

Evaluating environmental drivers and synchrony of Arctic shorebird demographic rates to inform conservation management

Kayla L. Davis^{1,2} | Richard B. Lanctot³ | Sarah T. Saalfeld³ | Elise F. Zipkin^{1,2} 

¹Department of Integrative Biology,
Michigan State University, East Lansing,
Michigan, USA

²Ecology, Evolution, and Behavior
Program, Michigan State University, East
Lansing, Michigan, USA

³Migratory Bird Management Division,
U.S. Fish and Wildlife Service,
Anchorage, Alaska, USA

Correspondence

Kayla L. Davis
Email: davisk93@msu.edu

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Abstract

Many Arctic-breeding shorebirds are assumed to be declining, yet obtaining reliable estimates of species' demographic rates and trends is difficult because of challenges collecting data in remote breeding regions and throughout the annual cycle. For many vulnerable species, data limitations impede efforts to determine appropriate management actions in the face of ongoing environmental change. Integrated population models (IPMs) offer an approach to maximize the utility of available data by providing a framework for estimating demographic rates and environmental drivers of population change, while also accounting for sources of uncertainty. Here, we used an IPM to estimate demographic rates, synchrony, and population trends of Arctic-breeding shorebirds within the context of climatic and management-related changes. We estimated species-specific breeding population sizes, adult survival rates, number of adults gained into the breeding population through recruitment (i.e., the sum of immigration and reproduction), as well as the effects of environmental drivers on demographic traits for three shorebird species nesting near Utqiagvik, Alaska, over an 18-year study period (2005–2022). We found that the annual number of adults recruiting into the breeding population was important for maintaining local populations, and that local environmental factors and management regimes had strong effects on demographic rates. The timing of snowmelt had a notable effect on (1) fecundity, (2) the number of adults recruited for two of the three species, and (3) adult survival during the following year for one species. Predator removal increased fecundity of all three species but had limited effects on subsequent local population sizes. The Pacific Decadal Oscillation, a broad-scale climate metric, affected adult survival differently across species, with a positive and negative effect for one species each, and a negligible effect for the other. Unlike adult recruitment and fecundity that varied synchronously among species, annual adult survival varied asynchronously. Our results suggest that differences in survival were likely related to conditions experienced during nonbreeding periods arising from dissimilar migratory routes, stopover

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sites, and nonbreeding season ranges. Future work should focus on incorporating additional environmental factors on the nonbreeding grounds to determine when and where these species could benefit most from management interventions.

KEY WORDS

Arctic-breeding shorebirds, demographic rate synchrony, integrated population model, nonbreeding season

INTRODUCTION

Widespread species declines are diminishing global biodiversity and altering ecosystem processes at unprecedented rates (IPBES, 2019; Rosenberg et al., 2019; UNEP-WCMC, 2024). One of the primary challenges of the Anthropocene is determining where and when to enact conservation actions to effectively mitigate and reverse ongoing declines (Ceballos et al., 2015; Hoffmann et al., 2010; Seddon et al., 2016). Conservation of small and declining populations requires identifying the environmental factors that influence population dynamics, as well as quantifying and predicting how populations and communities are likely to respond to variations in environmental conditions and management interventions. However, natural resource managers often lack the resources necessary to make such assessments and are thus forced to base conservation and management decisions on what is logistically feasible, even though science-based evidence may be lacking (Martin et al., 2018). Migratory species are particularly at risk of experiencing declines due to the time, energy, and direct mortality risks of migration (Alerstam & Lindström, 1990). Further, long-distance migratory species are exposed to a wide range of threats, from coastal habitat loss and degradation (Studds et al., 2017), mortality from harvest (Andres et al., 2022; Watts et al., 2015), disease (Ramey et al., 2022), and exposure to pollutants (Henkel et al., 2014; Perkins et al., 2016, 2023). Identifying limiting factors and quantifying their influences on population dynamics of migratory species is challenging because individuals are often difficult to follow throughout the annual cycle.

Because migratory species face myriad natural and human-generated threats throughout the year, identifying the limiting phase(s) of the annual cycle is especially important for determining appropriate management actions (Smith et al., 2023). For many migratory species, management actions are typically easier to implement during the breeding season compared to other times of the annual cycle when individuals have less defined territories and are more mobile. Breeding season interventions generally seek to increase reproductive output (Dinsmore et al., 2014), yet these management strategies are only

effective for increasing population size if the demographic rates they target (e.g., fecundity) contribute to population growth. If population growth is limited by reproductive success, management interventions targeting nest and chick survival via implementation of predator exclusion (Smith et al., 2011) or predator removal methods (Lennox et al., 2018) are likely to be effective at increasing population growth. Alternatively, if population growth is limited by adult survival, management actions targeting other periods of the annual cycle, such as during migration and other nonbreeding periods, could potentially increase population sizes most effectively. Comparing the demographic rates of sympatric-breeding species can also help uncover how environmental factors impact population and community dynamics including phases of the annual cycle that may be limiting for individual species. For example, synchrony in the demographic rates of several species could indicate similar responses to conditions throughout the annual cycle (Weegman et al., 2022), such as a shared response to climate (Jansen et al., 2020; Robinson et al., 2013) or predation (Raimondo et al., 2004). On the other hand, asynchronous demographic rates among sympatric species might indicate differential responses to environmental variation (Youngflesh et al., 2021) occurring on the breeding grounds, migration, or nonbreeding grounds.

The demographic data required to rigorously estimate how vital rates and the effects of environmental variables impact population growth are not typically available for species that are rare or that breed at low densities in remote regions (Oppel et al., 2014; Saunders et al., 2018). Analytical methods, such as integrated population models (IPMs), that can leverage sparse datasets are critical to estimate species' demographic rates and their environmental drivers, providing insights into how to abate and reverse population declines (Davis et al., 2023; Oppel et al., 2014; Saunders et al., 2021). For small and declining populations, it is especially important to use as much available data as possible to inform estimates of demographic rates, and IPMs offer a powerful approach for leveraging multiple data types to increase the accuracy and precision of biological estimates (Zipkin & Saunders, 2018).

IPMs may be particularly beneficial for shorebirds, which have experienced some of the most severe

population declines across bird taxa, with many Arctic-breeding species considered threatened (Rosenberg et al., 2019). Arctic-breeding shorebirds undergo some of the longest migrations of any birds and, thus, face unique challenges (Conklin et al., 2017). Anthropogenic-mediated changes in the climate of the Arctic have been especially pronounced compared to other ecosystems. For example, temperatures in the Arctic have risen between two and four times faster than global temperatures (Ballinger et al., 2020; Rantanen et al., 2022) leading to earlier, longer, and drier summers (Taylor et al., 2018)—a trend that is expected to continue (IPCC, 2013). Phenology in Arctic systems is strongly associated with climate and weather conditions, and the timing of snowmelt is a key factor influencing invertebrate emergence (Saalfeld & Lanctot, 2017; Tulp & Schekkerman, 2008). As seasonal snowmelt advances, invertebrate prey emerge earlier, potentially allowing insectivorous birds, such as some shorebird species, to lay eggs sooner after arrival to the breeding area following spring migration (Kwon et al., 2019; Sénéchal et al., 2011). For those species that can adjust their arrival schedules, this could lead to higher reproductive success and recruitment, benefiting shorebird populations (Weiser, Brown, et al., 2018a, but see Reneerkens et al., 2016, Saalfeld et al., 2019). However, predator communities in the Arctic are also changing due to range expansions of generalists (e.g., red foxes [*Vulpes vulpes*]: Killengreen et al., 2011; Kubelka et al., 2022; Stickney et al., 2014; Common Ravens, [*Corvus corax*]: Backensto, 2010), which could reduce reproductive success and survival of shorebirds that have traditionally benefitted from low predation pressure at high latitudes (McKinnon et al., 2010). Arctic-breeding shorebirds also face considerable risks during migration due to habitat loss and degradation at stopover locations (Dahl, 2014; Studds et al., 2017). Shorebird migratory pathways and nonbreeding locations vary by species; thus, different shorebird species breeding in the same location may experience very different environmental risks and stressors when away from the breeding grounds (Santos et al., 2023). Determining the limiting periods of the annual cycle and the environmental factors that influence population dynamics is thus necessary to prioritize management actions that can slow or reverse population declines. Comprehensive analyses of multiple species incorporating broad-scale and seasonal environmental variables are needed to evaluate the complex interactions among the many forces acting on shorebird communities throughout the annual cycle.

In this paper, we use an IPM to estimate demographic rates and population trends for three sympatric species of Arctic-breeding shorebirds over an 18-year study period (2005–2022) near Utqiagvik, Alaska: American golden-plover (AMGP; *Pluvialis dominica*), the *arcticola* subspecies of dunlin (DUNL; *Calidris alpina*), and

semipalmated sandpiper (SESA; *Calidris pusilla*). Our objectives were to (1) estimate and compare the demographic rates to examine synchrony among species; (2) determine the relative influence of broad-scale climate and assess the effects of local-level weather and intensive management on the demographic rates of each species; and (3) determine the demographic drivers of variations in population growth for each species and if/how these differ among species. Evaluating synchrony in demographic rates can help pinpoint whether management strategies are likely to benefit the entire community and help to identify key differences among species. For example, synchrony of demographic rates could indicate that interventions focused on the breeding period, when birds are experiencing similar conditions, could be beneficial to the shorebird community; whereas asynchronous rates among species could indicate that nonbreeding season conditions are more influential in driving demographic rate variation. Further, understanding the impacts of environmental factors on shorebird population dynamics and which demographic rates contribute most to population growth will inform management and conservation actions for these and other Arctic-breeding shorebird species in decline.

METHODS

Study species

The American golden-plover, the *arcticola* subspecies of dunlin (hereafter dunlin), and semipalmated sandpiper are all listed as species of high conservation concern by the Alaska Shorebird Group (2019) and are also listed as Birds of Conservation Concern by the US Fish and Wildlife Service (USFWS, 2021). Available evidence from various stages of the annual cycle (breeding season, migratory stopovers, and nonbreeding periods) indicates that the American golden-plover and dunlin have suffered declines in recent decades (Alaska Shorebird Group, 2019; Johnson et al., 2021; Weiser et al., 2020), likely due to habitat loss and harvest (both legal and illegal) at migratory stopover sites and on the nonbreeding grounds (Brown et al., 2017; Lagassé et al., 2020; Reed et al., 2018). The western population of semipalmated sandpiper that breeds at the Utqiagvik study site is likely stable (Smith et al., 2012; Weiser et al., 2020).

All three study species breed in the arctic and subarctic tundra, with some variation in habitat use from drier (American golden-plover) to moist vegetation (dunlin and semipalmated sandpiper, Cunningham et al., 2016). All species are monogamous and territorial during breeding, and there is relatively strong site fidelity to specific

breeding territories across successive seasons, particularly among males (Saalfeld & Lanctot, 2015). Age at first breeding is generally one year for American golden-plovers (Johnson et al., 2021) and two years for dunlin and semipalmated sandpipers; although some may breed in their first year (Hicklin & Gratto-Trevor, 2020; Weiser et al., 2020). Nests of all three species consist of shallow

scrapes and typically contain four eggs. All species may renest if nests are lost early in the breeding season (Gates et al., 2013; Naves et al., 2008).

Although the three species share similar natural history traits on the breeding grounds (Saalfeld & Lanctot, 2015), they differ dramatically in their migration pathways and location of their nonbreeding grounds

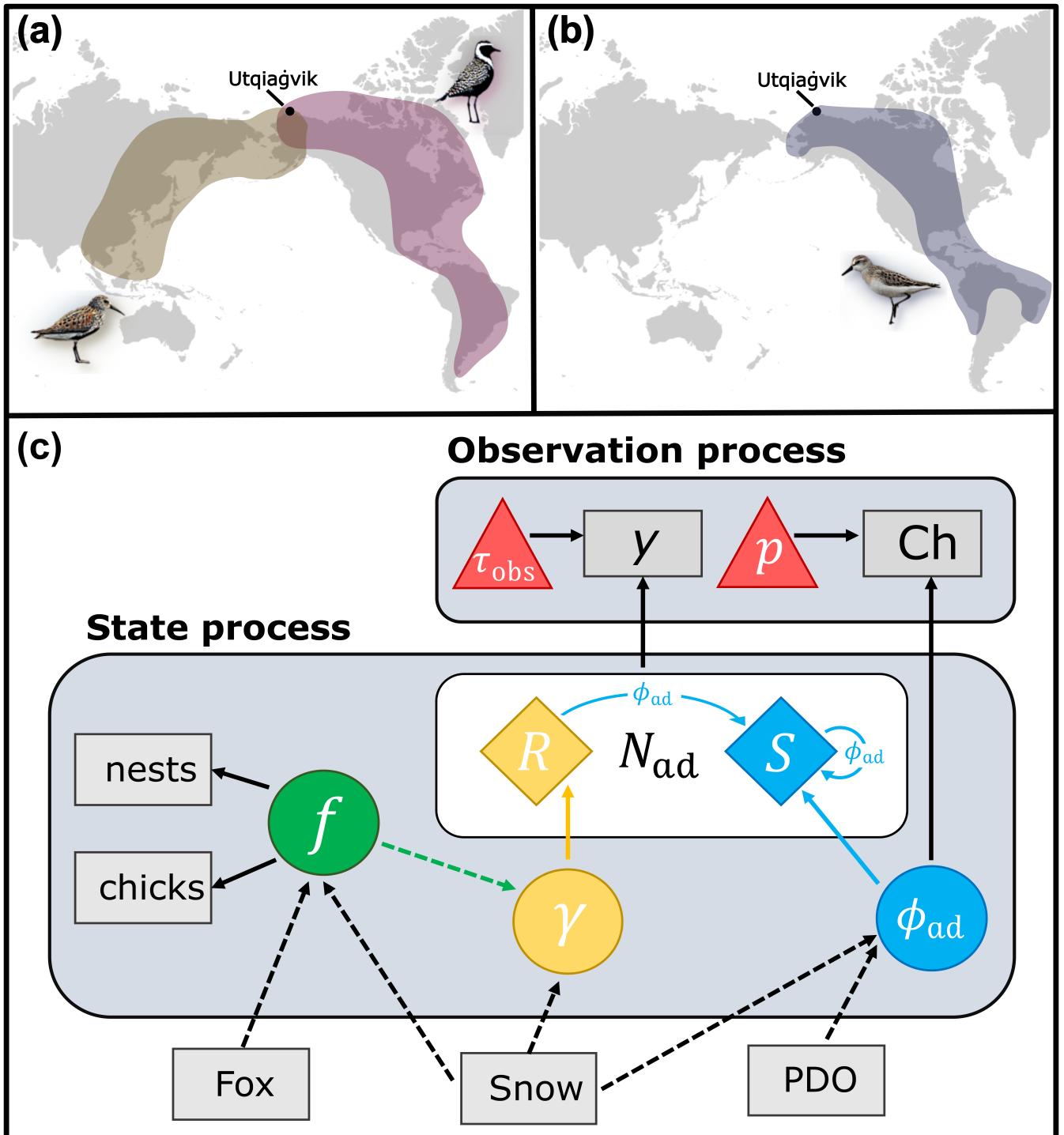


FIGURE 1 Legend on next page.

(Figure 1a,b; Hicklin & Gratto-Trevor, 2020; Johnson et al., 2021). Thus, comparing environmental drivers of demographic rates and demographic synchrony of these species could reveal key differences among species that would help pinpoint factors limiting population growth, as well as the stages of the annual cycle where targeted conservation and management should occur.

During southbound migration, American golden-plovers take a trans-Atlantic flight between their Arctic-breeding grounds in North America and their nonbreeding grounds in the pampas region of Argentina and Uruguay; birds use one or more stopovers in the eastern Arctic of Canada to build energy stores before departure. Northbound migration occurs along the midcontinental flyways that cross the Amazon, Gulf of Mexico, and the middle of North America. Other birds migrate north via a western route that crosses the Andes and continues offshore of South America before diverting east to intersect the inland route north of Central America (Johnson et al., 2021; Lamarre et al., 2021). From the northern Alaska and Yukon breeding range, dunlin move to western Alaska to stage before migrating south along the East Asian–Australasian Flyway to nonbreeding grounds located in Japan, Taiwan, the Koreas, and China. During northbound migration, dunlin travel north along the East Asian–Australasian Flyway into Russia before heading east across the Bering Strait to breeding grounds in Alaska (Gill et al., 2013; Lagassé et al., 2020, 2022). Semipalmated sandpipers breeding in northern Alaska migrate south across a rather large longitudinal gradient through the interior of North America and then winter from Peru to French Guiana. They take the same route back to the breeding grounds during northward migration (Brown et al., 2017).

Data collection

Field data on shorebird breeding demography and environmental conditions were consistently collected within five 36-ha study plots located to the southeast of Utqiagvik, Alaska, U.S. ($71^{\circ}18' N$, $156^{\circ}45' W$; Figure 1a,b) from 2005 to 2022 (see Saalfeld & Lanctot, 2015 for plot selection and data collection methods). Demographic data (i.e., nest count, adult survival, and nest success) and environmental data (i.e., timing of snow melt and predator removal) were available each year, except for the 2020 season when field work was limited due to COVID-19. We aggregated data on local (e.g., snowmelt) and global climate metrics (e.g., Pacific Decadal Oscillation [PDO]) to capture potential environmental factors influencing population dynamics during the breeding period and throughout the annual cycle, respectively. A fox removal effort took place on the study site between 2005 and 2016 as part of an effort to reduce nest mortality of a threatened sea duck species. We included a fixed effect to distinguish between years with low or no removal effort and years with high removal effort to assess the influence of this management strategy on the fecundity of shorebird species. Demographic and environmental data collection are described in further detail below.

Demographic data collection

Nest count data

Between late May and early July each year, observers located nests by systematically visiting each plot almost daily for 4 h/day. Adults suspected to be nesting or that

FIGURE 1 (a) Annual range of American golden-plovers (burgundy) and the *arcticola* subspecies of dunlin (brown). (b) Annual range of semipalmated sandpipers (navy). In panels (a) and (b) the black dot indicates the location of Utqiagvik, Alaska, where the data were collected during 2005–2022. (c) Directed acyclic diagram of the Arctic shorebirds life cycle and the integrated population model (IPM) framework. There are two categories of adults that make up the breeding population in a given year (N_{ad}): (1) adults recruited through reproduction and immigration (R) and (2) adults who were previous breeders at the study site and returned (S). The total breeding population is estimated with a state-space model using the annual count of breeding pairs (y), determined by the number of nests. The true number of breeding pairs in the population is linked to the observed survey data through an observation process that incorporates imperfect detection during surveys (τ_{obs}). Fecundity is estimated outside of the joint likelihood of the IPM with covariates including predator removal in each year (Fox) and annual snowmelt date (Snow). Annual estimates of demographic parameters in the IPM include the expected number of new recruits to the population (γ ; yellow), which is estimated from nest and chick data with covariates including snowmelt date (Snow) and fecundity from the previous season $t - 1$ (f); and annual recapture/resighting probability (p) and adult survival (φ_{ad} ; blue), which is estimated with a Cormack-Jolly-Seber model using the mark-recapture data (capture histories: Ch) with snowmelt date (Snow) and the Pacific Decadal Oscillation (PDO) covariates. Data are shown in light gray. Solid black arrows depict how the demographic data inform model parameters. Dashed arrows depict how the covariates are incorporated in the model, and colored arrows (green, yellow, and blue) show how the model parameters are connected. American golden-plover image (a) by Peter Wilton, used under a Creative Commons Attribution 2.0 license. Dunlin image (a) by Jevgenis Slihto, used under a Creative Commons Attribution 2.0 license. Semipalmated sandpiper image (b) by Mdf/Wikimedia Commons used under a Creative Commons Attribution-ShareAlike 3.0 license.

were flushed from nests were followed to locate nests. In addition, two observers dragged a rope across each plot at least once to flush incubating adults that were reluctant to leave their nests. Nests were also found opportunistically by observers banding birds or collecting other environmental data. Information on likely nest locations was shared among observers to maximize the number of nests found within the study plots (see Saalfeld & Lanctot, 2015 for more details on methodology). Once found, nest locations were recorded using handheld global positioning system (GPS) units. We used the total nest count (excluding known renesting attempts) combined across all plots as the observed number of breeding pairs, or population size, for each year. Although this is an imperfect observation of annual population size, it reflects the standardized and arduous nest searching approach developed by the Arctic Shorebird Demographics Network to maximize the detection of nests (S. C. Brown et al., unpublished data).

Adult survival data

Adults were captured at nests on the five survey plots using a bow-net (Priklonsky, 1960), and individuals were banded with a U.S. Geological Survey metal band and a unique combination of colored leg bands and a single dark green flag. Chicks were also banded with a metal band and a single, year-specific cohort color band; chicks rarely returned to their natal site to breed in successive years (Saalfeld & Lanctot, 2015). We documented adults returning to breed at the site in subsequent years by conducting opportunistic resightings both on and off plots using binoculars, spotting scopes, or by taking pictures throughout the breeding season. The majority of resightings occurred during nest initiation when adults were actively displaying and easily found or when they flushed and returned to nests (usually <3 m from an observer). Adults were also recaptured at nests, and additional opportunistic resightings were recorded away from plots (e.g., when walking from roads to plots). Resights/recaptures were recorded every year during the breeding season (excluding 2020), and each year was considered a separate occasion for estimating annual demographic rates. The mark-recapture and resighting data provided information on the apparent survival probability of adults.

Nest success data

After nests were located, observers checked nests every 3–5 days until 3–4 days prior to the estimated hatch date

(as determined by egg flotation or egg laying), at which time nests were checked every two days until signs of hatching were observed (e.g., small cracks or pips), and daily thereafter. Evidence of hatching included visually locating chicks in or near the nest, the breeding pair acting defensive or “broody,” or the presence of egg fragments or caps indicative of hatching. Observers recorded the number of chicks that left the nest and the number of eggs remaining in the nest. The number of hatched eggs, hereafter chicks, was used to estimate annual fecundity rates.

Environmental data collection

We gathered data on both the local environmental conditions and the global climate metrics as potential drivers of shorebird population dynamics. We calculated the Julian date when plots were 20% covered with snow during the breeding season each year by first estimating the percent snow cover in 36 50 × 50 m quadrats distributed throughout each study plot every 2–5 days until ≤10% snow cover remained. We then regressed the mean snow cover across all quadrats within each plot against the day of the year to predict the date when 20% snow cover remained on each plot. We averaged these dates across all study plots for each year (see Saalfeld & Lanctot, 2015 for details on snow cover data and methods) to get a yearly date of snowmelt. We evaluated the effect of snowmelt because the timing of this phenomenon influences a suite of shorebird activities, including establishing territories and timing of nest initiation (Saalfeld & Lanctot, 2017; Smith et al., 2010), and is associated with shorebird reproductive success (Meltofte et al., 2007; Piersma et al., 2003; Saalfeld et al., 2019, 2021).

We also evaluated support for an effect of the PDO as a broad-scale, global climate metric on shorebird demographic rates. The PDO measures the long-term climatic fluctuation of the Pacific Ocean and is characterized as having a warm phase associated with warmer than usual sea surface temperatures (SSTs) along the Pacific coast of North America and cooler than usual SSTs in the north, west, and southern Pacific; a pattern that is reversed during the cool phase (Wang & Schimel, 2003). These climate patterns influence weather at the breeding areas for all three species in northern Alaska. The PDO also has strong correlations to weather events in East Asia and the Pacific coast of the Americas and moderate correlations with weather along the Atlantic coast of North America and the Caribbean (Wang & Schimel, 2003)—areas that some of the Alaska-breeding shorebird species inhabit during the nonbreeding season. These climate patterns affect processes that impact abundances of lower

trophic-level taxa, including invertebrate species that are important prey for shorebirds (Anderson et al., 2021; Tulp & Schekkerman, 2008). If the PDO is an important driver of adult nonbreeding season survival, we would expect to see variation in the direction of the effect for each species due to their differing migratory pathways and nonbreeding season ranges that have different conditions under positive and negative values of the index. In contrast, we would expect similar responses to PDO across species if PDO is an important driver of adult breeding season survival. We downloaded monthly PDO values from the NOAA National Climate Data Center (NOAA, 2023). To calculate annual PDO values, we considered the start of the shorebird calendar year to be 1 July of year t because the bulk of the nesting was completed by early July each year. We averaged monthly PDO values from 1 July of year t to 30 June of year $t + 1$ to estimate the effects of climate influence on adult survival during the nonbreeding season.

Within the Arctic, shorebird nesting densities at Utqiagvik are higher than at other locations (Lanctot et al., 2016), which could result in higher predation pressure at this location compared to other sites with lower nest densities (Catlin et al., 2019; Tinbergen et al., 1967). However, predation pressure was also likely lower between 2005 and 2016, when a predator removal program was implemented to increase the nesting success of the threatened Alaska-breeding population of Steller's eider (*Polysticta stelleri*). Predator removal consisted of shooting and trapping adult arctic fox (*Vulpes lagopus*) and their young by Animal and Plant Health Inspection Service staff from mid-May to mid-July across the greater Utqiagvik area that included the shorebird nesting plots. Arctic foxes are known predators of shorebird nests (Liebezeit & Zack, 2008; McKinnon & Béty, 2009), and their removal likely enhanced shorebird nest survival. Yearly fox removal efforts varied in duration, spatial extent of trap deployment, and number and type of traps deployed (Barto et al., 2016). We summarized fox removal data into a binary categorical variable indicating years of high removal efforts and years of low or no removal efforts: 0 = no or low effort; 1 = medium or high effort. All years of fox removal (2005–2016) were categorized as high except for 2009, which was categorized as a low effort year due to the discontinued use of leg hold traps to reduce bycatch (Saalfeld & Lanctot, 2015). The fox removal data were obtained from Saalfeld and Lanctot (2015) and annual reports compiled by the United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services.

Model overview

We developed species-specific IPMs (one IPM for each species) to estimate population abundance, adult survival, the number of adults (i.e., breeding pairs) gained to the population through recruitment (i.e., the sum of immigration and reproduction), and population growth rates within a unified model for all three shorebird species (Figure 1c). Here, we defined population abundance as the number of breeding pairs, adult survival as the apparent survival probability that individuals marked as adults survived and returned to the breeding population from year t to year $t + 1$, the number of adults recruited as the annual number of new breeding pairs to the population of a given species, and population growth as the ratio of population abundance in year $t + 1$ to year t . Hereafter, all references to adult survival indicate apparent survival estimates as it was not possible to distinguish between death and permanent emigration out of the study area. We used a stage projection matrix model with a pre-breeding survey (i.e., only adults included in the population) to decompose shorebird demography into state processes. Parameters were assumed to be equal for all individuals of the same species (i.e., no individual heterogeneity or differences among sexes). Although some demographic rates (e.g., adult survival) are likely to vary between the sexes, limited data prevented the estimation of separate demographic rates by sex. We used a Cormack-Jolly-Seber (CJS) model to estimate adult survival with the mark-recapture data and a state-space model to inform breeding pair population size using the nest counts derived from intensively searching plots. The nest and chick counts from the nest monitoring efforts were used in a Poisson regression model to estimate fecundity (i.e., the number of chicks hatched per breeding pair; fecundity model; Figure 1c). We estimated species' annual fecundity outside of the IPM joint likelihood because very few individuals that hatched at the study site returned to breed there (hereafter called the fecundity model). For example, across all three species, only 11 of the 2998 birds banded as chicks were ever recaptured as adults over the study period. Despite the limited return of birds banded as chicks, it is likely that fecundity measured at the study site reflects the fecundity of the surrounding areas. Therefore, we included the fecundity (estimated outside of the IPM) as a fixed-effect covariate on the number of adults recruited into the local population in the following years (the next year for American golden-plovers and two years for dunlin and semipalmated sandpipers, based on age at first breeding) to evaluate whether a strong year class at the study site had any effect on the future breeding population size. We describe each of the sub-models and the overall IPM model fitting below.

Fecundity model

Nest success data (i.e., chick counts) were used to estimate annual fecundity (f_t), or the number of chicks hatched per breeding pair. The number of chicks observed in each year, chicks_t , was assumed to follow a Poisson distribution constrained by the number of monitored nests, nests_t :

$$\text{chicks}_t \sim \text{Poisson}(\text{nests}_t \times f_t). \quad (1)$$

We evaluated support for local environmental variables on fecundity (Snow and Fox) via fixed effects:

$$\log(f_t) = \alpha_f + \beta_{f1} \times \text{Snow}_t + \beta_{f2} \times \text{Snow}_t^2 + \beta_{f3} \times \text{Fox}_t, \quad (2)$$

where α_f is expected fecundity given average covariate values, β_{f1} is the effect of the Julian date (hereafter “date”) of 20% snow cover at the study site in year t (Snow_t), β_{f2} is the quadratic effect of the date of 20% snow cover at the study site in year t (Snow_t^2) to examine whether fecundity peaks at certain snowmelt dates during the breeding season, and β_{f3} is the effect of a binary variable representing high fox removal effort years ($\text{Fox}_t = 1$ in high years and 0 otherwise). All covariates on fecundity and hereafter were standardized to have a mean of zero and a SD of one.

Integrated population modeling framework

Our life cycle model includes two categories of adults (Figure 1c): adults who were previous breeders and survived to return (S) and new adults recruited into the population through reproduction and immigration (R). For the initial population size in the first year of sampling, we assumed the number of pairs ($N_{\text{ad},1}$) was drawn from a Poisson distribution with an expected value equal to the observed breeding pair population size in year one (y_1):

$$N_{\text{ad},1} \sim \text{Poisson}(y_1). \quad (3)$$

For years >1 :

$$N_{\text{ad},t} = S_t + R_t, \quad (4)$$

where $N_{\text{ad},t}$ is the total number of pairs in year t , dependent on the number of surviving adults (breeding pairs) who return to breed (S_t) and the number of new adults (breeding pairs) recruited into the population (R_t). The number of surviving adults, S_t , is a function of the

apparent survival probability of adults from year $t-1$ to $(\varphi_{\text{ad},t-1})$ and the total number of adults in year $t-1$ ($N_{\text{ad},t-1}$):

$$S_t \sim \text{Binomial}(\varphi_{\text{ad},t-1}, N_{\text{ad},t-1}). \quad (5)$$

We estimated annual adult survival probabilities ($\varphi_{\text{ad},t}$) from individual mark-recapture-resight data using a CJS submodel. Individual capture histories follow a multinomial distribution with cell probabilities that are a function of survival (φ_{ad}) and recapture (p) probabilities (Schaub & Kéry, 2021). Recapture probability was fixed to zero (i.e., there was zero probability of being recaptured or resighted) in 2020 when fieldwork was limited due to COVID-19. In the remaining years, recapture probability was allowed to vary by year using an annual random effect.

We evaluated support for local environmental variables (Snow_t in year t and Snow_{t-1} in year $t-1$) and a broad-scale climate variable (PDO) on adult survival:

$$\text{logit}(\varphi_{\text{ad},t}) = \alpha_{\text{ad}} + \beta_{\text{ad}1} \times \text{Snow}_t + \beta_{\text{ad}2} \times \text{Snow}_{t-1} + \beta_{\text{ad}3} \times \text{PDO}_t + \varepsilon_{\text{ad},t}, \quad (6)$$

where α_{ad} is expected adult survival for average covariate values, $\beta_{\text{ad}1}$ is the fixed effect of the date of 20% snow cover at the study site in year t (Snow_t), $\beta_{\text{ad}2}$ is the fixed effect of the date of 20% snow cover in year $t-1$ (Snow_{t-1}), and $\beta_{\text{ad}3}$ is the fixed effect of the PDO in year t (PDO_t). We also included an annual random effect for environmental stochasticity, $\varepsilon_{\text{ad},t}$.

The annual number of adults recruited, R_t , is drawn from a Poisson distribution with an expected value, γ_t :

$$R_t \sim \text{Poisson}(\gamma_t), \quad (7)$$

in which

$$\log(\gamma_t) = \alpha_R + \beta_{R1} \times \text{Snow}_t + \beta_{R2} \times \text{Snow}_t^2 + \beta_{R3} \times f_{t-x}, \quad (8)$$

where α_R is the expected number of new adult breeding pairs at average covariate values, β_{R1} is the effect of the date of 20% snow cover at the study site in year t (Snow_t), β_{R2} is the quadratic effect of the date of 20% snow cover at the study site in year t (Snow_t^2) to examine whether adult recruitment peaks with certain snowmelt dates during the breeding season, and β_{R3} is the effect of fecundity in year $t-x$ (f_{t-x}), where x is one for American golden-plovers and two for dunlin and semipalmated plovers.

We used a hierarchical state-space model to separate the observed time series of breeding pair counts into the

biological process describing population size and an observation process describing the imperfect detection of breeding pairs (Schaub & Kéry, 2021). The true number of breeding pairs in the population is linked to the observed survey data through an observation process that incorporates imperfect detection during surveys. We modeled the observation process as a normal distribution conditional on the state process for years $t > 1$:

$$y_t \sim \text{Normal}(N_{\text{ad},t}, \tau_{\text{obs}}), \quad (9)$$

where y_t is the observed number of breeding pairs in year t and τ_{obs} is the observation error or sampling variance in annual detection probabilities. This approach allows for modeling both an under and over count; over counting is less likely because nests were marked when they were found; although, it is possible we did not detect renesting by the same pairs. We multiplied the likelihoods of the survival and population sub-models (CJS and state-space models) to obtain the joint likelihood for the IPM.

Estimating population growth rate and demographic synchronies

We calculated annual population growth rates (λ_t) for breeding pairs by dividing the total breeding pair population size (N_{ad}) in year $t + 1$ by the total breeding pair population size in year t :

$$\lambda_t = \frac{N_{\text{ad},t+1}}{N_{\text{ad},t}}. \quad (10)$$

We used the geometric mean of log-transformed annual λ_t estimates to calculate historic (last 5 and 10-year) growth rates as well as the growth rates following high fox removal years and years with low or no fox removal.

To assess the relative contributions of demographic processes to variation in annual population growth, we examined correlations between population growth rates and adult survival, number of adults recruited, and fecundity (which was not a parameter in the IPM) for each species. We calculated the Pearson correlations (r) between the demographic parameters and population growth rates using the mean estimates from each model iteration, and we calculated the probability that the correlation coefficients were positive $p(r > 0)$ or negative $p(r < 0)$.

We assessed pairwise synchrony of demographic rates among species by examining the correlations between adult survival, adult recruitment, and fecundity of each species pair. We calculated the Pearson correlations (r) between the demographic parameters for each species

using the mean estimates from each model iteration, and we calculated the probability that the correlation coefficients were positive $p(r > 0)$ or negative $p(r < 0)$.

Model fitting

We used a Bayesian framework for inference and parameter estimation, and we fit the IPM (Schaub & Kéry, 2021) in program JAGS (Plummer, 2003), using the R package jagsUI (Kellner, 2016). We assessed the overall fit of the IPM by comparing the demographic rates estimated from the independent likelihood components for survival and fecundity with those from the integrated analysis (Horswill et al., 2022; Appendix S1: Figure S1).

For shorebird adult survival, we specified vague beta priors ($\text{alpha} = 3$, $\text{beta} = 3$), where 99% of the prior density fell between approximately 0.1 and 0.9. We used the same beta (3, 3) prior for mean recapture probability for all species. For the mean number of adults recruited into the population, we used uniform priors, the upper bound of which was the species' mean population size during the study period (AMGP: 0–8; DUNL: 0–31; SESA: 0–25). For mean fecundity, we used uniform priors (0–4), as shorebird clutch size is rarely more than four chicks (Hicklin & Gratto-Trevor, 2020, Johnson et al., 2021; see Appendix S1: Figures S2–S4 for prior specification testing). We used normal priors ($\text{Normal}(0, 3.2)$) with a mean of 0 and a SD of 3.2 for all covariate effects on adult survival probability, the number of adults recruited into the population, and fecundity for all species. We used gamma priors for the SD of the random year effects on adult survival probability ($\text{Gamma}(2, 0.25)$) and recapture probability ($\text{Gamma}(2, 0.25)$), and we specified gamma priors for the SD of the observation error in the counts of breeding pairs ($\text{Gamma}(2, 2)$).

For each species, we ran three chains for 450,000 iterations after a burn-in of 350,000 iterations, an adaptation phase of 10,000, and we thinned chains by 10, resulting in a posterior distribution of 30,000 values for each model parameter. Model convergence was determined using the Rhat statistic (Gelman & Hill, 2006) and visual inspection of chains. Convergence (Rhat values < 1.1) was obtained for all estimated parameter values. Posterior distributions were summarized by their means and 95% credible intervals (CRIs) unless otherwise noted. We interpreted population growth rate and pairwise species correlations as “significant” based on whether 95% CRIs overlapped zero. For covariate effects on demographic parameters, we report the proportion of the posterior greater than or less than zero and considered a relationship important when the proportion of the posterior distribution greater than or less than zero was 0.90 or more.

RESULTS

Demographic rates and environmental drivers

All three species' population sizes fluctuated substantially over the 18-year study period. Population sizes for all species peaked around the early- to mid-2010s (Figure 2a–c): American golden-plover increased from one breeding pair (CRI: 0, 3) in 2005 to a peak of 20 pairs (CRI: 16, 23) in 2009; dunlin had two peaks with 39 pairs in 2009 (CRI: 35, 41) and 40 in 2013 (CRI: 37, 42); and semipalmated sandpiper also had two peaks in the same years as dunlin (2009: 37 pairs, CRI: 32, 41; 2013: 44 pairs, CRI: 36, 48). Population growth appeared to stall in the early 2010s for American golden-plover and semipalmated sandpiper, with both reaching very low numbers by 2022 (AMGP: 6 pairs, CRI: 3, 9; SESA: 5 pairs, CRI: 2, 9). In contrast, dunlin declined to a minimum of 20 (CRI: 17, 22) pairs in 2018 and 2019 but then increased in the last years of the time series to 34 (CRI: 31, 36) pairs in 2022 (Figure 2a–c).

The annual number of adults recruited into the population (via reproduction and immigration) varied by species (Figure 2d–f), with American golden-plovers gaining an average of five pairs annually (CRI: 2, 7), dunlin gaining an average of 14 pairs annually (CRI: 10, 17), and semipalmated sandpipers gaining 7 pairs annually (CRI: 4, 10). Peaks in annual estimates of the number of adult recruits coincided with peaks in estimated population size for all three species (Figure 2d–f). There was a limited effect of snowmelt on the number of adults recruited for semipalmated sandpipers, but a considerable quadratic effect for dunlin ($p(\beta_{R2} < 0) = 1.00$) and American golden-plover ($p(\beta_{R2} < 0) = 0.99$), suggested that the peak adult recruitment occurred when snowmelt was around 5–7 June (Julian day: 156–158; Figure 3a). Fecundity in the previous breeding season ($t - 2$) was an important predictor of the eventual number of adults recruited for semipalmated sandpipers ($p(\beta_{R3} > 0) = 1.00$; Figure 3b) but was not supported for the two other species.

Annual apparent adult survival was relatively low for all three species but was quite different in the level of inter- and intra-variability among species (Figure 2g–i). American golden-plover adult survival averaged 0.55 (CRI: 0.43, 0.68), although annual estimates were relatively imprecise and highly variable over the study period, which is likely related to our relatively low recapture rates (mean: 0.42, CRI: 0.29, 0.56; range: 0.38–0.48). Dunlin mean adult survival was highest (0.65, CRI: 0.60, 0.70) and the least variable among years. Semipalmated sandpiper mean adult survival was slightly lower (0.58, CRI: 0.50, 0.66) and was the second most variable.

Recapture rates of dunlin were relatively high (mean: 0.69, CRI: 0.62, 0.76; range: 0.59–0.78), and semipalmated sandpiper recapture rates were in the middle (mean: 0.50, CRI: 0.42, 0.59; range: 0.43–0.58). The PDO index had a negligible effect on dunlin survival, but positive PDO, which is associated with El Niño-like conditions, was correlated with higher adult survival ($p(\beta_{ad1} > 0) = 0.94$) in American golden-plovers, and negative PDO (associated with La Niña-like conditions) was correlated with higher adult survival ($p(\beta_{ad1} < 0) = 0.98$; Figure 3c) in semipalmated sandpipers. There were negligible effects of snowmelt date in the previous year on adult survival for all species, but for semipalmated sandpiper, adult survival was higher when snowmelt was earlier in the current season ($p(\beta_{ad3} < 0) = 0.92$; Figure 3d).

Fecundity was relatively constant across years with high fox removal for each species but differed dramatically from years with low or no fox removal (Figure 3e). Overall, mean fecundity was much higher when foxes were removed, ranging from 2.40 to 2.91 chicks/breeding pair, compared to years when fox removal effort was low or did not occur, when it ranged from 0.29 to 1.25 (Figure 3e). Within species, American golden-plover had the greatest difference in mean fecundity (chicks per breeding pair) between years with high fox removal (average 2.40) and years with low or no fox removal (average = 0.29; Figures 2j and 3e), followed by dunlin (high = 2.91, low/no = 1.08; Figures 2k and 3e) and semipalmated sandpiper (high = 2.76, low/no = 1.24; Figures 2l and 3e). Fecundity of dunlin decreased linearly with the date of snow melt (DUNL: $p(\beta_{f1} < 0) = 0.97$). In contrast, fecundity increased until 5 June (Julian date of 156) for semipalmated sandpipers and then declined after that date ($p(\beta_{f2} < 0) = 1.00$, Figure 3f). There was a negligible effect of snowmelt on the fecundity of American golden-plover.

Population growth rates and demographic rate synchronies

Despite interannual population fluctuations, the geometric mean of annual population growth (λ_{geo}) indicated slight population growth for dunlin ($\lambda_{geo} = 1.03$, CRI: 1.01, 1.06), with more substantial increases in the last five years (since 2018 $\lambda_{geo} = 1.07$, CRI: 1.04, 1.10). Semipalmated sandpiper populations were stable over the duration of the study ($\lambda_{geo} = 1.01$, CRI: 0.94, 1.10); however, they declined substantially in the second half of the study period (since 2013: $\lambda_{geo} = 0.85$, CRI: 0.77, 0.90; since 2018 $\lambda_{geo} = 0.74$, CRI: 0.62, 0.85). The American golden-plover population grew throughout the study period ($\lambda_{geo} = 1.30$, CRI: 1.02, 1.71), but like the semipalmated sandpiper declined in the second half of the study period

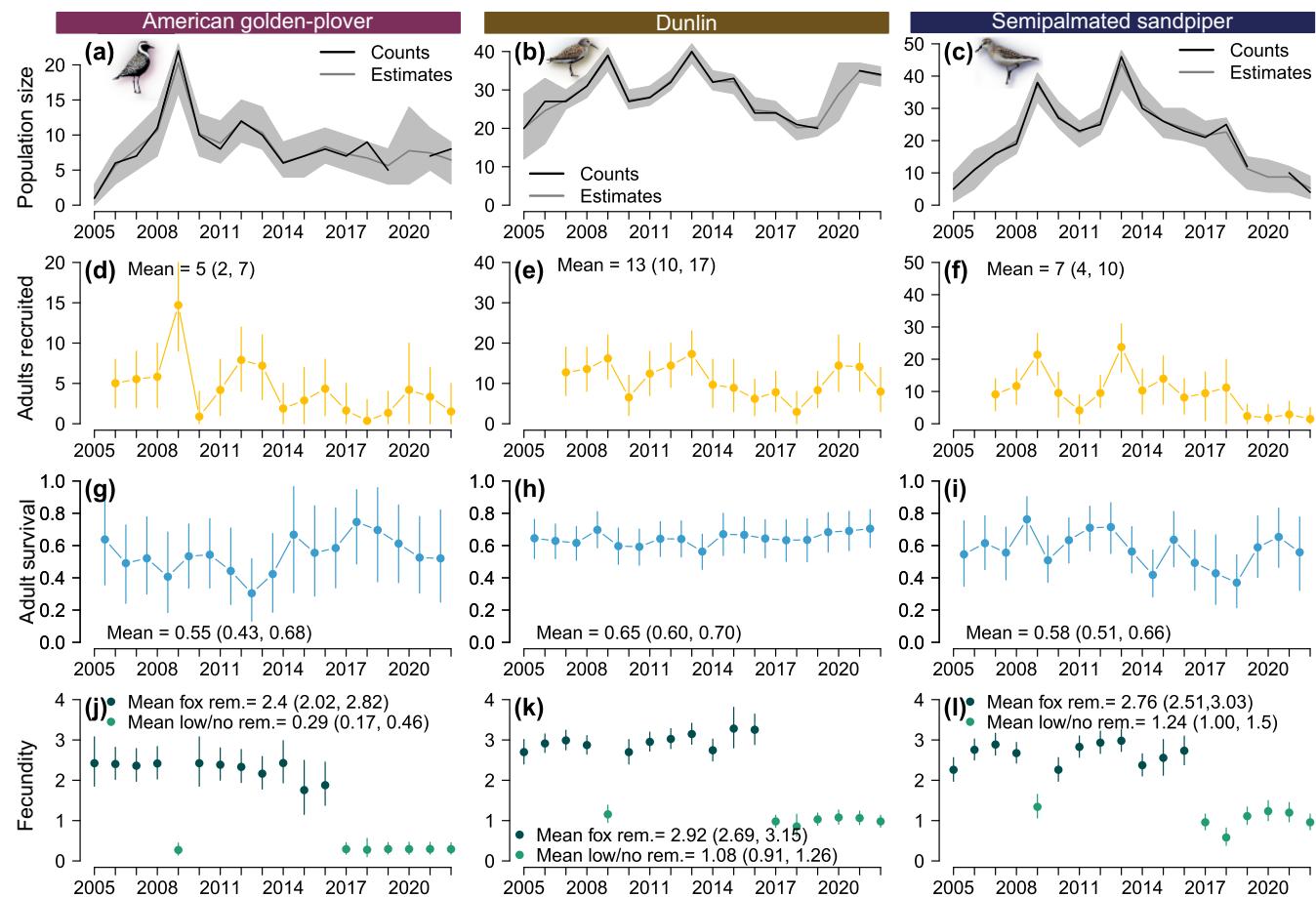


FIGURE 2 Demographic parameters for American golden-plovers (burgundy column), dunlin (brown column), and semipalmated sandpipers (navy column) estimated from a long-term study at Utqiagvik, Alaska, 2005–2022. (a–c) Estimates of shorebird population size (breeding pair abundance estimates, gray line) and 95% credible intervals (light gray shading) with observed pair counts (nest counts excluding known renests, black line), (d–f) annual number of adults (pairs) recruited to the population, (g–i) annual apparent adult survival probabilities, and (j–l) fecundity (chicks per breeding pair) estimated from chick counts. In (j–l), dark green indicates fecundity estimates in years with high fox removal, and light green shows fecundity estimates in years with low or no fox removal. Solid points with vertical lines indicate mean annual estimates with 95% credible intervals. American golden-plover image (a) by Peter Wilton, used under a Creative Commons Attribution 2.0 license. Dunlin image (b) by Jevgenis Slipto, used under a Creative Commons Attribution 2.0 license. Semipalmated sandpiper image (c) by Mdf/Wikimedia Commons used under a Creative Commons Attribution-ShareAlike 3.0 license.

(since 2013: $\lambda_{\text{geo}} = 0.94$, CRI: 0.86, 0.98; since 2018 $\lambda_{\text{geo}} = 0.97$, CRI: 0.82, 1.10).

Fox removal had differing effects on the breeding population size across species. Surprisingly, the geometric mean of population growth rate of dunlin was higher in years following low to no fox removal than it was following years with high fox removal efforts ($p(\lambda_{\text{fox}} > \lambda_{\text{no fox}}) = 0.00$). However, fox removal had positive effects on the population growth rate at the study site in the year following removal for semipalmated sandpiper ($p(\lambda_{\text{fox}} > \lambda_{\text{no fox}}) = 0.99$) and perhaps a slightly positive effect for American golden-plover ($p(\lambda_{\text{fox}} > \lambda_{\text{no fox}}) = 0.67$).

Few of the demographic rates were strongly correlated with population growth rate for any of the species (Figure 4). Fecundity was the only parameter correlated

with population growth rate for American golden-plover ($r = 0.25$ [CRI: 0.12, 0.47], Figure 4c); however, data for this species were relatively sparse, leading to imprecise estimates of adult survival and population growth rates. For dunlin and semipalmated sandpiper, adult recruitment was positively correlated with population growth rate (DUNL: $r = 0.77$ (CRI: 0.53, 0.88); Figure 4e and SESA: $r = 0.76$ (CRI: 0.45, 0.87); Figure 4h). Fecundity was also positively correlated with population growth rate in semipalmated sandpipers ($r = 0.46$ (CRI: 0.11, 0.59), Figure 4i).

Across all species combinations, adult recruitment and fecundity across the full time series were positively correlated between most species (Figure 5a–c,g–i), indicating a high degree of demographic synchrony in these

rates. The number of adult recruits for American golden-plover and dunlin was the most strongly correlated ($r = 0.62$, CRI: 0.20, 0.81), with the lowest correlation estimated between semipalmated sandpiper and dunlin ($r = 0.22$, CRI: 0.19, 0.64; Figure 5a–c). Among

demographic rates, adult survival displayed the lowest synchrony (Figure 5d–f), with all between-species correlations having 95% CRIs that widely overlapped zero. The binary effect of fox removal explained nearly all variation in fecundity, and consequently, correlation coefficients

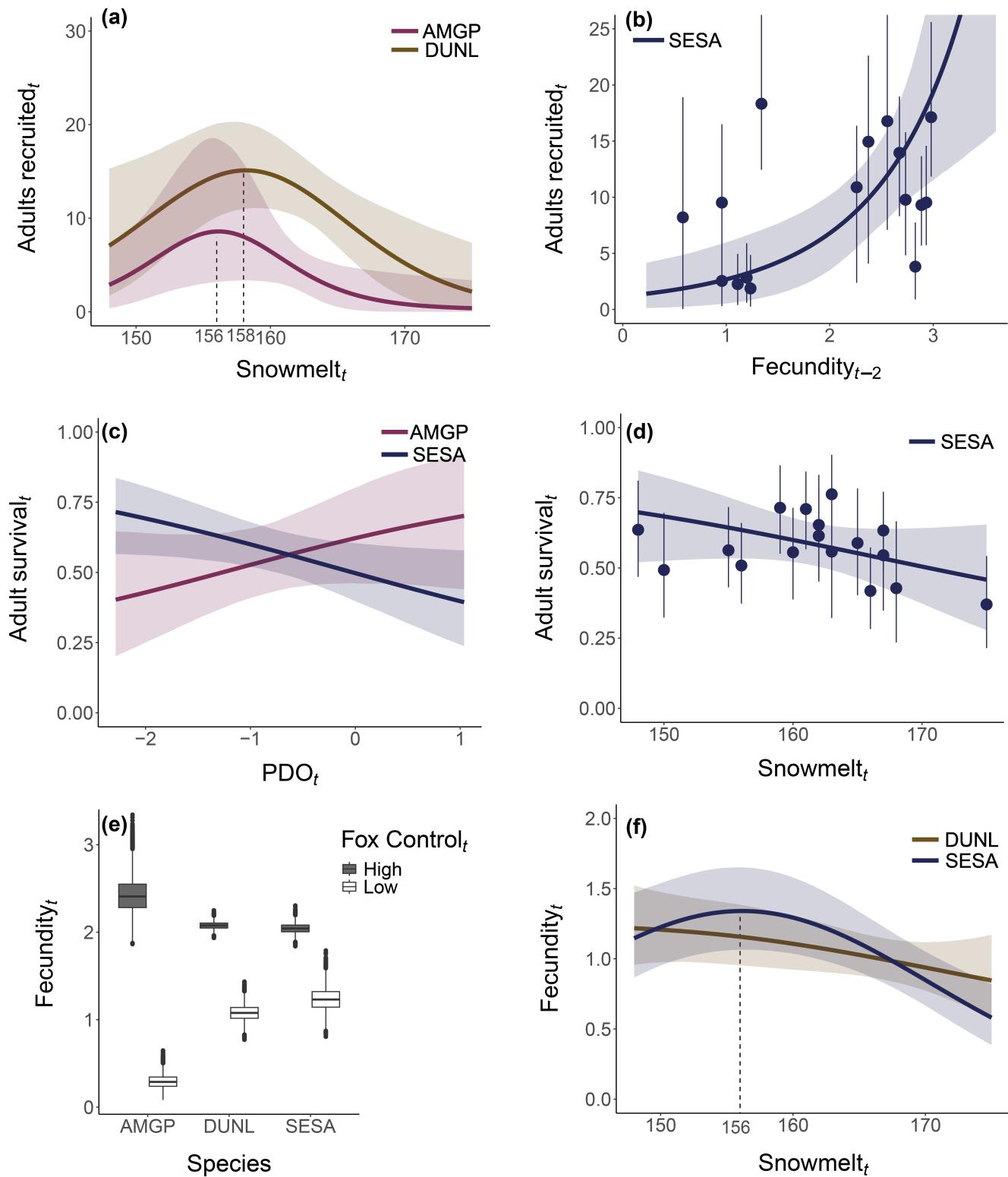


FIGURE 3 Legend on next page.

for species pairwise fecundity correlations were 1.00 for the full time series that included both years with low or no fox removal efforts and with high fox removal efforts (Figure 5g–i; see Appendix S1: Figure S5 for species pairwise correlations within years of high vs. low/no fox removal).

DISCUSSION

We estimated Arctic-breeding shorebird demographic rates and their environmental drivers for three sympatrically breeding species: American golden-plover, dunlin, and semipalmated sandpiper, revealing that species' population trends varied over time. Although local populations were estimated to be stable or increasing over the 18-year study period, two out of three species showed declines over the most recent decade in the time series. Environmental conditions at the breeding site, including timing of snow melt and predator removal, had important effects on breeding season demographic rates (e.g., adults recruited and fecundity), which were highly synchronous among species. However, fecundity within periods of low to no fox removal efforts compared to periods with high fox removal varied asynchronously, indicating that large benefits of fox removal were shared across the community, but smaller differences in fecundity among the species were likely due to differential responses to other environmental variables. Adult survival, which reflects conditions throughout the annual cycle, also varied asynchronously among species. The PDO had opposite effects on adult survival, suggesting that factors outside of the breeding season differentially affect species and that conditions along

the migratory pathways and nonbreeding ranges for these species are likely to be important factors influencing survival.

Mean adult survival estimates were generally low across species, yet species results were relatively consistent with previously published estimates of apparent survival for Arctic-breeding shorebirds. Few estimates are available for American golden-plover, but our estimates of apparent adult survival (0.30–0.74) were similar to other golden-plover species (0.55–0.80; Johnson et al., 2001, Piersma et al., 2005), albeit containing much more variability, with critically low adult survival in some years. Adult survival estimates for dunlin were consistent with previously published estimates for the species (0.59–0.70 for the current study versus 0.41–0.74 for previously published estimates; Hill, 2012). Similarly, for semipalmated sandpiper, our estimates were relatively consistent with the literature (0.37–0.71 for the current study versus 0.56–0.66 for previously published estimates; Sandercock & Gratto-Trevor, 1997, Sandercock et al., 2000). However, as with the American golden-plover, a handful of low survival estimates for the semipalmated sandpiper in our study over the last decade are outside the range of what has been reported previously. Weiser, Lanctot, et al. (2018b) conducted an analysis of shorebird survival across many sites in the Arctic using a spatially explicit Cormack-Jolly-Seber analysis that allowed estimation of true survival. They found that true survival estimates during a five-year period (2010–2014) for American golden-plover and semipalmated sandpiper were higher than the apparent survival estimates reported here and in the previous literature. This suggests that permanent emigration from our study site likely

FIGURE 3 Demographic parameters for American golden-plovers (AMGP), dunlin (DUNL), and semipalmated sandpipers (SESA) in relation to snow melt, Pacific Decadal Oscillation (PDO), and fox removal efforts estimated from a long-term study at Utqiāġvik, Alaska, 2005–2022. (a) Expected number of adults recruited (new breeding pairs) into the population as a function of the Julian date of 20% snowmelt on the breeding grounds for American golden-plover (burgundy) and dunlin (brown). Earlier snowmelt increased recruitment until ~5 June (Julian date = 156) for American golden-plover and ~7 June (158) for dunlin. Shading shows 95% credible intervals. (b) Estimated number of adults recruited as a function of fecundity in year $t - 2$ for semipalmated sandpiper (navy); shading shows 95% credible intervals. Points show the estimates of annual number of adults recruited with 95% credible intervals. Semipalmated sandpiper recruitment was positively correlated with fecundity in the breeding season two years earlier. (c) Estimated apparent adult survival as a function of the PDO for American golden-plover (burgundy) and semipalmated sandpiper (navy). Apparent adult survival was positively correlated with PDO in American golden-plovers and negatively correlated with PDO in semipalmated sandpipers. Shading shows 95% credible intervals. (d) Estimated apparent adult survival as a function of the Julian date of 20% snowmelt at the breeding site for semipalmated sandpiper (navy); shading shows 95% credible intervals. Points show the annual apparent adult survival estimates with 95% credible intervals. Semipalmated sandpiper apparent adult survival was negatively correlated with snowmelt date. (e) Boxplots showing posterior medians, interquartile range and 95% credible intervals of fecundity estimates (chicks per breeding pair) under high (gray) versus low or no (white) fox removal efforts for American golden-plover, dunlin, and semipalmated sandpipers. High predator removal effort resulted in substantially higher fecundity compared to years with low or no fox removal. (f) Estimated fecundity as a function of the Julian date of 20% snowmelt at the breeding site for dunlin (brown), and semipalmated sandpiper (navy), shown in years with low/no fox removal. Earlier snowmelt resulted in increased fecundity until ~5 June (Julian date = 156) for semipalmated sandpiper, and dunlin fecundity decreased linearly with later snowmelt. Shading shows 95% credible intervals.

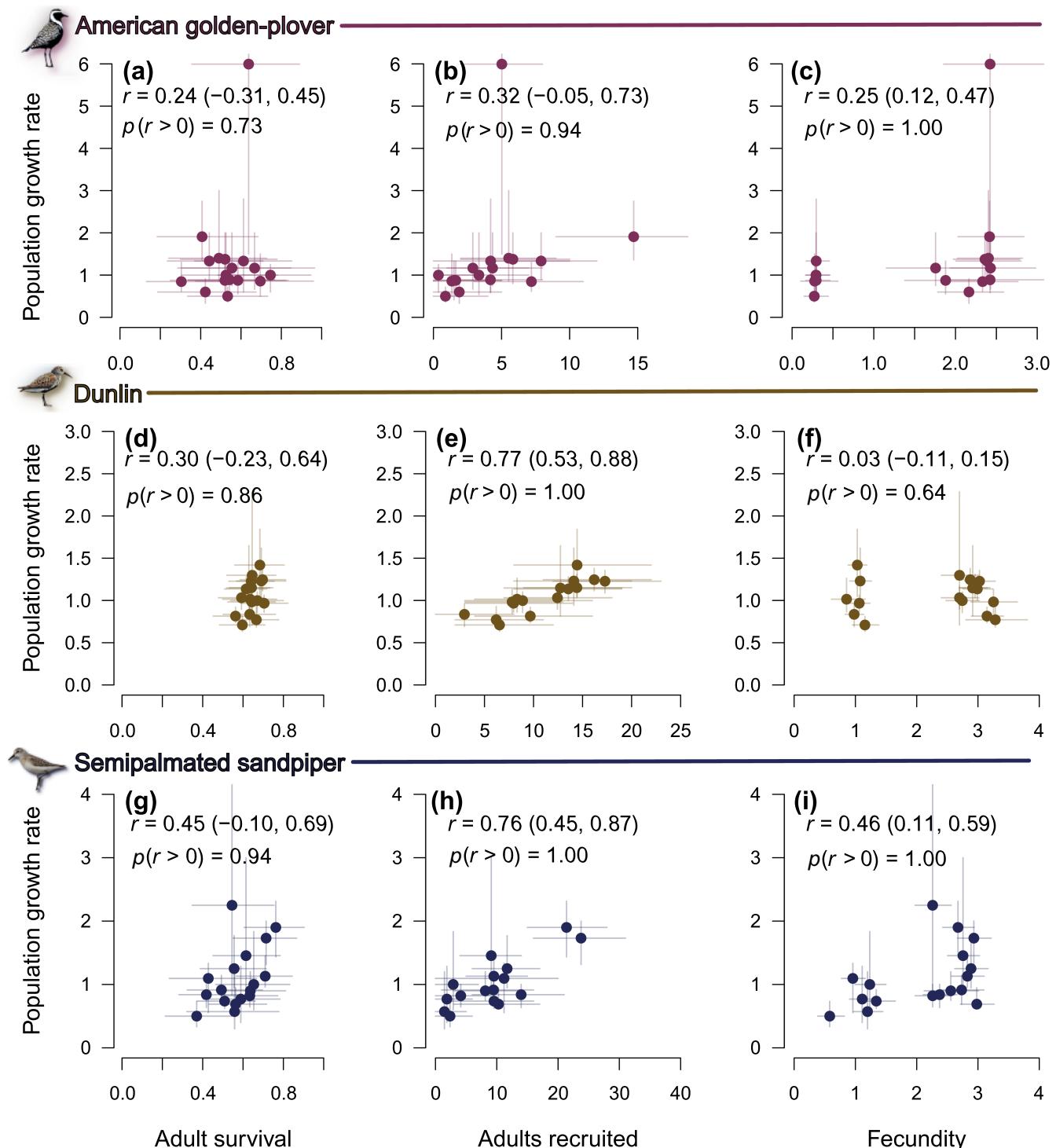


FIGURE 4 Posterior means of the annual population growth rate (λ_t) at Utqiagvik, Alaska, (2005–2022) plotted against (1) the posterior means of annual adult survival for each species (left column); (2) number of adults recruited for each species (middle column); and (3) fecundity (right column). Posterior means of the correlation coefficients (r) with associated 95% credible intervals and the probabilities that estimates are positive $p(r > 0)$ are given for each parameter correlation. Horizontal and vertical lines show the extent of 95% credible intervals for each annual estimate. American golden-plover image (top row) by Peter Wilton, used under a Creative Commons Attribution 2.0 license. Dunlin image (middle row) by Jevgenis Slihto, used under a Creative Commons Attribution 2.0 license. Semipalmated sandpiper image (bottom row) by Mdf/Wikimedia Commons used under a Creative Commons Attribution-ShareAlike 3.0 license.

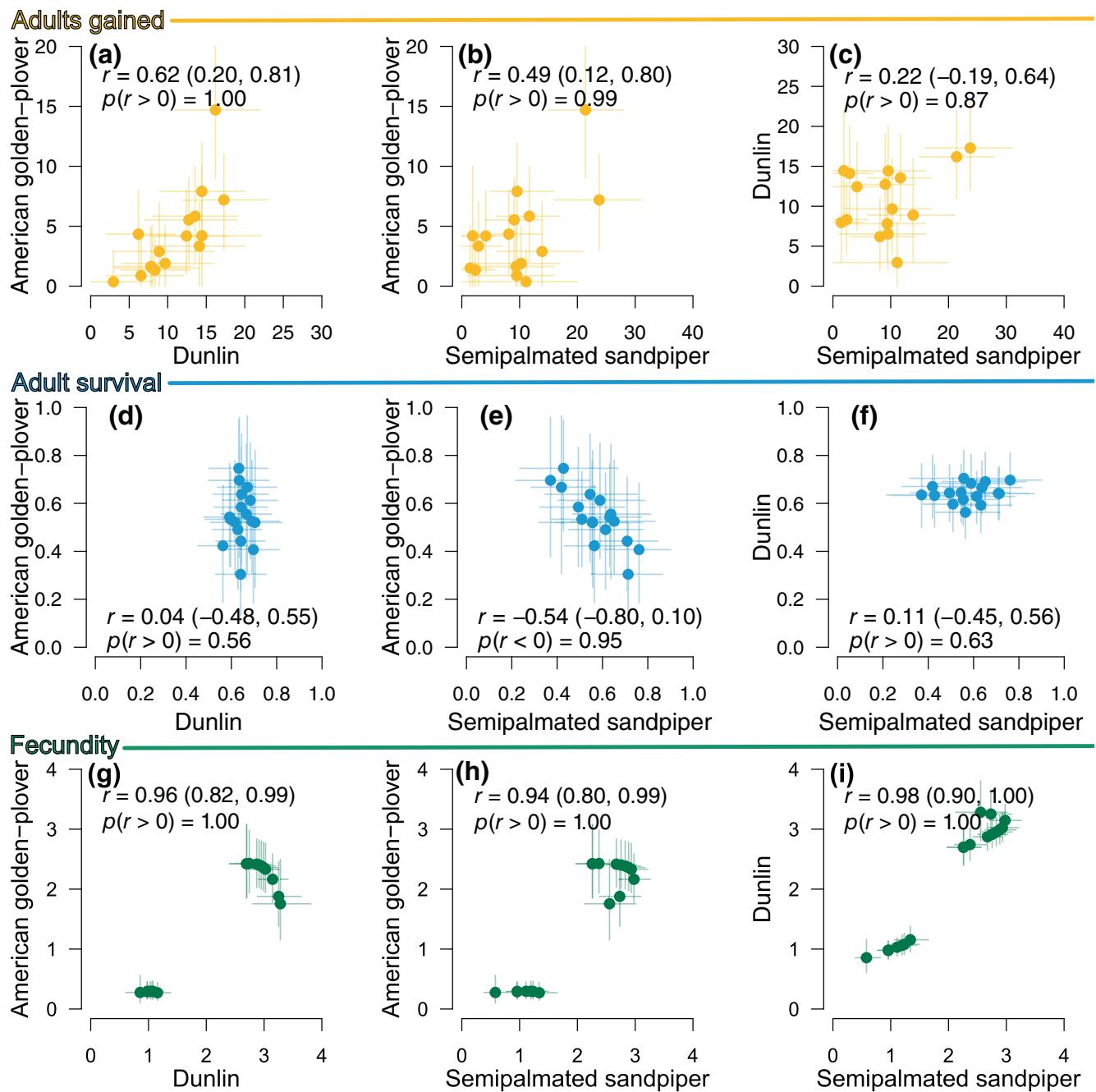


FIGURE 5 Pairwise species comparisons of American golden-plover, dunlin, and semipalmated sandpiper demographic rates at Utqiagvik, Alaska, 2005–2022, including means and 95% credible intervals for adult recruitment (yellow; a–c), apparent adult survival (blue; d–f), and fecundity (green; g–i). The pairwise correlation coefficients (r ; means and 95% credible intervals) as well as the probabilities that estimates are positive $p(r > 0)$ are given for each species pair.

contributed to our low apparent survival estimates for plovers and semipalmated sandpipers.

Shorebirds generally have high breeding site fidelity, particularly among males in monogamous mating systems like the three species we studied (Kwon et al., 2022), but when nests fail, birds may disperse to new areas in subsequent years (Sandercock et al., 2000; Weiser, Lanctot, et al., 2018b). Nesting density at the

Utqiagvik study site is relatively high compared to other monitoring sites in the Arctic (Lanctot et al., 2016), potentially leading to higher predation pressure and subsequent nest failures compared to other areas in the breeding ranges (e.g., dry, inland areas [Saalfeld et al., in review]). American golden-plovers had particularly low fecundity compared to the other species, especially in years with low or no fox removal. Nest failure could be

driving permanent emigration of American golden-plovers, and perhaps to a lesser extent, the other species, from this breeding location. However, if nest failure alone was driving our estimates of apparent survival, we would expect greater synchrony in adult survival estimates among species and a demarcation in survival for years with low or no fox removal effort when fecundity was very different. Yet there was little correlation among apparent survival estimates between species. Thus, environmental conditions along the different migratory pathways and nonbreeding ranges are likely also contributing to variation in adult survival among species. Future studies attempting to understand Arctic-breeding shorebird population dynamics should consider ways to disentangle mortality from permanent emigration, perhaps by using resightings of birds away from the breeding grounds (Barker, 1997), including sex-specific estimates of survival, and incorporating additional environmental variables from outside of the breeding season to better understand the role of emigration and potential nonbreeding season mortality.

IPMs allow estimation of “hidden parameters,” or additional parameters for which no specific data exist (Schaub & Kéry, 2021). Here, we took advantage of this benefit of IPMs and estimated the number of adults of each species that entered the population each year through recruitment, the sum of local reproduction and immigration. Although estimating such additional parameters is a benefit of IPMs, it is important to acknowledge the limitations of estimating parameters that are not directly informed by data. Such parameters are especially sensitive to violations of underlying model assumptions, lack of fit, or unmodeled variation in other parameters (Riecke et al., 2019). They also tend to have strong correlations with population growth rate (Paquet et al., 2021). Consequently, our adult recruitment parameter should be interpreted as “adults recruited + bias” (Paquet et al., 2021).

Our estimates of the number of adults recruited included both individuals hatched within the study area as well as immigrants. Natal recruitment is extremely limited in these shorebird species (Weiser et al., 2020), and almost none of the individuals banded as chicks returned to the study area (e.g., only 7 of 1722 dunlin, 4 of 1046 semipalmated sandpiper, and 0 of 230 American golden-plover chicks banded at the study site were resighted in a subsequent year during the 18-year study period). Thus, “the number of adults recruited” as we defined it in our model refers to new adults entering the population, including those new to the area and those that were not captured in a prior year and previously identified as breeders. Uncertainty in the number of adults recruited was high, especially for American golden-plovers, and it is likely that unmodeled

heterogeneity from other model parameters was absorbed into this additional parameter (Riecke et al., 2019). Thus, caution should be used when interpreting these results. In some years, the number of adults recruited made up as much as 88% of the breeding population at this site; average estimates were 46% (AMGP), 36% (DUNL), and 40% (SESA). While it is likely that some portion of these birds had previously bred in our study area and were simply not captured (especially in years with high nest predation when time to capture birds was limited), this finding and the low apparent adult survival estimates suggest birds breed over a much larger portion of the Arctic region than encompassed by the study area. Indeed, despite these species being considered site faithful, movement into and out of the study area may be more common than previously thought.

The environmental variables that we evaluated as potential drivers of shorebird population dynamics had varying levels of support; however, the timing of snowmelt had important effects on at least one demographic rate of all species. Two species (American golden-plover and dunlin) experienced higher rates of adult recruitment during years of earlier to average snowmelt, and semipalmated sandpipers experienced higher adult recruitment following high fecundity two years prior. Adult recruitment was lower for all species in years when snow melted exceptionally early or exceptionally late. It is possible that too early snowmelt could reduce the population of breeding adults because of the potential for a trophic mismatch between chick hatch and invertebrate emergence (Saalfeld & Lanctot, 2017) as these shorebirds are unable to advance their migration schedule (Both & Visser, 2001). Similarly, a very late snowmelt could also lead to fewer adults breeding, likely due to birds settling in other areas (McGuire et al., 2020). This line of reasoning assumes that birds are able to assess habitat conditions over a relatively vast area and settle in areas with appropriate phenological conditions—a behavior typically reserved for opportunistic shorebird species with polygynous or polyandrous mating systems and not monogamous species like those studied here (Kempenaers & Valcu, 2017; Pitelka et al., 1974; Saalfeld & Lanctot, 2015). However, the high number of adults immigrating into our study area suggests that even monogamous species may be deciding if an area is suitable for settling (see also Kwon & Kempenaers, 2023). The location of our study site in north central Alaska, a site centrally located in the dunlin breeding range, should lend itself well to discovery by dunlin as they travel east from Asia (Lagassé et al., 2020). Semipalmated sandpipers, in contrast, are approaching the end of their migration and might only breed in our study area if other available areas are snow-covered or saturated with individuals (Brown et al., 2017). It is possible that there are unique features in

the Utqiāġvik area that coincide with the snow-free years (e.g., lemming numbers that provide alternative food to predators of shorebirds, not analyzed in this study) that also cause birds to settle (Pitelka & Batzli, 2007). Two species (dunlin and semipalmated sandpiper) experienced increased fecundity (i.e., greater hatch success) during years of earlier snowmelt, perhaps due to increased access to food and/or reduced predation pressure as a result of higher nest densities in early snowmelt years. In addition, semipalmated sandpipers exhibited increased adult recruitment following high fecundity two breeding seasons earlier, suggesting that semipalmated sandpipers produced in the areas surrounding the study site could be joining the study population. A similar result was found in an 11-year study at Prudhoe Bay, Alaska; here nest density increased significantly with nest success rates two years previously (fig. 7, in Troy, 1996).

Local-scale predator management played an important role in increasing fecundity for all three shorebird species but did not generally translate into site-level increases in the number of breeding pairs. Population-level responses in years following predator management varied across species, likely due to unmeasured variables that limited post-hatch survival. Our study evaluated fecundity at chick hatching; thus, we could not assess survival to fledging or any factors affecting post-hatch survival. The impacts of management actions taken at a site level are difficult to discern at a population level given that Arctic-breeding shorebirds disperse and breed over a region much larger than the study area (Kempenaers & Valcu, 2017; Lanctot & Weatherhead, 1997). While predator removal can be an effective tool to increase reproductive output in birds, it is likely that any positive impact on the population would require implementation of the management technique over large areas (Côté & Sutherland, 1997; Dinsmore et al., 2014).

We evaluated the effect of the PDO on shorebird adult survival as an attempt to evaluate the influence of environmental conditions experienced throughout the annual cycle. The PDO affects the climate at the breeding locations of these shorebird species, leading to similar conditions experienced by shorebirds breeding in the same area. However, because these species use different migratory pathways and nonbreeding ranges, the PDO likely had different effects on each species during the nonbreeding season because of differences in conditions under positive and negative values of the index in nonbreeding areas. We found that the PDO had no effect on dunlin adult survival, a positive effect on American golden-plover adult survival, and a negative effect on semipalmated sandpiper adult survival. Thus, positive values of the index were associated with higher adult survival for American golden-plovers and lower survival for semipalmated sandpiper, and the opposite relationship

under negative values. Positive phases of the PDO are associated with El Niño-like conditions, a phenomenon that brings plentiful rains to the pampas region of southeast South America and drought to much of northern South America (Grimm et al., 2000), where American golden-plovers and semipalmated sandpipers spend the nonbreeding season, respectively. Negative phases of the PDO are associated with La Niña-like conditions, which reverse the precipitation patterns observed under El Niño conditions (Grimm et al., 2000). The relationships observed between the PDO and plover and semipalmated sandpiper survival suggest that PDO values associated with drought conditions during the nonbreeding season could negatively impact shorebird survival. In addition, negative PDO tends to bring cooler waters to the Pacific coast of South America, where some semipalmated sandpipers spend the nonbreeding season. Cool conditions in this region increase oceanic upwelling, bringing nutrient-rich waters to the coastline and enhancing primary productivity that can also increase shorebird prey availability (Pennington et al., 2006). These climate events are strongly linked to primary productivity and the abundance of invertebrates (Polis et al., 1997), influencing prey availability for shorebirds in the nonbreeding season, ultimately impacting survival and migration (Anderson et al., 2021).

Long-distance migratory birds, like Arctic-breeding shorebirds, spend the majority of their annual cycle outside of their breeding ranges, and conditions during the nonbreeding period may have carryover effects that can impact demographic rates during subsequent breeding seasons (Masero et al., 2017; Szostek & Becker, 2015, but see Senner et al., 2014). There is growing concern that stopover and nonbreeding habitat loss is leading to population declines of shorebirds (e.g., dunlin; Studds et al., 2017); but other risk factors, like legal and illegal harvest (McDuffie et al., 2022; Watts et al., 2015) and habitat loss due to sea level rise and expanding aquaculture, are also possible causes of declines (Brown et al., 2017). Although knowledge gaps remain, an increasing volume of tagging data can help elucidate migration routes, stopovers, and connectivity questions for migrating species (Harrison et al., 2024; Scarpignato et al., 2023). For species in which tags are not small enough, information from Motus technology, although less informative than satellite-derived GPS and platform transmitting terminal (PTT) tags, as well as recent advances using publicly available volunteer-collected data (e.g., eBird) can help identify important areas for conservation planning (Johnston et al., 2020; Schuster et al., 2019) during periods of the annual cycle when these birds are most vulnerable.

Taken together, our findings support the idea that shorebird survival is influenced by conditions during the

nonbreeding period in important ways. Although management interventions at the breeding area can be highly effective at increasing local reproductive output, actions during the nonbreeding season are needed to target adult survival. The inability to enact large scale interventions on remote Arctic-breeding grounds underscores the importance of enhancing conservation and management efforts during migration and nonbreeding seasons, which constitute the longest periods of the annual cycle, when birds are vulnerable to migratory stressors and unfavorable weather and resource conditions (Marra et al., 2015). For example, efforts can be made to protect, restore, and enhance intertidal habitats used by dunlin and semipalmated sandpipers during the nonbreeding season (see e.g., Jackson et al., 2024). Similarly, American golden-plovers could benefit from additional efforts to reduce harvest in the Caribbean and northeastern South America (AFSI, 2020; Reed et al., 2018). We recognize this full annual cycle approach to conservation presents financial and logistical challenges across continental and country borders and governmental agency jurisdictions. Nevertheless, urgent action is needed to identify where, when, and what conservation and management actions are likely to be most effective at reversing population declines for shorebirds.

AUTHOR CONTRIBUTIONS

Kayla L. Davis contributed to statistical analysis design and execution, writing (lead), and figure creation. Richard B. Lanctot contributed to field study design and data collection and curation, writing (supporting), and editing. Sarah T. Saalfeld contributed to field study design, data collection and curation, and writing and editing (supporting). Elise F. Zipkin contributed to advising, statistical analysis design and execution (advising), writing (advising), and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to disclose, and all authors have approved this work for publication. We certify that the submission is original work and is not under review at any other publication. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the US Fish and Wildlife Service.

DATA AVAILABILITY STATEMENT

Data and code for the analysis (Davis, 2025) are available in Zenodo at <https://doi.org/10.5281/zenodo.15277231>.

ORCID

Elise F. Zipkin  <https://orcid.org/0000-0003-4155-6139>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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