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Demographic models indicate the need for further research on vital rates to track status and trends of Arctic-breeding shorebirds

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Data availability: Analyses reported in this article can be reproduced using the values in Table 2 and a publicly available R script (Weiser 2020).

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Demographic models indicate the need for further research on vital rates to track status and trends of Arctic-breeding shorebirds

Running head: Modeling shorebird population trends

ABSTRACT

Conservation status and management priorities are often informed by population trends. Trend estimates can be derived from population surveys or models, but both methods are associated with sources of uncertainty. Many Arctic-breeding shorebirds are thought to be declining based on migration and/or overwintering population surveys, but data are lacking to estimate the trends of some shorebird species. In addition, for most species, little is known about the stage(s) at which population bottlenecks occur, such as breeding vs. nonbreeding periods. We used previously published and unpublished estimates of vital rates to develop the first large-scale population models for 6 species of Arctic-breeding shorebirds in North America, including separate estimates for 3 subspecies of Dunlin. We used the models to estimate population trends and identify life stages at which population growth may be limited. Our model for the *arcticola* subspecies of Dunlin agreed with previously published information that the subspecies is severely declining. Our results also linked the decline to the subspecies' low annual survival rate, thus potentially implicating factors during the nonbreeding period in the East Asian-Australasian Flyway. However, our trend estimates for all species showed high uncertainty, highlighting the need for more accurate and precise estimates of vital rates. Of the vital rates, annual survival had the strongest influence on population trend in all taxa. Improving the accuracy, precision, and

spatial and temporal coverage of estimates of vital rates, especially annual survival, would improve demographic model-based estimates of population trends and help direct management to regions or seasons where birds are subject to higher mortality.

Keywords: demography; fecundity; phalarope; plover; population modeling; sandpiper; survival; waders

Lay summary

- Documenting population trends is essential for evaluating conservation status of wild populations.
- Trends can be estimated with population surveys or by predicting population growth based on survival rates and fecundity, but both methods are challenging, especially for species with large or remote geographic distributions.
- We used recent broad-scale estimates of survival and fecundity to develop population models for 6 species of Arctic-breeding shorebirds.
- The *arcticola* subspecies of Dunlin is likely in severe decline, but our trend estimates for all species showed high uncertainty.
- Uncertainty around the values of annual survival rates was a key driver of the uncertainty around the trend estimates.
- Our work highlights the need for better estimates of annual survival, seasonal survival, juvenile survival, and breeding propensity for these Arctic-breeding shorebirds.

INTRODUCTION

Effective management and conservation of wildlife require knowledge of population trends. Trends can be estimated either through count-based population surveys, which measure abundance, or with demographic models, which use estimates of vital rates to predict the population growth rate. When repeated population surveys and vital rates are both available, Integrated Population Models (IPMs) can be used to evaluate trends (Schaub and Abadi 2010). However, when survey data are too sparse to develop an IPM, vital rates can be used in a demographic model. The output can then be compared to estimates from population surveys to provide multiple lines of evidence for a population trend. Through a sensitivity or elasticity analysis (de Kroon et al. 1986, Caswell 2001), demographic models can also be used to identify which vital rates have the strongest influence on population growth rate, thus directing research and management to key life stages and relevant geographic areas.

In long-lived species, adult survival often has a strong influence on the rate of population change, while reproductive rates are more influential for short-lived species (Sæther and Bakke 2000). The relative effect of each demographic parameter on population growth or decline depends on the mean and variance of the parameter; for example, high, constant survival rates drive population growth more strongly than low or variable rates (Sæther and Bakke 2000, Wisdom et al. 2000). If population growth is limited by reproductive success, management efforts might be most effective when focused on the breeding grounds. In contrast, if adult survival has the strongest influence on the rate of change, management actions might most effectively target areas where adult survival is limited.

Identifying the limiting stage of the annual cycle is especially crucial for migratory birds, which can be affected by different factors in breeding vs. nonbreeding areas (Hostetler et al.

2015). Arctic-breeding shorebirds undertake some of the longest migrations of any birds, making nonstop flights of up to 12,000 km to spend the nonbreeding season in the tropics or Southern Hemisphere (Henningsson and Alerstam 2005, Conklin et al. 2017). Nearly half of shorebird populations worldwide have shown long-term population declines associated with anthropogenic change, but population sizes and trends are not well quantified for many species (International Wader Study Group 2003, Andres et al. 2012b, Hua et al. 2015, Smith et al. 2020). Many Arctic-breeding shorebirds use remote areas during both the breeding and nonbreeding seasons, so conducting comprehensive surveys or studies of vital rates has been logistically challenging, especially on a scale relevant to the large breeding distributions of most species (Bart and Johnston 2012).

The Arctic Shorebird Demographics Network (ASDN) monitored shorebirds at 16 field sites across Alaska, Canada, and Russia in 2008–2014 (Brown et al. 2014, Lanctot et al. 2015). The ASDN produced the first comprehensive estimates of reproductive parameters for 21 species and of adult survival for 6 species of Arctic-breeding shorebirds (Weiser et al. 2018a, b). We supplemented these estimates with additional unpublished data from the ASDN and previous estimates of other demographic parameters to develop population models for 6 species of Arctic shorebirds. For each species, we estimated the rate of population change and compared our results to previous estimates of trends, which were often primarily based on population surveys in nonbreeding areas (Andres et al. 2012a, b; U.S. Shorebird Conservation Plan Partnership 2016). We also quantified the elasticity value of each vital rate to identify the demographic parameter(s) that had the strongest influence on population growth rate for each species. For influential parameters, we discuss the key gaps in knowledge that could become the focus of

future research. Our study provides the first flyway-scale estimates of population trends using demographic models, providing information to prioritize future research.

METHODS

The ASDN coordinated standardized data collection at 16 field sites in Alaska, Canada, and Russia (Figure 1). Methods for collection of field data are provided in detail by Brown et al. (2014) and summarized by Weiser et al. (2018a, b) and all raw data are publicly available (Lanctot et al. 2016). In the present analysis, we focus on 6 species of shorebirds for which key demographic rates, including rates of true annual adult survival corrected for emigration, have been estimated. The focal species were American Golden-Plover (*Pluvialis dominica*), 3 allopatric subspecies of Dunlin *(Calidris alpina pacifica, arcticola,* and *hudsonia*), Semipalmated Sandpiper (*C. pusilla*), Western Sandpiper (*C. mauri*), Red-necked Phalarope (*Phalaropus lobatus*), and Red Phalarope (*Ph. fulicarius*; Table 1). Over 95% of our data were from North American sites, so our study is primarily relevant to Nearctic-breeding populations. During migration, the *arcticola* subspecies of Dunlin uses the East Asian-Australasian Flyway and all of our other study populations use the 4 Americas flyways (Rodewald 2015). Where information on a particular vital rate was not available for one of our study species, we used estimates for the most closely related species; we evaluated the consequences of such uncertainty in vital rates in the population model as described below.

Estimating Vital Rates

To develop our population models, we used estimates previously derived from ASDN data from 2008–2014 for the mean values and variances of true annual survival rates of adults (corrected for emigration; Weiser et al. 2018b), and clutch size, daily nest survival rates, and

incubation duration for each species (Weiser et al. 2018a; Table 2). For most of our study species, adult survival estimates were drawn primarily from study sites in Alaska, as sample sizes and return rates were too low at sites in eastern Canada (Figure 1). We also used published estimates of renesting propensity (Gates et al. 2013), chick survival rates (Hill 2012; other studies provided survival rates by brood, not by chick), and juvenile survival rates (Warnock and Gill 1996, Fernández et al. 2003, Rice et al. 2007; Table 2), some of which were developed at or near our study sites in previous years. All vital rates were estimated independently by previous studies over various time periods, so we did not include estimates of covariance among vital rates.

We developed estimates of additional parameters for the population model from the ASDN dataset, which is publicly available (Lanctot et al. 2016). First, we estimated age of first return to the breeding grounds based on birds that we banded as chicks and later observed as adults at breeding sites (Supplemental Material Appendix A). For birds present in breeding areas, extreme weather conditions can cause >50% of females (e.g., 2 of 8 years in Gratto-Trevor 1991) or nearly all individuals (Schmidt et al. 2019) to forgo breeding. However, probability of attempting to breed is not well documented in our study species. For individuals that were present on the breeding grounds, we therefore assigned a moderately high annual nesting propensity (mean = 0.80) with moderate parameter uncertainty (SD = 0.10) and interannual variation (SD_{yr} = 0.20).

For nests that hatched at least one egg, we developed an estimate of the number of chicks hatched per nest by subtracting the species-specific mean estimate of eggs lost during incubation and the mean number of unhatched eggs per nest from the total clutch size (Weiser et al. 2018a) and assumed that all other eggs in the clutch hatched. We used a mean of 1:1 for the primary sex

ratios of eggs and assumed that there was no sex bias in mortality of eggs or chicks, as there is no evidence of biased sex ratios for any of our study species (Warnock and Gill 1996, Rubega et al. 2000, Hicklin and Gratto-Trevor 2010, English et al. 2014, Franks et al. 2014).

Arctic-breeding shorebirds can renest if their first clutch fails before hatching. However, rates of renesting are not well known and have been typically underestimated, as finding and identifying renests as such is challenging (Naves et al. 2008). One experimental study of radio-tracked *arcticola* Dunlin found that an average of 73% of females renested, depending on timing of failure of the clutch (Gates et al. 2013). Robust estimates were not available for our other study species, so we used the same rate of 73% across all species as the best available estimate. Renests are often expected to be less successful than initial nests due to seasonal declines in reproductive output, which are present in our study system and have been described based on the initiation date of the nest (Ruthrauff and McCaffery 2005, Hill 2012, Weiser et al. 2018a). We therefore calculated the mean difference in initiation dates between initial nests and renests for 57 documented renests in our dataset (Supplemental Material Appendix B). We used estimates of seasonal declines in breeding parameters (Ruthrauff and McCaffery 2005, Hill 2012, Weiser et al. 2018a) to evaluate how mean values of clutch size, incubation duration, daily nest survival, and chick survival changed from initial nests to renests (Table 2).

Model Structure

We modeled each shorebird species separately with a stochastic post-breeding projection matrix model (Caswell 2001). Population models typically model only the sex that could be limiting in the system, such as the number of female young produced per adult female (Caswell 2001). Modeling a single sex provides a common denominator among species with various breeding systems. Red and Red-necked phalaropes are polyandrous, so males are likely the

limiting sex for fecundity (Rubega et al. 2000, Tracy et al. 2002, Liker et al. 2013). Our other study species show obligate biparental care of the clutch through most of the incubation period and sex ratios are generally thought to be even (Warnock and Gill 1996, Hicklin and Gratto-Trevor 2010, Johnson and Connors 2010, Franks et al. 2014). For consistency, we therefore used male-based population models for all species. Female-based models for plovers and sandpipers would yield identical results for most of our study species, except that annual survival rates might be slightly lower for female than male Western Sandpipers (Weiser et al. 2018b).

Based on our observations of known-age breeders (Table 2), we structured the model for each species with up to 4 age classes: class J = juveniles (all species), 1 = yearlings, 2 = two-year-olds, and 3 = all age groups in which 100% of individuals were expected to breed. For species where all individuals were expected to breed as yearlings, only classes J and 3 were included in the model; likewise, for species in which all individuals were expected to breed as two-year-olds, the model included only classes J, 1, and 3. Age-specific probabilities of breeding resulted in age-specific values of fecundity, but we did not vary other vital rates (including annual survival) among classes because insufficient data were available to develop age-specific estimates. No information on density dependence of survival or fecundity is available for our study species, so we did not include density dependence in the model. Likewise, immigration and emigration rates are not known for these species, so we assumed that emigration and immigration would be balanced, on average, at our study sites, and thus modeled each population as if it were closed.

In the model for each species, transitions among ages were described by annual survival (*S)* of each age class. Fecundity (*F),* the number of male juveniles produced per adult male,

depended on a series of components of reproductive success. For initial nests (1), fecundity was defined as:

$$F_1 = P_a \cdot N \cdot H_1 \cdot E_1 \cdot C_1 \cdot 0.5,$$

where the probability of returning to the breeding area (P) varied by age class (a), N = nesting propensity for birds present in the breeding area, H = probability of the nest surviving to hatch (daily survival raised to the power of incubation duration in days), E = number of eggs expected to hatch (clutch size minus number of eggs lost during incubation and number of eggs remaining unhatched in a successful nest), C = survival rate of chicks to fledging, and 0.5 = sex ratio as the proportion of eggs that were expected to be male.

Renesting (laying a second clutch) has been documented in all of our study species if the first clutch fails before hatching (Lanctot et al. 2016). In one of our study taxa (*pacifica* Dunlin), a female that successfully hatches a clutch will sometimes desert her mate and produce a new clutch with a new mate (Jamieson 2011). There is no evidence of double-brooding in the other species, and our model assumed that fecundity was male-limited, so the possibility of female Dunlin double-brooding was not relevant to our models. We therefore assumed that in our male-based model, renesting occurred only after a clutch failed before hatching. Based on previous estimates that components of fecundity are lower for renests than initial nests (Hill 2012, Gates et al. 2013) and that reproductive output declines over the season (Weiser et al. 2018a), we defined each component of fecundity separately for initial nests and renests. We defined fecundity of the renesting attempt (2) similarly to the initial nest, but conditional upon on the probability of the first nest failing and the probability of renesting (R):

$$F_2 = P_a \cdot N \cdot (1 - H_1) \cdot R \cdot H_2 \cdot E_2 \cdot C_2 \cdot 0.5.$$

Total fecundity across the initial nest and renest was then taken as the sum of F_1 and F_2.

Our model was stochastic, incorporating estimates of demographic variance instead of using fixed mean values to estimate population trajectories. For each vital rate, we incorporated variance among replicates based on the SD estimated by previous studies or for this study, representing uncertainty in the parameter estimates. Data on variation among years were rarely available, so we applied a relatively small interannual SD to rates that were expected to vary little among years, such as annual survival, and relatively larger values for components of fecundity (Table 2). We drew values from a normal distribution when appropriate, or from a beta distribution for values constrained to range from 0 to 1.

Model Execution

We used the mean values of each vital rate (Table 2) to produce a deterministic calculation of the stable age structure for each model. We used that stable structure as the starting distribution for each model. We simulated 1000 replicates of 20 years to fully represent interannual variation and parameter uncertainty for each species. In each replicate and year, we calculated the population size (N), values of each major vital rate (survival *S* and fecundity *F* by age class), and an estimate of stochastic elasticity (*e*), which indicates the relative contribution of each vital rate to population growth (de Kroon et al. 1986). We used the *popbio* package version 2.6 (Milligan and Stubben 2007) to calculate λ (function "lambda"), *e* of major vital rates (survival and net fecundity; function "elasticity"), and *e* of lower-level vital rates (function "vitalsens") for each year and replicate. We averaged values of N, *S*, *F*, and *e* across years within replicates and then across replicates, and calculated the 95% CIs from the distribution of simulated values across replicates.

Given the large uncertainty around many of vital-rate estimates, we then simulated additional scenarios where we reduced each vital rate by half in turn and calculated λ in each

case. These additional scenarios explicitly demonstrate the potential implications of the uncertainty inherent in the estimates we used for many vital rates. We tested reduced vital rates in these simulations to represent worst-case scenarios in terms of population trends in these species of conservation concern.

We conducted all simulations and calculations in R v. 3.6.1 (R Core Team 2019) and our script to run the stochastic matrix model simulation is publicly available ([the authors] 2020).

RESULTS

Estimates of Vital Rates

Based on the age at return of locally banded chicks (corrected for detection probability; Supplemental Material Appendix A), we estimated that in sandpipers, most individuals would return to breed in their first year (42–57%) or second year (33–36%), with the remainder (7–16%, highest in Dunlin) delaying breeding until their third year (Table 2, Supplemental Material Table S1), which broadly agreed with previous estimates (Hilden and Vuolanto 1972, Reynolds 1987, Schamel and Tracy 1991, Warnock and Gill 1996, O'Hara et al. 2005, Hicklin and Gratto-Trevor 2010). We expected 89% of Red-necked Phalaropes to return in their first year and the remaining 11% in the second year. Although numbers of returning birds banded as chicks were small (5–16 individuals per species), our estimates agreed with previous assessments with even smaller samples (Supplemental Material Appendix A). We had no information on returning American Golden-Plovers or Red Phalaropes banded as chicks and there was no previous information on age at return in those species. We therefore assumed all American Golden-Plovers returned in their first year because few are thought to spend the boreal summer in nonbreeding areas (Johnson and Connors 2010), and we assumed that Red Phalaropes would

show the same age at first breeding as Red-necked Phalaropes. Our models therefore contained a single adult age class for American Golden-Plovers, 2 for phalaropes, and 3 for sandpipers (Table S1).

In successful nests in the ASDN dataset, 90–98% of eggs were expected to hatch for each species (Table 2). For birds observed to renest following failure of the initial clutch, the renest was initiated an average of 13-20 days after the first clutch was laid (Table 2, Supplemental Material Table S2). As per previously published estimates, adult survival rates showed some variation among species, while adult fecundity showed less variation (Figure 2). Subadult fecundity varied depending on the expected age at first breeding for each species. We used a juvenile survival rate of 0.45 (SD = 0.10, interannual SD = 0.05), which was the average from 3 previous studies (Warnock et al. 1997, Fernández et al. 2003, Rice et al. 2007), across all species due to a lack of species-specific information. The implications of the uncertainties around our vital rate estimates are detailed in the elasticity and sensitivity analyses as reported below.

Model Results

The main population models predicted that 38–45% of the post-breeding population (i.e. just before fall migration) of each species would be comprised of juveniles (Supplemental Material Table S3). Simulated population growth rates averaged near or above $\lambda = 1.00$ (stable to increasing) for 7 out of 8 taxa (Figure 2a; Table 1), although the distributions of simulated λ were large in most cases (Figure 3). In contrast, *arcticola* Dunlin were expected to be declining ($\lambda = 0.83$; 95% CI = 0.64–1.03), which would result in the population reaching ~3% of the current size after 20 years in the absence of density dependence.

Variation among taxa in population growth rates closely matched the variation in adult survival rates (Figure 2a,b). Correspondingly, elasticity values (*e*) were highest for survival rates

of adults in all taxa, although juvenile survival was similarly influential for *arcticola* Dunlin, (Figure 4a). In the other taxa, *e* was moderate for juvenile survival and lower for fecundity. In all taxa with multiple age classes, *e* averaged higher for fecundity of adults than subadults due to the different probabilities of breeding (Figure 4b). Among lower-level components of fecundity, the strongest effects on λ were from annual nesting propensity and components of the initial nesting attempt, followed by age at first breeding (Figure 5a,b). Components of a renesting attempt had the smallest elasticity values (Figure 5c).

Scenarios in which we halved each vital rate in turn provided additional evidence of the effect of each vital rate on λ. In all species, when adult survival was halved, λ was significantly lower than in the main scenario and also significantly lower than 1 (Figure 6). Halving the other vital rates did not significantly change the population growth rate, but variance was large and the change in the mean was often biologically meaningful, sometimes switching a mean estimate of population growth to decline.

DISCUSSION

We used previously published and new estimates of vital rates to develop the first continental-scale population models for 6 species of Arctic-breeding shorebirds. Our models demonstrated the strong influence of the estimated annual survival rate on the predicted population trend, emphasizing the importance of accurately and precisely estimating this parameter as well as managing for conditions to maximize survival when working to prevent or mitigate population declines. Uncertainty in all parameters, especially annual survival, resulted in wide uncertainty around our estimated population trends, indicating the need for further information on most life-history stages of Arctic-breeding shorebirds.

Our models estimated stable to increasing populations for most of our study taxa, which often contradicted previous estimates. However, uncertainty was large around our trend estimates, and only the estimate for Western Sandpiper was significantly different from zero. Uncertainty around estimates of population size or trend from nonbreeding surveys is also often high (Andres et al. 2012b), so the appearance of a discrepancy between our trend estimates and those from previous studies could simply be due to chance. The uncertainty around our estimates was typically due to small sample sizes relative to the magnitude of variation inherent in the population. Variation around adult survival estimates was large partly due to difficulties in distinguishing between mortality and detectability of marked individuals. Moreover, the vital rates that we used were drawn from multiple years at multiple study sites that spanned a wide range of longitude. Thus, the uncertainty around the vital-rate estimates also included spatial and temporal heterogeneity present in the dataset.

These uncertainties highlight the need for further study of Arctic-breeding shorebirds. Study of the most influential vital rates, such as adult survival, will be especially important for understanding population trends and any causes of decline. While annual rates of survival have been estimated for our study species (Weiser et al. 2018b), uncertainty around those estimates was large. Moreover, estimating seasonal (not just annual) survival rates would help identify when during the annual cycle these birds are most susceptible to mortality, which can then focus management actions on the most relevant periods and regions to mitigate any ongoing or expected population declines.

After annual survival, our models indicated that juvenile survival is also a potentially important parameter in driving population trends. Juvenile survival is thus far poorly known for most Arctic-breeding shorebirds (only 3 of our study species at a small number of locations;

Warnock et al. 1997, Fernández et al. 2003, Rice et al. 2007) and is difficult to evaluate given the apparently low natal site fidelity in these species, but could become easier to monitor as tracking technology continues to advance. The moderate influence of the first nest attempt on population trend also indicates that ongoing monitoring of reproductive success is warranted and further efforts would be useful to define spatiotemporal patterns in the probability of breeding, especially if changing Arctic habitat and phenology has the potential to produce large changes in these vital rates (Galbraith et al. 2014, Senner et al. 2017, Wauchope et al. 2017, Kwon et al. 2019, Saalfeld et al. 2019).

In addition to considering the uncertainty around the estimates, comparing our trend estimates to previous work is further complicated by the possibility that the sites at which we estimated vital rates and the surveyed overwintering sites might not be equally representative of the population of interest. First, migratory connectivity is not well described for some of our study species, so vital rates measured at our breeding sites might not be directly relevant to the population counts from monitored overwintering sites. Second, in some cases, the estimates of vital rates used in our study were drawn primarily from a subset of sites, with sample sizes often much larger in Alaska than eastern Canada, and thus do not equally represent the breeding ranges of our study species. Third, site-selection bias could play a role in the estimates of trend from both breeding and overwintering areas. Study sites are often selected to maximize sample sizes of the species of interest, and thus may represent high-quality sites in years of relatively high abundance rather than representing the overall population (Fournier et al. 2019). Our breeding sites were often selected based on a combination of accessibility and bird availability, and thus might represent high-quality sites with relatively high vital rates. The same issue could apply to overwintering population surveys if monitored sites were chosen due to an initial abundance of

the target species. If that initial abundance was partly due to chance, then there may appear to be a population decline over time as those sites revert to their long-term mean (Fournier et al. 2019). The potential effects of representativeness and methodology on trend estimates are an important consideration when evaluating the management needs of wild populations. When the full breeding or wintering range of a species cannot be surveyed, using multiple lines of evidence could be helpful to best define population trends.

Despite the uncertainty around our trend estimates, we note that our mean estimate of trend for *arcticola* Dunlin agreed with previous estimates that the subspecies is severely declining (Andres et al. 2012b, U.S. Shorebird Conservation Plan Partnership 2016). This subspecies shows much lower mean annual survival rates than our other study taxa (Weiser et al. 2018b), and our simulations highlighted the importance of this vital rate in driving population trend, suggesting that low annual survival is likely playing a key role in the decline of this subspecies. Our other study species have higher annual survival rates despite being sympatric with *arcticola* Dunlin on the breeding grounds, and the other subspecies of Dunlin we examined also had higher annual survival. Of all our study taxa, *arcticola* Dunlin are the only group to use the East Asian-Australasian Flyway (Gill et al. 2013). Many shorebirds in that flyway are declining, possibly as a result of habitat loss in the Yellow Sea and other crucial stopover and wintering areas which has reduced annual survival rates (Piersma et al. 2016, Studds et al. 2017). Our findings of a likely-declining trend corresponding with low annual survival in *arcticola* Dunlin corroborate this previous evidence that reduced annual survival may be depressing population trends for species using this flyway.

Conclusion

While our models aimed to estimate population trends for Arctic-breeding shorebirds, the uncertainty around our trend estimates highlights the need for more accurate and precise estimates of vital rates from future field studies. Despite the uncertainty, our models corroborate the evidence for a severe decline in *arcticola* Dunlin, which use the imperiled East Asian-Australasian Flyway. Our models also quantified the importance of annual adult survival in driving population trends. Improving the accuracy, precision, and spatial and temporal coverage of estimates of vital rates, especially annual or seasonal adult survival, would improve demographic model-based estimates of population trends and help direct management to regions or seasons where populations are limited.

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To maintain double-blind review, the citation for the code used in this analysis is provided in the unblinded title page document.

Table 1. Population trends of 6 species of Arctic-breeding shorebirds studied at 16 field sites in Alaska, Canada, and Russia, 2008–2014. Question marks indicate uncertainty in trend estimates, as data were often sparse.

			Current population trend		
Common name	Scientific name	Species code	Previous estimates*	This study†	
American Golden-Plover	*Pluvialis dominica*	AMGP	Uncertain	Uncertain	1.01 (0.47–1.32)
Dunlin‡	*Calidris alpina pacifica*	DUNLpac	Stable	Uncertain	1.19 (0.89–1.35)
	C. a. arcticola	DUNLarc	Strong decline	Strong decline?	0.83 (0.64–1.03)
	C. a. hudsonia	DUNLhud	Stable	Uncertain	1.19 (0.88–1.35)
Semipalmated Sandpiper	*C. pusilla*	SESA	Stable to increase	Uncertain	1.04 (0.84–1.23)
Western Sandpiper	*C. mauri*	WESA	Uncertain	Increase	1.13 (0.97–1.28)
Red-necked Phalarope	*Phalaropus lobatus*	RNPH	Stable to decline?	Uncertain	1.08 (0.77–1.32)
Red Phalarope	*Ph. fulicarius*	REPH	Uncertain	Uncertain	1.15 (0.64–1.37)

* Previous estimates of short-term population trends, generally from years ~2000–2015 (Smith et al. 2020; Andres et al. 2012a, b; U.S. Shorebird Conservation Plan Partnership 2016).

† Numeric values are the population growth rate (λ) given as mean (95% CI).

‡ Three allopatric subspecies of Dunlin (Cramp and Simmons 1983, Miller et al. 2015) were modeled separately in this study.

Table 2. Vital rates used to parameterize the population models for 6 species of shorebirds. Species codes are defined in Table 1. Numbers in parentheses indicate inter-replicate SDs representing uncertainty in parameter estimates; where not given, a constant value was used.

Vital rate	Group	AMGP	DUNLpac	DUNLarc	DUNLhud	SESA	WESA	RNPH	REPH	Inter-annual SD	Source*
Prob. first returning to breeding site	Age 1	-	0.56 (0.10)	0.56 (0.10)	0.56 (0.10)	0.67 (0.10)	0.60 (0.10)	0.89 (0.10)	0.89 (0.10)	0.02	1
	Age 2	-	0.28 (0.10)	0.28 (0.10)	0.28 (0.10)	0.26 (0.10)	0.33 (0.10)	-	-	0.02	1
	Adult†	1.00	0.16 (0.10)	0.16 (0.10)	0.16 (0.10)	0.07 (0.10)	0.07 (0.10)	0.11 (0.10)	0.11 (0.10)	0.02	1
Nesting propensity	All	0.80 (0.10)	0.80 (0.10)	0.80 (0.10)	0.80 (0.10)	0.80 (0.10)	0.80 (0.10)	0.80 (0.10)	0.80 (0.10)	0.20	2
Prob. 4-egg clutch	Initial nests	0.94 (0.02)	0.94 (0.02)	0.96 (0.01)	0.94 (0.02)	0.90 (0.02)	0.81 (0.04)	0.90 (0.03)	0.90 (0.02)	0.02	3
	Renests	0.89 (0.04)	0.35 (0.19)	0.13 (0.06)	0.33 (0.18)	0.78 (0.05)	0.36 (0.08)	0.87 (0.03)	0.72 (0.06)	0.02	3
Prob. 3-egg clutch	Clutches with <4 eggs	0.79 (0.02)	0.92 (0.02)	0.90 (0.02)	0.64 (0.02)	0.84 (0.02)	0.84 (0.02)	0.83 (0.02)	0.85 (0.02)	0.02	3
Prob. 2-egg clutch		0.15 (0.02)	0.08 (0.02)	0.11 (0.02)	0.29 (0.02)	0.14 (0.02)	0.15 (0.02)	0.17 (0.02)	0.10 (0.02)	0.02	3
Prob. 1-egg clutch		0.06 (0.02)	0 (0.02)	0 (0.02)	0.07 (0.02)	0.01 (0.02)	0.02 (0.02)	0.01 (0.02)	0.05 (0.02)	0.02	3
Sex ratio of eggs	All	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0	
Incubation (days)	Initial nests	26 (1)	21 (1)	21 (1)	21 (1)	19 (1)	20 (1)	20 (1)	19 (1)	1.00	3
	Renests	26 (1)	21 (1)	19 (1)	21 (1)	19 (1)	20 (1)	20 (1)	17 (1)	1.00	3
Daily survival rate	Initial nests	0.9770 (0.0056)	0.9870 (0.0052)	0.9778 (0.0052)	0.9825 (0.0048)	0.9826 (0.0037)	0.9776 (0.0050)	0.9806 (0.0043)	0.9792 (0.0045)	0.01	3
	Renests	0.9557 (0.0146)	0.7830 (0.1921)	0.8799 (0.0825)	0.9654 (0.0462)	0.9844 (0.0040)	0.9477 (0.0191)	0.9573 (0.0131)	0.9550 (0.0141)	0.01	3
Prop. eggs hatched	All	0.98 (0.01)	0.90 (0.01)	0.96 (0.01)	0.95 (0.01)	0.94 (0.01)	0.91 (0.01)	0.95 (0.01)	0.97 (0.01)	0.02	1
Prob. renesting	All	0.73 (0.20)	0.73 (0.20)	0.73 (0.20)	0.73 (0.20)	0.73 (0.20)	0.73 (0.20)	0.73 (0.20)	0.73 (0.20)	0.20	4
Time between first clutch and renest (days)	All	14	20	20	20	13	16	15	15	0	1
Chick survival	Initial nests	0.71 (0.07)	0.71 (0.07)	0.71 (0.07)	0.71 (0.07)	0.71 (0.07)	0.71 (0.07)	0.71 (0.07)	0.71 (0.07)	0.10	5
	Renests	0.23 (0.19)	0.23 (0.19)	0.23 (0.19)	0.23 (0.19)	0.23 (0.19)	0.23 (0.19)	0.23 (0.19)	0.23 (0.19)	0.10	5
Juvenile survival	All	0.44 (0.10)	0.44 (0.10)	0.44 (0.10)	0.44 (0.10)	0.44 (0.10)	0.44 (0.10)	0.44 (0.10)	0.44 (0.10)	0.05	6
Adult survival	All	0.72 (0.33)	0.94 (0.01)	0.54 (0.08)	0.95 (0.01)	0.76 (0.09)	0.91 (0.06)	0.78 (0.15)	0.86 (0.24)	0.02	7

* 1) This study (see also Lanctot et al. 2016), 2) Gratto-Trevor (1991), 3) Weiser et al. (2018a), 4) Gates et al. (2013), 5) Hill (2012), 6) Mean of values estimated by Fernandez et al. (2003), Rice et al. (2007), and Warnock et al. (1997), 7) Weiser et al. (2018b).

† Including all ages at which all individuals of a species were expected to return to the breeding grounds; ages 1 and 2 are shown separately only for species where some individuals delayed breeding.

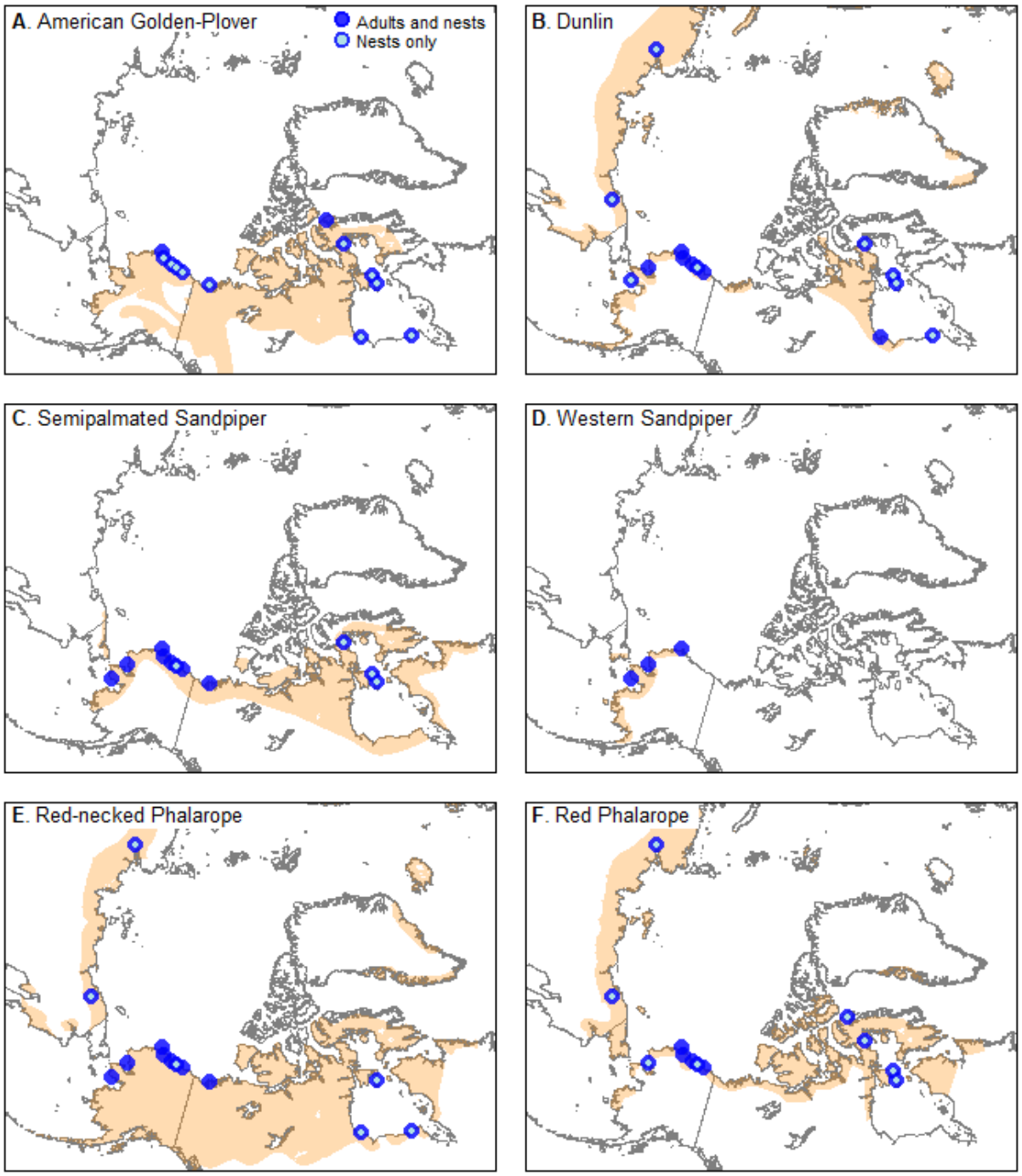

Figure 1. Locations of ASDN study sites (points) and breeding ranges (orange shading) of each species in Arctic Russia, Alaska, and Canada. Point type indicates whether data were collected for only nests or both nests and adult survival. Shapefiles for range maps were provided by BirdLife (BirdLife International and Handbook of the Birds of the World 2018). For each species, study sites are shown if we documented breeding, including some sites outside of the indicated breeding range.

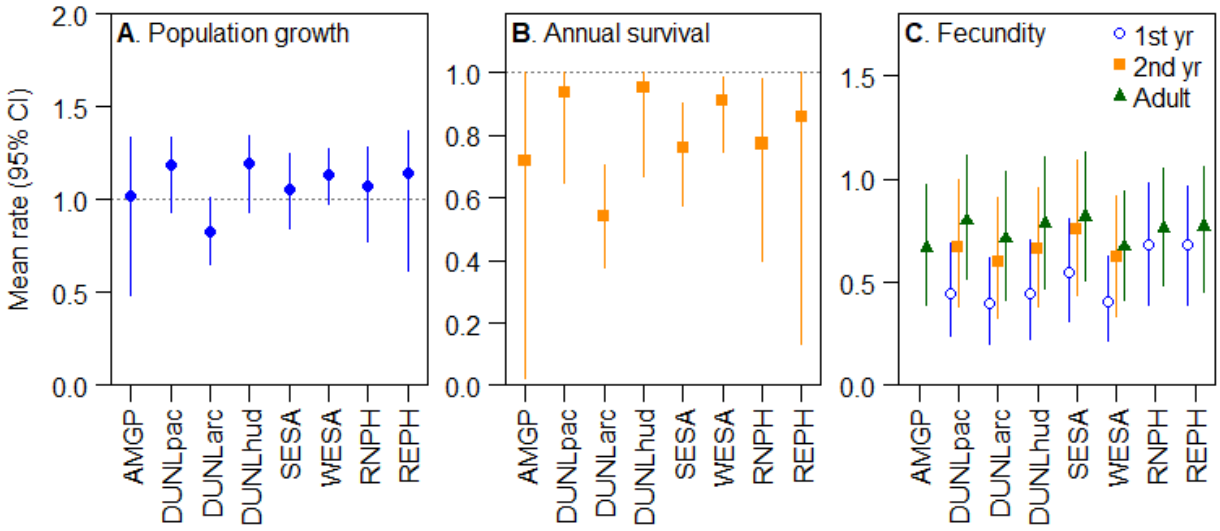

Figure 2. Annual population growth rate (λ, **A**) and transition rates (**B, C**) estimated by the population models for 8 taxa of shorebirds. Error bars show 95% CIs of the simulated values across 1000 replicates. A value of one (dotted line) indicates a stable population (**A**) or the maximum possible rate of annual survival (**B**). Fecundity is the number of male offspring produced per breeding male per year (**C**). Values for subadult age classes (1- and 2-year-olds) are shown only for species where breeding was delayed for some individuals. Species abbreviations are defined in Table 1.

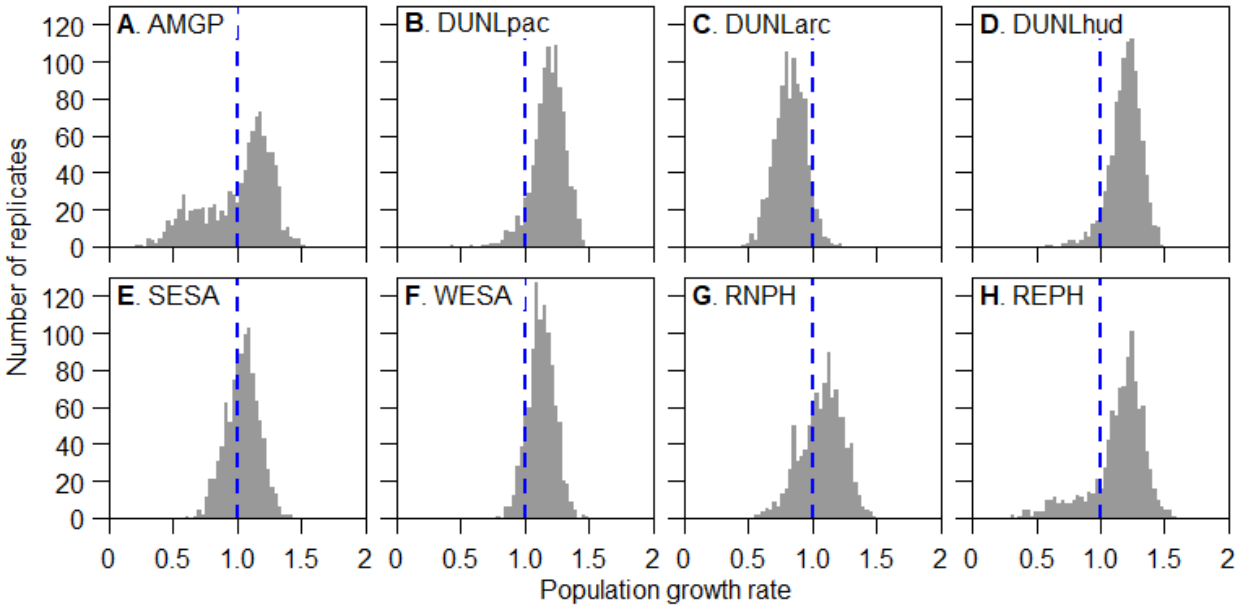

Figure 3. Distributions of simulated population growth rates (λ) across 1000 replicates for each species. A dashed reference line is shown at λ = 1.0 (stable population). Species abbreviations are defined in Table 1.

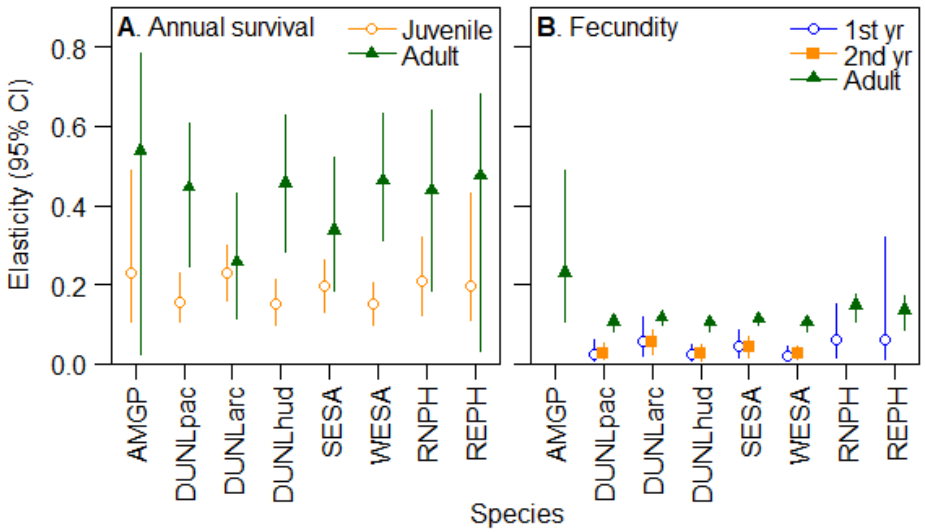

Figure 4. Elasticity of population growth rate to the annual survival (**A**) and overall fecundity (**B**) rates of each shorebird species in each age class. Error bars indicate 95% CIs of the simulated values across 1000 replicates. Species abbreviations are defined in Table 1.

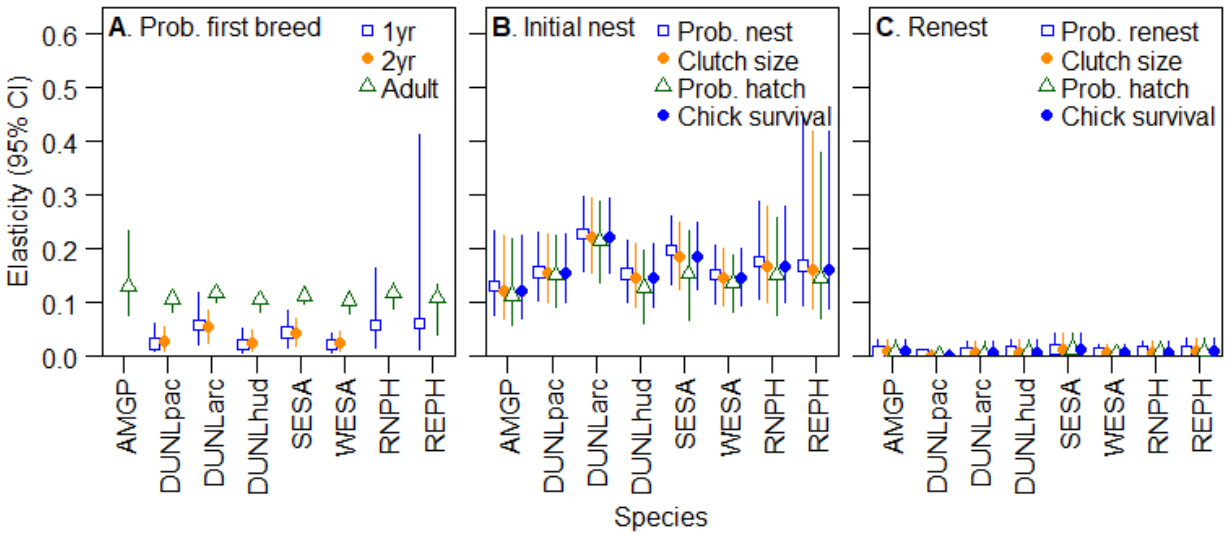

Figure 5. Elasticity of population growth to lower-level vital rates for each species. Panels show breeding propensity (**A**), parameters for the first nest of the season (**B**), and parameters for a renesting attempt (**C**). Error bars indicate 95% CIs of elasticity values across 1000 replicates. Species abbreviations are defined in Table 1.

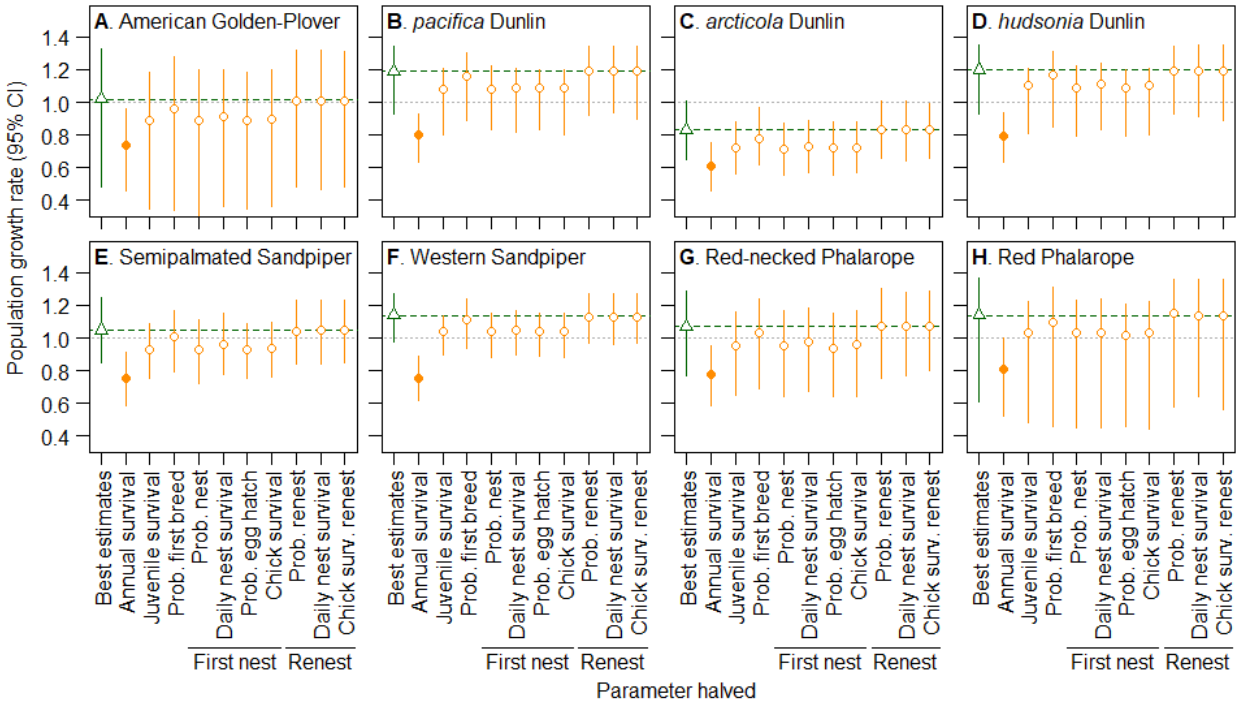

Figure 6. Simulated population growth rate (λ) under scenarios exploring the consequences of halving each vital rate in turn. For each species or subspecies (**A–H**), the first point (open triangle) shows λ estimated by the main population models using the best estimates of vital rates (Table 2) with a dashed horizontal reference line at the mean. All other scenarios, in which the indicated parameter was reduced by half, are shown with circles. A filled circle indicates an estimate of λ that was significantly different from the mean value from the main model. Error bars indicate 95% CIs across 1000 replicates. A horizontal reference line is provided at λ = 1 (stable population; pale gray dotted line).