supplemental Material Table S3). Across all species, 66% of individuals (1,292 of 1,967) were never resighted after the initial capture year. The remaining 34% (675 of 1,967) were seen in one or more subsequent years, with the proportion resighted lowest for Red Phalaropes (*Phalaropus fulicarius*; 10%) and highest for *pacifica* Dunlin (57%; Table 1). The sex ratio of known-sex individuals was female-biased for marked American Golden-Plovers (71% of sexed individuals) but approximately even for 3 species of sandpiper: 49% male for Dunlin, 52% for Semipalmated Sandpipers (*Calidris pusilla*), and 53% for Western Sandpipers. Sixteen percent of American Golden-Plovers, 40% of Dunlin, and 18% of Semipalmated Sandpipers were unsexed; the few unsexed Western Sandpipers were excluded from the analysis. Nest initiation dates spanned a 52-day period, May 13 to July 3, across all species and sites. We found nests for all birds during the initial capture year and for 85% of individuals observed to return following initial marking. Nest fate was determined for 1,998 (89%) of 2,246 documented nests. Of nests with a known fate, 68% hatched and 32% failed, with egg predation accounting for most failures (83%), followed by nest abandonment (10%) and other causes (≤ 2% each).

After accounting for imperfect detection and permanent emigration, mean estimates of survival were high for most species and subspecies ($S = 0.72$–0.98), except *arcticola* Dunlin ($S = 0.54$; Figure 2A). Probability of encounter was also high for most species ($p = 0.59$–0.95), but lower for *hudsonia* Dunlin ($p = 0.35$) and especially Red Phalaropes ($p = 0.06$; Figure 2C). The SD among nest or resighting locations across years was typically <500 m and frequently ~100 m (Figure 3). Dispersal estimates were largest for American Golden-Plovers, partly as a result of small sample size, as only 6 of 45 birds were observed after marking (Figure 3).

Grouping Variables

An effect of time-since-marking on S was not supported for any species ($\theta < 0.70$ in final models; Supplemental Material Table S4B). Site effects on S were supported in the final models for 2 of 8 taxa: Semipalmated Sandpipers ($\theta = 0.77 \pm 0.42$ at CAKR and 0.98 ± 0.13 at NOME) and Western Sandpipers ($\theta = 1.00 \pm 0.01$ at CAKR and 1.00 ± 0.00 at NOME; Supplemental Table S4B; Figure 2B). Site effects on p were supported in the final models for Semipalmated Sandpipers ($\theta = 0.95 \pm 0.22$ at COLV) and Red-necked Phalaropes (*Phalaropus lobatus*; $\theta = 0.95 \pm 0.21$ at CAKR; Figure 2D, Supplemental Material Table S4B).

As expected, females typically dispersed farther than males, showing larger variance among locations, in several species with male-territorial breeding systems (Figure 3, Table S5). Individuals of both sexes often dispersed farther following nest failure than following successful hatching. Unsexed individuals tended to disperse farther than sexed individuals, which was likely an artifact of the fact that birds seen in multiple years were more likely to be sexed by behavioral observations or morphometric comparisons than those observed in only one year. Similarly, individuals with an unknown nest fate tended to disperse farther than those known to hatch or fail, possibly because they had nested in an area where monitoring was less consistent, so the individual could have been missed even if it returned to the same area in the following year.

Even after accounting for the effects on dispersal, sex and nest fate of males affected S in Western Sandpipers (Figure 2A; Supplemental Material Table S4B). Males showed higher S than females ($\theta = 0.83 \pm 0.37$), and males that successfully hatched a nest showed higher S than males that failed or had an unknown nest fate ($\theta = 0.89 \pm 0.31$). Unsexed individuals that hatched a nest tended to have lower S than other groups in Semipalmated Sandpipers, while unsexed individuals showed lower p than sexed individuals in *hudsonia* Dunlin (Supplemental Material Table S4A). However, we dropped the effects of unsexed individuals from the final model as they were not biologically meaningful,

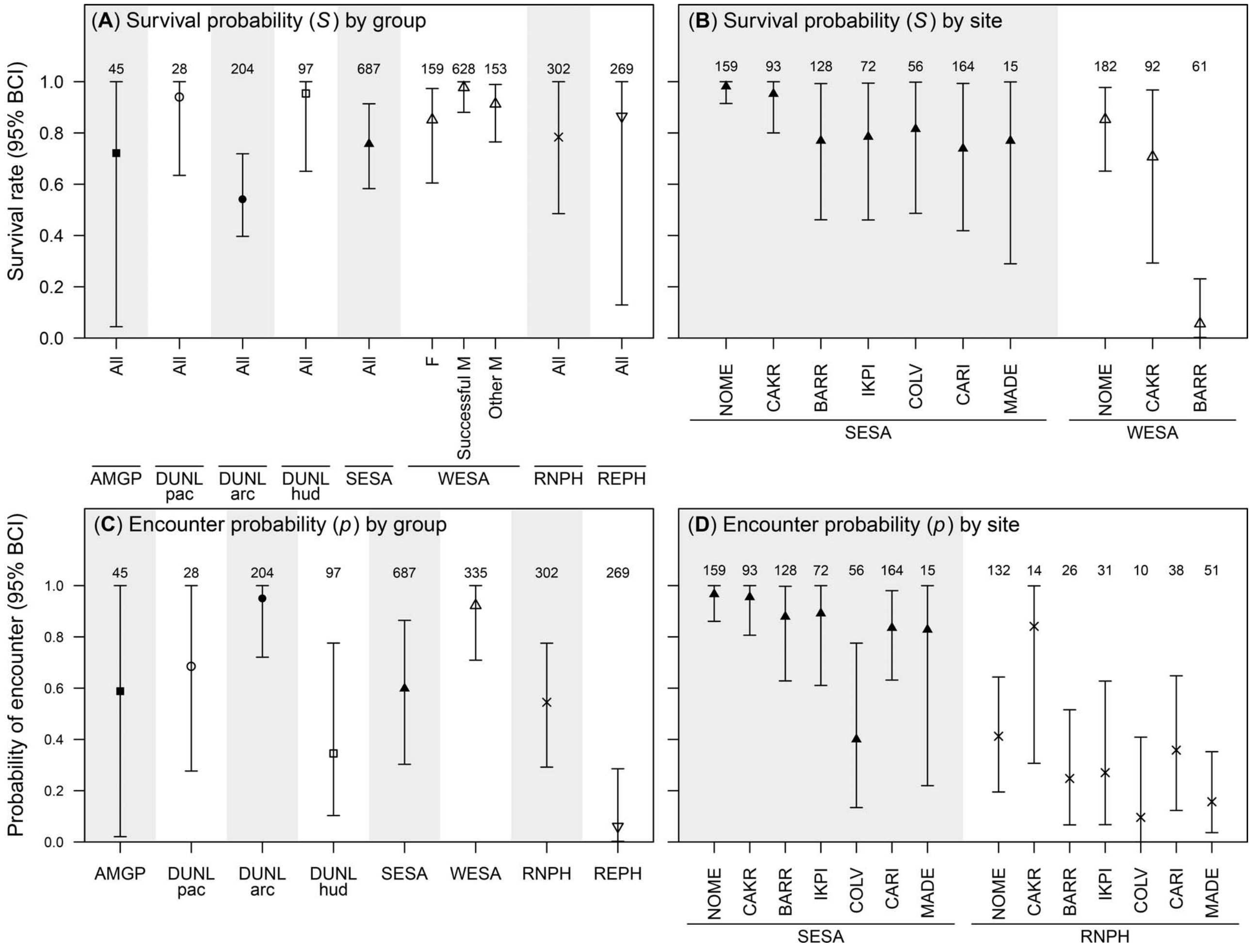

FIGURE 2. Mean estimates of survival rate (**A**) and probability of encounter (**B**) for 8 species and subspecies of shorebirds. Estimates are separated by nest fate (**A**) or by site (**B** and **D**) where group effects were supported in the final model for each species (Supplemental Material Table S4). Error bars show the 95% Bayesian credible intervals (BCI) of the estimates. Numbers along the top of each panel show sample sizes as the number of marked individuals, or the number of records of each nest fate for the nest-fate groups. Species codes are defined in Table 1.

but rather probably an artifact of sexing individuals by behavior or comparison with their mate (more likely if the individual was present for >1 year).

Environmental Variables

Across sites and years, timing of spring snowmelt ranged from May 22 to July 20 and mean temperature during the nest-initiation period ranged from 0.53 to 6.19°C (Supplemental Material Figure S1A,B). Within each site, the timing of snowmelt varied by 2–30 days among years (mean across sites = 8.8 ± 8.5 days) and mean temperatures varied by 0.61–5.30°C (mean across sites = 3.06 ± 1.68°C), indicating substantial interannual variation at most sites. Timing of snowmelt was not correlated with temperature during the nest initiation period ($r = 0.006$, $P = 0.212$). We found no support for effects of timing of snowmelt or temperature during the nesting season on S of any species ($\theta \leq 0.57$; Supplemental Material Table S4A).

Ecological Variables

Annual mean observations of arvicoline rodents across all sites ranged from 0 to 0.25 individuals per person-hour and included 3 species of lemmings and voles (Supplemental Material Table S2, Supplemental Material Figure S1C). Avian predators were mainly gulls and jaegers, and were more frequently observed (0.44–68.48 observations per person-hour) than foxes (0–0.53 per person-hour; Supplemental Material Table S2, Supplemental Material Figure S1D,E). Standardized indices of abundance of arvicolines, mammalian predators, and avian predators were not correlated ($|r| < 0.01$, $P > 0.09$). Mean expected survival of Semipalmated Sandpipers was lower in years of high abundance of arvicoline rodents

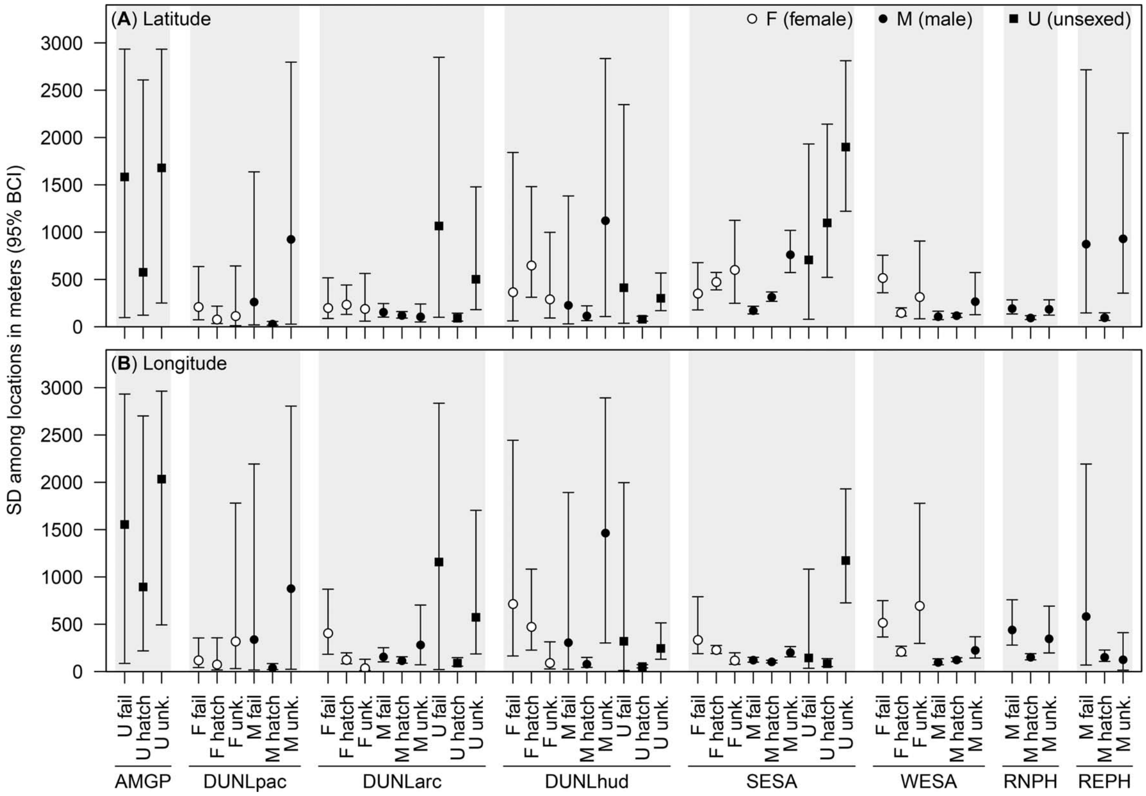

FIGURE 3. Estimates of dispersal, measured as the SD in meters among locations where each individual was observed, from the spatially explicit Cormack–Jolly–Seber model. Individuals of each species or subspecies are grouped by sex and nest fate (horizontal axis). Species codes are defined in Table 1.

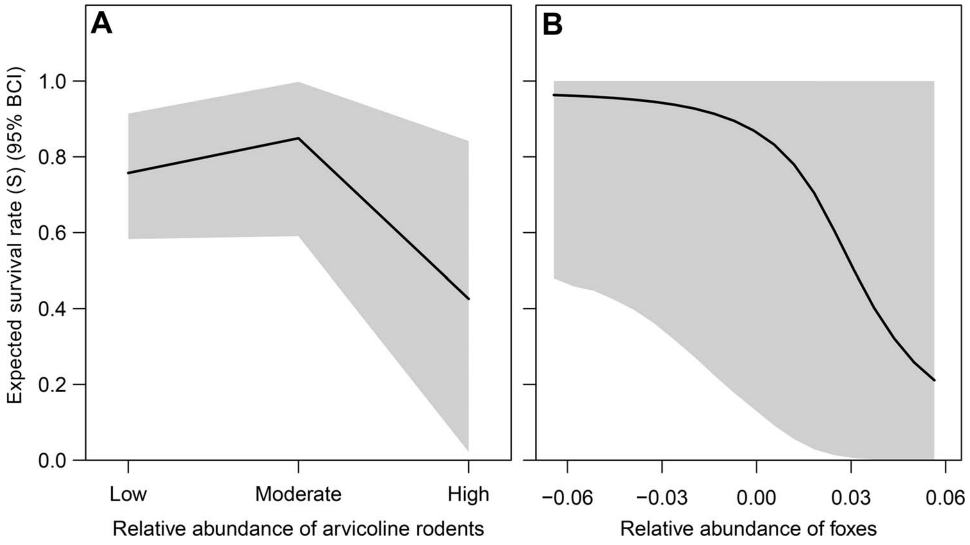

FIGURE 4. Relationships between survival rates of shorebirds and ecological variables. The effect of arvicoline abundance was supported for Semipalmated Sandpipers (**A**), and the effect of fox abundance was supported for Red Phalaropes (**B**). Shaded bands indicate 95% Bayesian credible intervals. Survival rates were modeled on the logit scale and abundance of foxes was standardized, but values here are shown on the natural scale (categorical for arvicoline rodents; difference from the site-specific mean for fox abundance).

than in years with low or moderate abundance ($\theta = 0.79 \pm 0.41$; Figure 4A, Supplemental Material Table S4B). Mean expected survival of Red Phalaropes declined sharply with higher-than-average fox abundance, but credible intervals were wide ($\theta = 0.90 \pm 0.29$; Figure 4B, Supplemental Material Table S4B). We found no effects of abundance of avian predators on S of any species ($\theta \leq 0.49$; Supplemental Material Table S4A).

DISCUSSION

Our study provides the first broad-scale estimates of annual survival for 6 species of Arctic-breeding shorebirds. Our estimates were drawn from spatially explicit models that accounted for both imperfect detection and permanent emigration to provide estimates of true survival, rather than apparent survival as typically assessed by mark–recapture studies (Schaub and Royle 2014). We also tested for relationships between survival rates and individual, environmental, and ecological variables in breeding areas. We found few effects of sex or nest fate on S after accounting for the effects on dispersal; no effects of other individual or environmental variables; and only 2 effects of ecological variables. Thus, for most species, conditions in the Arctic had negligible effects on adult annual survival, indicating that variation in mortality of adult shorebirds is explained either by conditions during migration or in overwintering areas, or by Arctic conditions not measured by our study.

Mean estimates of survival were generally high for our study species, as expected for iteroparous birds with a lifespan of several years (Sæther and Bakke 2000). Most of our estimates were substantially higher than previously published estimates of apparent survival (ϕ): $S = 0.54–0.95$ for Dunlin versus previous estimates of $\phi = 0.41–0.74$ (Warnock et al. 1997, Hill 2012), $S = 0.76$ versus previous estimates of $\phi = 0.56–0.66$ for Semipalmated Sandpipers (Sandercock and Gratto-Trevor 1997, Sandercock et al. 2000), and $S = 0.85–0.98$ versus previous estimates of $\phi = 0.49–0.78$ for Western Sandpipers (Sandercock et al. 2000, Fernández et al. 2003, Johnson et al. 2010). Little previous information is available for phalaropes (Rubega et al. 2000, Tracy et al. 2002), but our estimates of $S = 0.78$ and 0.86 for Red-necked and Red phalaropes, respectively, are similar to those of the similarly sized sandpipers. No previous estimates of survival were available for American Golden-Plovers, but our estimate of $S = 0.72$ is near the high end of the range of reported rates of apparent survival for other golden-plover species ($\phi = 0.55–0.80$; Johnson et al. 2001, Piersma et al. 2005). The higher estimates from our study are explained primarily by our use of a spatially explicit Cormack–Jolly–Seber model, which accounts for permanent emigration (Schaub and Royle 2014). Similarly, previous shorebird studies that have disentangled site fidelity from survival have produced estimates of true survival that are much higher than estimates of apparent survival (LeDee et al. 2010, Taylor et al. 2015).

In contrast, our mean estimate of survival was substantially lower for the *arcticola* subspecies of Dunlin than for our other study species ($S = 0.54$). Our estimate was similar to a previous estimate of apparent survival of *arcticola* Dunlin at one of our study sites ($\phi = 0.41$ for females, 0.60 for males; Hill 2012). Despite large sample sizes, we found no effects of any variable on survival of this subspecies, suggesting that conditions outside the Arctic might be driving the low survival rate. Unlike the other taxa in our study, which migrate within the Western Hemisphere, *arcticola* Dunlin use the East Asian–Australasian Flyway, where stopover habitat for migrating shorebirds is being rapidly lost (Yang et al. 2011). Palearctic species that use the Yellow Sea are experiencing significant population declines (Piersma et al. 2016). While our study could not conclusively test for an effect of mortality during migration, our surprisingly low estimate of annual survival for *arcticola* Dunlin across several breeding sites suggests the possibility that habitat loss and degradation on the migratory route or wintering grounds could be suppressing annual survival to unsustainably low levels. Further investigation is urgently needed to determine the mechanisms underlying the low annual survival rates, which could explain the ongoing population decline (Andres et al. 2012).

We found no support for effects of most of the 9 variables we tested on survival or encounter probability in the majority of our study species. In some cases (American Golden-Plover and *hudsonia* and *pacifica* Dunlin), small sample sizes also might have prevented detection of effects. For most other species, the high annual survival rates resulted in little residual variation in survival that could be explained by the variables we tested. Thus, any effects of variables were likely small and difficult to detect, even if present. Environmental and ecological conditions on the breeding grounds therefore appear to have little influence on adult survival, even when they affect reproductive phenology or success (Meltofte et al. 2007, Smith et al. 2010, Liebezeit et al. 2014, Senner et al. 2017). Similarly, the lack of regional variation in survival indicated that local conditions were not driving annual survival rates for most species. The demographic buffering hypothesis predicts that stabilizing selection should minimize the response of important demographic parameters (e.g., adult survival in iteroparous organisms; Sæther and Bakke 2000) to environmental variation (Morris and Doak 2004). In our study species, adult survival rates would therefore be expected to be relatively invariant, at least within the scope of the environmental conditions encompassed by our study. More extreme conditions than those we measured, including conditions expected to arise as a result of climate change, could still affect adult survival rates.

In contrast to the majority of species, 2 of our study species displayed regional variation in survival. First, we found evidence that Semipalmated Sandpipers had higher survival in western Alaska than in northern Alaska and western Canada. This finding is at least partly in agreement with a previous investigation that found increasing nest densities of Semipalmated Sandpipers in parts of western and northern Alaska (Smith et al. 2012). Counterintuitively, however, the previously documented increase in breeding density in northern Alaska occurred at the same site at which we found comparatively low survival rates (Utqiaġvik/Barrow, Alaska). Increasing densities at this site could have instead resulted from increased nest survival with the implementation of fox removals for waterfowl conservation, allowing more nests to survive long enough to be found by field crews, rather than a true population trend (Smith et al. 2012). Our results therefore suggest that the western (Alaskan) population of Semipalmated Sandpipers may not be demographically homogeneous. Second, annual survival of Western Sandpipers showed regional variation, with much lower rates at the northern edge of the breeding range than at 2 sites in western Alaska. The lower survival at the edge of the breeding range could result from increased mortality in marginal habitat. Alternatively, lower survival could indicate a higher probability of long-distance dispersal, which would not be detected in our study, if individuals show a more opportunistic settlement strategy at the edge of the range (Saalfeld and Lanctot 2015). If survival rates in northern Alaska do not improve as the species' climatic niche shifts northward (Wauchope et al. 2017), some regional factor might be suppressing survival, which could ultimately threaten population viability of the Western Sandpiper.

We found one effect of nest fate on adult survival: male Western Sandpipers that had hatched a nest showed higher annual survival than males that failed to hatch a nest or females with any nest fate. Other studies of shorebirds have commonly found that both sex and nest fate affected apparent survival, probably through an effect on site fidelity (Reed and Oring 1993, Sandercock and Gratto-Trevor 1997, Warnock et al. 1997, Flynn et al. 1999, Sandercock et al. 2000). However, correcting for sex-biased breeding dispersal was found to eliminate the differences between sexes in apparent survival estimates for 2 of our study species (Taylor et al. 2015). Similarly, the dispersal process of our model accounted for effects of sex and nest fate and eliminated the effects of those variables on S and p for most species. The remaining effects of sex and nest fate on survival of Western Sandpipers therefore suggest differences in true survival, not permanent emigration, unless there was substantial long-distance dispersal that was not well documented in our study. If there is a relationship between true survival and nest fate, it might stem from individual quality, such that a high-quality male is more likely than a low-quality male to both hatch a nest and survive until the following year (Cam et al. 2002). The lack of a relationship for females suggests that individual quality might be less important in determining nesting success and/or annual survival for female Western Sandpipers than for males.

We found effects of ecological covariates on survival rates of only 2 species. First, annual survival rates of Semipalmated Sandpipers were lower in years of high abundance of arvicoline rodents than in years with low or moderate abundance, which was the opposite of what we expected. Predation pressure on birds' nests is expected to be lower in years when arvicolines are abundant (Angelstam et al. 1984, Summers et al. 1998, Blomqvist et al. 2002), and we expected that predation pressure on adult shorebirds would either follow the same pattern or show no relationship with arvicoline abundance. Instead, our results suggest that an immediate numerical response of predators to abundant prey, such as higher reproductive rates or immigration to the local area (Gilg et al. 2006), might increase predation risk for adult Semipalmated Sandpipers in years of high arvicoline abundance. Further study with a longer time-series would more accurately describe the relationship between shorebird survival and abundance of alternative prey and allow for testing of lag effects, which would be useful to determine whether the alternative prey hypothesis applies to adult survival of other species of shorebirds in the Nearctic.

Annual survival was affected by abundance of predators in only one case, where Red Phalaropes experienced low survival when fox abundance was high. This result suggests that adult Red Phalaropes are either particularly susceptible to predation by foxes, or more likely than other species to leave the area (dispersing longer distances than could be documented in our study) when predators are abundant. Red Phalaropes show a highly opportunistic strategy for choosing breeding sites (Saalfeld and Lanctot 2015) and are thus more likely than other species to disperse to a new location when local conditions are unfavorable. However, uncertainty in the estimated effect size was high, and we resighted few Red Phalaropes, so the apparent relationship could have been influenced by chance or individual variation.

Our estimates of encounter probability were generally moderate to high ($p = 0.35$–0.95). In contrast, our estimate of $p = 0.06$ for Red Phalaropes was much lower. While resighting leg bands is difficult in phalaropes because they typically forage while swimming, obscuring the legs, the encounter probability we estimated for the ecologically similar Red-necked Phalarope was on par with our estimates for shorebirds that forage on land. Instead, the low encounter probability for Red Phalaropes could have stemmed from a high probability of temporary emigration from our study areas that results from an opportunistic settlement strategy (Saalfeld and Lanctot 2015). With spatially explicit CJS models, survival estimation is now feasible for species with low site fidelity, so low values of p will likely become more common in the literature. However, large sample sizes of marked birds will still be necessary for precise estimates when only a small proportion returns to the study area.

Conclusion

Our broad-scale, spatially explicit estimates of annual adult survival provide the first opportunity to investigate patterns in adult survival of Arctic-breeding shorebirds across North America. Estimates of annual survival were generally high after accounting for imperfect detection and permanent emigration, and some variables (particularly sex and nest fate) did not affect survival after accounting for the effects on dispersal. Survival was affected by local conditions in only a few cases, suggesting that either conditions elsewhere in the annual cycle are more influential, or variables other than those we tested, such as food availability, habitat quality, or disease might be more important than previously thought. However, as conditions continue changing in the Arctic, it is possible that the variables we tested may become more influential as conditions are pushed past the climatic niche in which our study species evolved. Further investigation of how survival is affected by conditions at migratory stopovers and overwintering sites will be crucial for understanding the demography of Arctic-breeding shorebirds.

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Author contributions: RBL, SCB, BKS, HRG, JB, DBL, JRL, EN, JR, NRS, DHW, and PFW conceived the study and designed the methods. All authors conducted the research. ELW analyzed the data. ELW and BKS wrote the paper with input from other authors.

Data deposit: Data from the Arctic Shorebird Demographics Network, including all data used in this study, are publicly available at the NSF Arctic Data Center at https://arcticdata.io/catalog/#view/doi:10.18739/A2CD5M.

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