

Ydenberg, R. C., and L. Hemerik. 2024. Over-summering as a risk effect reducing population growth in a long-distance migrant shorebird. *Avian Conservation and Ecology* 19(2):19. <https://doi.org/10.5751/ACE-02735-190219>

Copyright © 2024 by the author(s). Published here under license by the Resilience Alliance. Open Access. CC-BY 4.0

Research Paper

Over-summering as a risk effect reducing population growth in a long-distance migrant shorebird

Ronald C. Ydenberg¹  and Lia Hemerik² 

¹Centre for Wildlife Ecology, Simon Fraser University, ²Biometris, Wageningen University

ABSTRACT. That anti-predator behavior can have large demographic consequences (called risk effects) is theoretically well-founded and experimentally supported. Here we investigate whether this mechanism could be contributing to population declines reported over recent decades for many shorebird species, especially long-distance migrants. Sandpipers are known to have adjusted behavioral and morphological traits to counter the migratory danger posed by the increase in abundance of an important predator, the Peregrine Falcon (*Falco peregrinus*), ongoing steadily since the mid-1970s. Individuals in some shorebird species skip migration and breeding (over-summer), remaining instead on or near non-breeding areas. Over-summering can be considered an anti-predator tactic because it avoids all exposure to predators during migration, though at the expense of a foregone breeding season. We hypothesize that over-summering by the Semipalmated Sandpiper (*Calidris pusilla*) has increased during recent decades as migration became more dangerous. A stage-structured matrix population model based on survival rates measured in Perú 2011–2017 indicates that Semipalmated Sandpiper population growth is negative at current over-summering levels (adults 19%, yearlings 28%). A substantial proportion of the large reduction in their numbers since 1980 could theoretically be accounted for if over-summering levels rose to this level after ~1980. Though good data are scanty, the historical level of over-summering appears to have been lower. The powerful ecological effects of apex predators have been recognized in many systems, but to date the recovery of falcon populations has not been considered as a possible factor in shorebird declines. Closer scrutiny of this hypothesis is warranted.

Un estivage prolongé comme effet de risque réduisant la croissance de la population d'un limicole migrateur au long cours

RÉSUMÉ. Ce comportement anti-prédateur qui peut avoir d'importantes répercussions démographiques (appelées « effets de risque ») est bien étayé par la théorie et documenté dans la pratique. Dans le cas présent, nous étudions si ce mécanisme pourrait contribuer au déclin de populations constaté ces dernières décennies chez de nombreuses espèces de limicoles, en particulier les migrateurs au long cours. De fait, on sait que les bécasseaux ont ajusté leurs traits comportementaux et morphologiques pour contrer le danger en migration que représente l'augmentation de l'abondance d'un prédateur notable, le Faucon pèlerin (*Falco peregrinus*), qui se poursuit sans relâche depuis le milieu des années 1970. Chez certaines espèces de limicoles, des individus sautent la migration et la reproduction (ils sur-estivent), préférant rester sur des sites de non-reproduction, ou à proximité de ceux-ci. Le sur-estivage peut être considéré comme une stratégie anti-prédatrice car il permet d'éviter toute exposition aux prédateurs durant la migration, bien que cela implique de renoncer à une saison de reproduction. Nous émettons l'hypothèse que le sur-estivage par le Bécasseau semipalmé (*Calidris pusilla*) a augmenté au cours des dernières décennies à mesure que la migration devenait plus risquée. Un modèle de matrice de population structurée par stade basée sur les taux de survie mesurés au Pérou sur la période 2011-2017 indique que la croissance de la population de Bécasseaux semipalmés est négative au niveau actuel de sur-estivage (adultes 19 %, juvéniles 1re année 28 %). Une proportion considérable du fort déclin des effectifs mesuré depuis 1980 pourrait en théorie s'expliquer si les niveaux de sur-estivage avaient augmenté à un niveau aussi important depuis les années 80. Bien que les données fiables soient rares, le niveau historique de sur-estivage semble avoir été plus faible. Les puissants effets écologiques des super-prédateurs ont été reconnus dans bien des systèmes, mais à ce jour, le rétablissement des populations de faucons n'a encore jamais été considéré comme une cause possible du déclin des limicoles. Cette hypothèse mériterait des investigations plus approfondies.

Key Words: *matrix population model; over-summering; population decline; population dynamics*

INTRODUCTION

Individuals in some species of long-distance migrant shorebirds are well-known to spend the (boreal) summer on low-latitude non-breeding areas rather than migrating to the Arctic to breed (termed “over-summering”). Most explanations invoke the idea that over-summering occurs when migration and/or breeding is unlikely to succeed (Summers et al. 1995). Factors such as parasite infection (McNeil et al. 1994, Wille and Klaassen 2022), poor condition, sterility, injury or illness (Wetmore 1927), sexual

immaturity (Eisenmann 1951, Soto-Montoya et al. 2009, Ayala-Perez et al. 2021), inexperience or low foraging prowess (Puttick 1979, Hockey et al. 1998), low-quality plumage (Johnson and Johnson 1983), large carry-over effects (Piersma 2019), and predation danger (Ydenberg et al. 2022) have all been suggested as factors possibly lowering the expectation of breeding success.

Fernández et al. (2004) and O'Hara et al. (2005) were the first to make explicit the idea that shorebird over-summering might

provide a fitness benefit offsetting the cost of foregoing a breeding opportunity. Over-summering birds have higher survival than migrants (Tavera et al. 2020), may be able to avoid carry-over effects contingent on migration (e.g., by allowing molt at a more advantageous time; O'Hara et al. 2002), and might be able to explore the non-breeding region to develop good local knowledge (Battley et al. 2020). For over-summering to be adaptive, such benefits must exceed the costs by a margin great enough to compensate in fitness terms for the foregone breeding season. Ydenberg et al. (2022) demonstrate that the magnitude of the survival advantage differs between Semipalmated (*Calidris pusilla*) and Western Sandpipers (*C. mauri*) over-summering at Paracas in Perú, as well as between age groups within each species, in a manner consistent with the strikingly different over-summering patterns of these groups. They point out that two large, independent studies both find that the survival of migrant Semipalmated Sandpipers over the 6-month breeding and migration season (April–September) is lower by a remarkable 0.15–0.17 than that of the closely-related Western Sandpiper. They suggest that the low survival of the former is attributable to the introductions after 1975 of Peregrines (*Falco peregrinus*) to the large and important Atlantic coast staging areas used by migrating shorebirds. Scores of Peregrine pairs now breed in the Bay of Fundy (Hope et al. 2020), and along the mid-Atlantic coastal plain (Virginia, Delaware, Maryland, New Jersey; Watts et al. 2015), regions historically free of breeding Peregrines. This rising migratory danger has made over-summering increasingly advantageous.

Semipalmated and Western Sandpipers are well-documented to have made safety-enhancing adjustments to migratory behavior (Ydenberg et al. 2004, Hope et al. 2020), and even wing morphology (Ydenberg et al. 2023) as falcon numbers rose after the mid-1970s (Ydenberg et al. 2017). Over-summering can also be considered a form of anti-predator behavior that avoids all migratory exposure to predators. In a large data set collected in 2011–2017 at Paracas, Perú, Tavera et al. (2020) estimated over-summering by 19% of adult and 28% of yearling Semipalmated Sandpipers. Unfortunately, there is little historical information with which to evaluate the hypothesis that historical levels were lower. In the most detailed account, McNeil (1970, see his Fig. 24) reports low numbers (~10%) of this species present in summer in Venezuela. Two accounts from Brazil report levels of 0% (Barbieri 2007: years 2003–2004) and 8% (Fedrizzi et al. 2004: years 1990–1997). (In each case the value reported is the number over-summering as a percentage of that present in winter. No age-specific details are given.) In Suriname, Haverschmidt (1955) reports that “many” remain throughout the northern summer, and Spaans (1984) reports “mass over-summering” by yearlings, but neither gives any details on ages or numbers. Rice et al. (2007) reports that no Semipalmated Sandpipers over-summer in Puerto Rico. Low levels of over-summering are reported for small (< 50 g) shorebird species in surveys made during the 1970s and 1980s in South Africa (0.6–5.2%; Summers et al. 1995). These data suggest that over-summering was undertaken historically by a small fraction of individuals in small-bodied shorebird species. The reported rates are all lower than that currently measured for Semipalmated Sandpipers at Paracas.

Shorebirds over-summering in the southern hemisphere non-breeding regions do so unseen by studies in the northern hemisphere (which constitute the large majority), with the

consequence that its conservation significance may be overlooked (Martínez-Curci et al. 2020, Navedo and Ruiz 2020, Tavera et al. 2020). For migrant species, events at one location and life history stage are inextricably linked to others (Sheehy et al. 2010), and intermittent breeding should be explicitly considered in demographic models, especially in declining populations (Lee et al. 2017, Öst et al. 2018). Nor has over-summering been the subject of much theoretical analysis (Shaw and Levin 2011, 2013). Here we develop a matrix population model to investigate the effect of over-summering on shorebird demography. Our intent is to investigate the degree to which the hypothesized recent increase in over-summering might be able to have contributed to the large decline (~80%) measured in Semipalmated Sandpipers since 1980 (Morrison et al. 2012).

METHODS

Model description

The model developed here simulates a population of Semipalmated Sandpipers, based on parameters measured at Paracas, Perú (Tavera 2020, Tavera et al. 2020), a non-breeding location. Several thousand Semipalmated Sandpipers are present at Paracas, including birds from eastern, central, and western breeding populations (Tavera et al. 2016). Our approach was inspired by Hitchcock and Gratto-Trevor's (1997) stage-structured model of a breeding population of Semipalmated Sandpipers at La Pérouse Bay in Arctic Canada, which accurately simulated the decline censused at that location from 1983 to 1993.

The simulated population is enumerated annually on 1 October, at the start of the annual cycle. This runs October to September, is divided into “winter” (alternatively “non-breeding”; October–March), and “summer” (alternatively “breeding”; April–September) seasons. Individuals are classified as “juveniles” during the summer of their birth, and are censused as such at the start of the subsequent annual cycle (at ~4 months of age). The juvenile classification extends through the non-breeding (October–March) season, until they by definition become “yearlings” on April 1 (at ~10 months of age). The yearling designation distinguishes them from the new generation of juveniles that will be born during the coming summer. In much shorebird literature these age classes are together termed juveniles or immatures, but are distinguished here because they face rather different circumstances. Yearlings by definition become “adults” at the start of their second non-breeding season (i.e., at ~16 months of age) and are censused as such. Adults that are older were born three or more breeding seasons earlier, and in each intervening summer either migrated to the Arctic, or over-summered on the non-breeding area.

The numbers of juveniles, over-summering adults, and migrating adults censused at the start of annual cycle t are represented by $J(t)$, $A_o(t)$, and $A_m(t)$, respectively. The sub-scripts “o” and “m” refer to “over-summering” and “migration” during the preceding summer. The population's demography is modeled with the matrix equation

$$\begin{pmatrix} J(t+1) \\ A_o(t+1) \\ A_m(t+1) \end{pmatrix} = M \begin{pmatrix} J(t) \\ A_o(t) \\ A_m(t) \end{pmatrix} \quad (1)$$

Where

$$M = \begin{pmatrix} S_J F_Y \sqrt{S_{Ym}} (1 - p_{Yo}) S_{JN} & S_J F_A \sqrt{S_{Am}} (1 - p_{Ao}) S_{AN} & S_J F_A \sqrt{S_{Am}} (1 - p_{Ao}) S_{AN} \\ S_{Yo} P_{Yo} S_{JN} & S_{Ao} P_{Ao} S_{AN} & S_{Ao} P_{Ao} S_{AN} \\ S_{Ym} (1 - p_{Yo}) S_{JN} & S_{Am} (1 - p_{Ao}) S_{AN} & S_{Am} (1 - p_{Ao}) S_{AN} \end{pmatrix} \quad (2)$$

The derivation of matrix M is detailed in Appendix 1. Matrix equation (1) incorporates winter and summer survival probabilities, modified by the probabilities of over-summering or migrating, and reproduction by adults and yearlings. With terms in matrix M numbered as follows for ease of reference,

$$\begin{pmatrix} J(t+1) \\ A_o(t+1) \\ A_m(t+1) \end{pmatrix} = \begin{pmatrix} (3) & (6) & (9) \\ (1) & (4) & (7) \\ (2) & (5) & (8) \end{pmatrix} \begin{pmatrix} J(t) \\ A_o(t) \\ A_m(t) \end{pmatrix} \quad (3)$$

Equation (2) can be understood with the aid of the transition diagram (Fig. 1). Eggs are hatched in June on Arctic breeding grounds. (Note that the annual cycle begins 1 October, so the juveniles in the census of year t were born in year $t - 1$.) The parameter S_J represents the proportion of eggs hatched that survive the hatchling period and southward migration, to be censused as $J(t)$ juveniles in October. Juveniles survive the subsequent 6-month non-breeding period (October–March) with probability S_{JN} by definition becoming yearlings at the transition to the summer season on 1 April.

Yearlings decide at this point whether they will migrate or over-summer. A proportion over-summer (P_{Yo}), surviving until the start of the following non-breeding season with probability S_{Yo} . These by definition become adults on 1 October and are tallied as part of the cohort $A_o(t+1)$ (term 1 in eqn 3). The remaining portion $(1 - P_{Yo})$ migrate and survive the migratory round-trip with probability S_{Ym} . (Survival in each direction is assumed to be $\sqrt{S_{Ym}}$, the square root of round-trip survival.) Each surviving northward migrant produces F_Y (female) hatchlings (term 3 in eqn 3). Yearlings that survive the entire migration graduate to adulthood at the end of the breeding season and are tallied as part of the adult cohort $A_m(t+1)$, at the start of the next annual cycle (term 2 in eqn 3).

Yearlings and adults that over-summered in annual cycle t survive from October until April of annual cycle $t + 1$ with probability S_{AN} . A portion of these (P_{Ao}) over-summer in annual cycle $t + 1$, survive the (boreal) summer with probability S_{Ao} , and are tallied as part of the adult cohort A_o (term 4) in October. Those that did not over-summer (part $1 - P_{Ao}$) migrate, survive the north- and southward migrations and breeding period in the Arctic with probability S_{Am} , and are tallied as part of the adult cohort A_m in October (term 5). Survival of the northward migration is $\sqrt{S_{Am}}$, and surviving adults each produce F_A female hatchlings. These migrate to Paracas and are censused in October as juveniles, having survived the hatchling period and the southward migration from the Arctic with probability S_J (term 6).

Yearlings and adults that migrated and bred in annual cycle t survive the non-breeding period of annual cycle $t + 1$ with probability S_{AN} . A portion (P_{Ao}) over-summer, survive the summer period with probability S_{Ao} , and join the adult cohort A_o (term 7) in October. Those that did not over-summer (portion $1 -$

P_{Ao}) migrate, survive the round-trip migration and breeding period in the Arctic with probability S_{Am} , and join A_m in October (term 8). Adult migrants survive the northward trip to the Arctic with probability $\sqrt{S_{Am}}$, each producing F_A female offspring who are censused in October as juveniles, having survived the hatchling period and the southward migration from the Arctic with probability (S_J) (term 9).

Model analysis

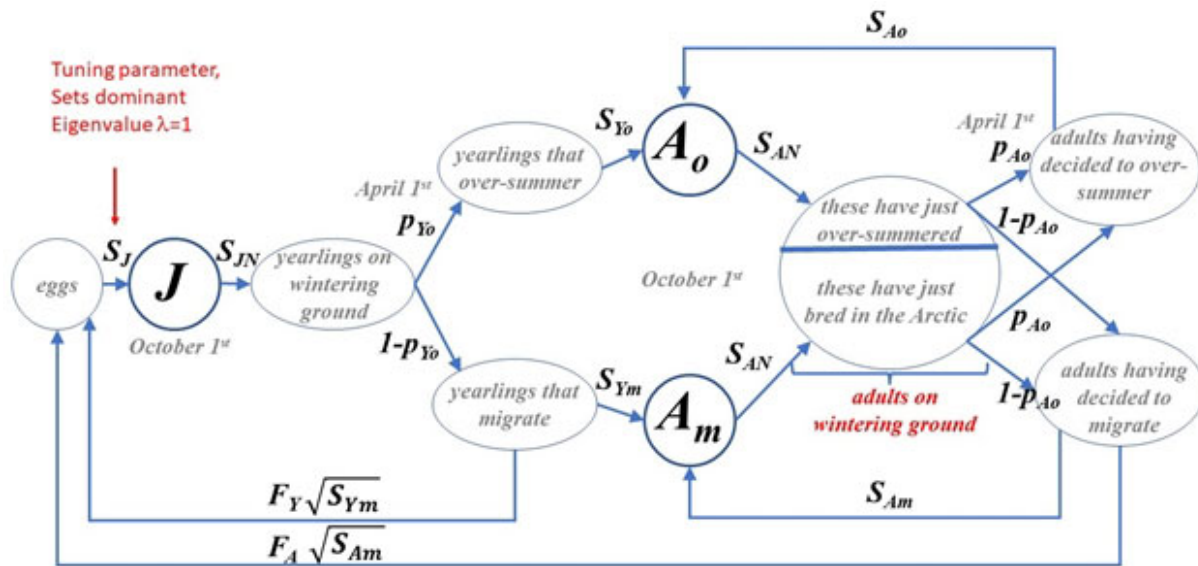
Survival parameters were estimated in a population of Semipalmated Sandpipers at Paracas, Perú. Monthly visits of about a week were made in 2011 to 2015 to Paracas, during which 1963 Semipalmated Sandpipers were captured and marked, and 3229 re-sightings made. The analysis of these data is described in Tavera et al. (2020), and parameter value estimates are summarized in Table 1. The exception is the parameter S_J (survival from hatch through the initial southward migration), the value of which is unknown. Shorebird clutch size and hatching success have been measured in many field studies, but hatchlings are precocial and leave the nest soon after hatch, moving to feeding areas on the tundra. This makes it difficult to measure their progression through the post-hatching and migratory periods that precede their arrival at non-breeding areas. This entire process is compressed for model purposes into a single parameter, S_J , used in our analyses as a tuning parameter (see below).

Population trajectories were simulated using matrix equation 1. For numerical calculations each model run was initiated with 500 individuals in each age/migration class and run for 200 generations. A stable age distribution was quickly attained (< 10 generations). Parameters were numerically evaluated over generations 101–200. The population growth factor and age distribution calculated numerically closely match the eigenvector and eigenvalues derived analytically using the characteristic equation reported in Appendix 2.

To evaluate the impact of over-summering on population growth we used four “baseline” cases (Table 2) with assumed historical over-summering rates ranging from low (Baseline Case 1: adult 1%, yearling 5%) to high (Baseline Case 4: adult 10%, yearling 20%). For each case we adjusted (“tuned”) S_J to set λ equal to 1.000, in effect assuming that the historical rate of over-summering supported a stable population. In subsequent simulations, the assumed historical over-summering rates were raised to that measured at Paracas (yearlings 0.28, adults 0.19), the value of λ re-evaluated, and the change (%) in population size that would be observed over 20, 30, 40, and 50 years calculated. We also report the number of years required to reduce the population size by 50%.

It is plausible that the value of the parameter S_J (the probability that a chick hatched in the Arctic survives until arrival on non-breeding areas after southward migration) declined after Peregrines were introduced to staging sites. We modelled a decline in the value of S_J by reducing it in 0.01 increments, using Baseline Case 4 (adult/yearling over-summering 0.10/0.20), as well as the currently-measured over-summering rates. At each value of S_J we calculated the consequent value of λ , the change (%) in population size that would be observed over 20, 30, 40 and 50 years, and the number of years required for population size to decline by 50%.

Fig. 1. Transition diagram for the modelled population. The state variables given in bold represent the number of juveniles $J(t)$, the number of over-summering adults $A_o(t)$, and the number of migrating adults $A_m(t)$ enumerated in the 1 October census. All parameters and their values are in Table 1. The decision to migrate and/or to over-summer is made 1 April. Survival during northward migration to the Arctic is denoted as $\sqrt{S_{Ym}}$ for yearlings and $\sqrt{S_{Am}}$ for adults. The parameter S_J is adjusted to set the population growth rate λ to 1.0000, enabling estimates of the impact of over-summering.



To assess the effects of stochasticity, we drew for each parameter a value from a uniform distribution (range $\pm 5\%$, $\pm 10\%$, $\pm 20\%$, or $\pm 50\%$) centered on the value reported in Table 1. We entered these into eqn 1, ran the simulation for 100 years, and determined the population growth factor. We report the mean and distribution of population growth factors of 1000 such simulations.

RESULTS

The estimated value, 95% confidence interval, elasticity, and sensitivity of each parameter are reported in Table 1. As expected, the population growth factor (λ) is positively related to all survival parameters, and negatively related to the rate of over-summering. Also as expected, λ is more sensitive to adult than to yearling parameter values, and more sensitive to the survival of migrants than of over-summering birds. The population growth factor λ is most sensitive to changes in adult non-breeding survival.

To assess the impact of an increase in over-summering rate the value of survival from hatch until arrival at non-breeding was tuned to set λ to 1.000 in each of the four baseline historical cases. The tuning value varies with the over-summering rate, ranging from 0.4743 in the lowest (Baseline Case 1) to 0.5017 in the highest (Baseline Case 4; see Table 2). When the level of over-summering is raised from the presumed historical level to that currently measured at Paracas (adults 19%; yearlings 28%), the population growth factor λ falls below 1.000. The impact is surprisingly large. Even for Baseline Case 4 (the highest historical level of over-summering), the population size over 20–50 years would be reduced by 29.3–58.0%, and only 41 years would be required to

reduce the population size by half. The impact is even greater for Baseline Case 1 (the lowest historical level of over-summering): the population size over 20–50 years would be reduced by 49.5–81.8%, and only 21 years would be required to reduce population size by half. Baseline Cases 2 and 3 lie in between these values.

The sensitivity of the population growth factor to the value of S_J is 0.313 (Table 1). With the over-summering rate set to that in Baseline Case 4 (adult/yearling over-summering 0.10/0.20) the value of S_J required to tune λ to 1.000 is 0.5017 (Table 3). As S_J is lowered in 0.01 increments from 0.5100 to 0.4700 (i.e., beginning just above 0.5017), λ declines from 1.005 to 0.979. At the lowest level of S_J the population size falls by 34.3–65.0% over 10–50 years. The effect is stronger if based on the over-summering rate currently measured at Paracas (adult/yearling over-summering 0.19/0.28; Table 3). The value of S_J tuning λ to 1.000 is 0.5307 (which would make population growth strongly positive in any of the other scenarios modeled here). As S_J is dropped from 0.5400 to 0.4700 (0.01 increments) λ declines from 1.0055 to 0.9639, and the population declines over 10–50 years ranges from 52.1% to 84.1%. In the deterministic simulations (Table 2), the time required to halve the population size when the level of over-summering is raised from the presumed historical level to that currently measured at Paracas ranges from 21 to 41 years (Baseline Cases 1–4, respectively).

The effect of adding stochasticity is summarized in Table 4. With the value of S_J set to that tuning λ to 1.000, and other parameter values randomly drawn from uniform distributions ($\pm 5\%$, $\pm 10\%$, $\pm 20\%$, $\pm 50\%$) about the measured value reported in Table 1, the median durations for population size to decrease by half are

Table 1. Symbols, definitions, and values of model parameters. The value for S_j is that tuning the dominant eigenvalue to 1.000 at the rate of over-summering currently measured at Paracas. Sensitivity and elasticity values obtained using this value of the tuning parameter. Sources of other parameter values are given in the footnotes below.

Symbol	Description	Value	95% CI	Sensitivity	Elasticity
S_j	survival from hatch until arrival at non-breeding area	0.5307	n/a	0.589	0.313
S_{jN}^j	juvenile non-breeding survival (Oct-Mar)	0.829	0.643–0.929	0.377	0.313
S_{yo}^j	survival of over-summering yearlings (Apr-Oct)	0.810	0.701–0.885	0.097	0.078
S_{ym}^j	survival of migrant yearlings (Apr-Oct)	0.670	0.54–0.79	0.299	0.2
S_{jN}^a	adult non-breeding survival (Oct - Mar)	0.894	0.838–0.945	0.769	0.687
S_{yo}^a	survival of over-summering adults (Apr-Oct)	0.894	0.839–0.932	0.117	0.104
S_{am}^a	survival of migrant adults (Apr-Oct)	0.679	0.625–0.728	0.678	0.46
P_{yo}^j	probability that a yearling over-summerers	0.28	0.23–0.33	-0.046	-0.013
P_{yo}^a	probability that an adult over-summerers	0.19	0.18–0.21	-0.17	-0.032
F_y^{Ao}	female eggs hatched by a yearling	0.835	not reported	0.081	0.068
F_a^{Ao}	female eggs hatched by an adult	1.5	not reported	0.163	0.245

The parameter S_j (the survival of offspring from hatch until arrival at the non-breeding area) is used in the model to tune the value of λ to 1.000. It was not measured and uncertainty could not be estimated.

Survival rate estimates are based on 3229 re-sightings of 1963 marked semipalmated sandpipers made at Paracas, Péru, 2011–2015, and reported in Table 3 of Tavera et al. (2020).

Over-summering rates are the complements of the migration rates of yearling and adult semipalmated sandpipers made at Paracas 2011–2015, reported in Tavera et al. (2020).

Breeding parameters (the number of female eggs hatched) were obtained from Gratto et al. (1983). Based on 213 nests measured 1980–1982 at La Pèrouse Bay, Manitoba, the mean adult clutch size is 3.9 and hatching success 77%. The expected number of hatched eggs is 3.00, of which half are assumed female. Yearling clutch size is 3.8 and hatching success 44%, making the expected number of hatched eggs 1.67, of which half are assumed female. Error terms were not reported.

Table 2. An increase in the rate of over-summering from presumed historical baselines to that currently measured at Paracas (yearling/adult 0.28/0.19) lowers the population growth rate of Semipalmated Sandpipers (*Calidris pusilla*). The impact is greater when the assumed historical level is lower (Case 1 lowest). Shown are the assumed adult and yearling over-summering rates in each of the four baseline cases; the “tuning” value of S_j is that required for each baseline case to set $\lambda = 1.000$. Shown is the value of λ that results when over-summering is raised from the baseline to the current level (adult/yearling = 0.19/0.28); and the consequent change in population size at that rate of growth over 20, 30, 40, and 50 year spans. The column labelled “time to 50%” is the number of years required for a population decline exceeding 50%.

Case	Over-summering, presumed historical baseline		S_j	λ	% change					time to 50%
	adult/yrig				20y	30y	40y	50y	50%	
1	0.01/0.05		0.4743	0.966	-49.5	-64.1	-74.5	-81.8	21	
2	0.05/0.10		0.4848	0.973	-42.5	-56.4	-66.9	-74.9	26	
3	0.075/0.15		0.4930	0.978	-36.4	-49.3	-59.5	-67.7	31	
4	0.10/0.20		0.5017	0.983	-29.3	-40.5	-50.0	-58.0	41	

127.9 y ($\pm 5\%$), 87.5 y ($\pm 10\%$), 46.5 y ($\pm 20\%$), and 11.4 y ($\pm 50\%$). These differ from each other because of the unequal effects of variation above and below the median (known as Jensen’s inequality). The 50% reduction time shortens with higher stochasticity because of the higher incidence of simulated populations going to extinction within the 100 year run. In all cases the resultant rate of growth is below 1.0.

DISCUSSION

The model presented here calculates the demographic impact of over-summering on the growth potential of a shorebird population. The basic finding that population growth rate is lowered by raising the level of over-summering was expected, but the magnitude of this effect is startling. If, for example, the over-

summering rate of Semipalmated Sandpipers recently measured at Paracas (Tavera et al. 2020; yearlings 28%, adults 19%) had risen from a historical rate of 10% for yearlings and 5% for adults, the population growth factor (λ) would have fallen to 0.973. Assuming that the population had been stable at the historical level, it would with the higher over-summering rate be expected to have fallen by 42.5% over 20 years, and by 66.9% over 40 years (Table 2). The impact is even larger if the historical over-summering rate was lower.

We are unable to calculate the current value of λ with complete confidence because we lack an independent estimate of the value of S_j (juvenile survival from hatch to arrival on the non-breeding area). Using the current over-summering rates for yearlings and adults, the tuning value of S_j required to keep the model population size stable is 0.5307. This value would in every other scenario considered here result in strong positive population growth.

Most of the evidence indicates that Semipalmated Sandpipers have undergone a strong decline in numbers since 1980. For example, aerial counts made along the coast of French Guyana (the center of the wintering range) during the non-breeding season in 1980 were repeated in 2008–2010 by the same observer using the same methods (Morrison et al. 2012). These data show a large decline (~80%) in the wintering population. Breeding populations censused in the Arctic (Hitchcock and Gratto-Trevor 1997), trends estimated at migratory staging sites (Bart et al. 2007), and large-scale indices compiled from surveys at many staging sites (Smith et al. 2023) all conclude that the population of Semipalmated Sandpipers has fallen by a large fraction.

The population growth factor estimated by Weiser et al. (2020) based on western Arctic breeding populations of Semipalmated Sandpipers does not differ significantly from 1.0. This could be because their estimates have great uncertainty, or because (in contrast to eastern Arctic breeding populations), those in the western Arctic are not declining (Hicklin and Chardine 2012).

Table 3. The impact of a decline in the value of SJ on λ , as well as the consequent change (%) in population size over 20, 30, 40 and 50 years. The upper portion of the table is calculated using baseline case 4, and the lower portion using the currently measured over-summering rates. The value of SJ tuning λ to 1.000 is 0.5017 for baseline case 4, and 0.5307 at the currently measured rates of over-summering. The value of SJ (slightly) exceeds this tuning value in the top row of each table, and λ thus exceeds 1.00.

Historical baseline Case 4 (adult/yearling) 0.10/0.20		% change			
S_j	λ	20y	30y	40y	50y
0.51	1.0053	11.25	17.34	23.76	30.54
0.50	0.9989	-2.27	-3.38	-4.49	-5.58
0.49	0.9923	-14.26	-20.60	-26.48	-31.92
0.48	0.9858	-24.87	-34.88	-43.56	-51.08
0.47	0.9792	-34.26	-46.70	-56.78	-64.96
Current (adult/yearling) 0.19/0.28		% change			
S_j	λ	20y	30y	40y	50y
0.54	1.0055	11.50	17.74	24.33	31.29
0.53	0.9996	-0.85	-1.27	-1.68	-2.10
0.52	0.9937	-11.92	-17.34	-22.42	-27.19
0.51	0.9878	-21.85	-30.91	-38.92	-46.00
0.50	0.9818	-30.73	-42.35	-52.02	-60.06
0.49	0.9758	-38.67	-51.97	-62.39	-70.55
0.48	0.9699	-45.77	-60.06	-70.59	-78.34
0.47	0.9639	-52.10	-66.85	-77.06	-84.12

Table 4. The impact of stochasticity on the population growth factor (λ). For each of four levels of stochasticity (uniform distributions ranging $\pm 5\%$, $\pm 10\%$, $\pm 20\%$, and $\pm 50\%$ about the mean parameter values reported in Table 1), the lower bound (minimum), median, and upper bound (maximum) of the distribution of dominant eigenvalues resulting from 1000 simulations is reported, as well as the time (years) required to reduce population size by 50%.

Range about mean	minimum	median	maximum	years to 50%
$\pm 5\%$	0.98996	0.99955	1.00894	127.9
$\pm 10\%$	0.9807	0.9977	1.0162	87.5
$\pm 20\%$	0.9556	0.9898	1.0268	46.5
$\pm 50\%$	0.8593	0.9429	1.0315	11.1

Comparing Weiser et al.'s (2020) simulations (see their Fig. 3E) with the values of λ simulated here (Table 4) suggests that the former have greater uncertainty. Their values of λ range from about 1.75 to 1.1, while the distribution at the greatest level of uncertainty ($\pm 50\%$) reported in Table 4 has a lower bound of 0.8993 and an upper bound of 0.9429 (median 0.9229). However the methods used to make these estimates differ, and a direct comparison requires caution.

Two conditions are required for the over-summering hypothesis developed here to be able to explain (a portion of) the population decline. First, the current over-summering rate must exceed the historical level. This is consistent with all the historical evidence available, which indicates that older estimates of the over-summering rate are more similar to Baseline Case 1 or 2 rather than to Case 3 or 4. The data are scanty, but the quantitative papers all report over-summering rates of 10% or less.

A second condition is that compensatory demographic feedbacks are absent, or limited in their impact. In principle any of the parameters listed in Table 1 could have changed in a compensatory

fashion. For example, adult non-breeding season survival S_{AN} (sensitivity of S_{AN} in Table 1 is 0.769) could have risen because of density-dependence as population numbers fell. Though the model developed here does not incorporate any of these possibilities, any compensatory changes that may have occurred are incorporated into the parameter estimates in Table 1, which are based on data collected in 2011–2017 (Tavera et al. 2020). If such changes occurred they may have lessened the rate of population decline, but they have not been powerful enough to offset it.

There are sound theoretical reasons to expect the level of over-summering by Semipalmated Sandpipers to have increased. The analyses of Shaw and Levin (2011, 2013) on delayed maturity and intermittent breeding in migrant species associate skipped breeding with low migratory survival. An “environmentally cued condition-based threshold” decision model (Tomkins and Hazel 2007) of shorebird over-summering (Ydenberg, in press) reaches the same conclusion. Two recent and independent estimates both show that the migratory survival of Semipalmated Sandpipers is lower by a large margin than of the closely-related and ecologically similar Western Sandpiper (summarized in Ydenberg et al. 2022).

Over-summering can be considered a form of anti-predator behavior, increasing survival at the expense of reproduction. In an illustrative example, DeWitt et al. (2019) found that porcupines *Erethizon dorsatum* had slower growth, delayed maturity, and reduced fecundity in regions of Wisconsin where populations of their specialist predator, fishers *Pekania pennanti*, had recovered. They hypothesize that as fishers increased in abundance porcupines became more cautious, which increased their survival but lowered the rate of population growth. Analogously, over-summering by Semipalmated Sandpipers improves individual survival but delays maturity and lowers breeding frequency, the joint impact of which lowers the growth rate of the population. Creel et al. (2019) term such population consequences of defensive actions “risk effects.”

Creel et al. (2019) outline how the total impact of predators on a prey population is the sum of direct predation mortality and risk effects. In other systems (reviewed by Preisser et al. 2005), the impact of risk effects on prey populations is several times that of direct predation mortality, suggesting that most of the demographic impact of Peregrines on sandpipers can be expected to arise from risk effects. Direct killing by Peregrines is assumed by the hypothesis outlined in Ydenberg et al. (2022) to contribute to the low migratory survival of Semipalmated Sandpipers, and the model developed here estimates the magnitude of the resultant risk effect. Direct killing on staging sites is described by Dekker et al. (2011), but its extent has not been quantified. Descriptions by Page and Whitacre (1975) and Dekker et al. (2011, 2012) of falcons hunting groups of shorebirds over extended periods indicate that this could be substantial.

The recovery of Peregrine populations in the Americas is ongoing (e.g. Ydenberg et al. 2017) and could be considered a hemispheric analog of the reintroduction of wolves into Yellowstone National Park (see Creel et al. 2019). The extensive popular and scientific literature on wolf re-introduction emphasizes its powerful direct and indirect ecological effects, and active debate and investigation of these effects continues. Peregrine recovery has received far less attention. Most accounts are popular, (justly) depicting this as a heroic rescue from near-extinction. Little scientific attention has been given to its basic ecology (though see Watts et al. 2015), and the possibility of powerful ecological effects such as those we raise here has hardly been considered. Closer scrutiny of the influence of this apex predator is warranted.

Acknowledgments:

We thank Darcy Visscher for discussion on risk effects, and Dov Lank for feedback on the model and many aspects of shorebird biology.

LITERATURE CITED

- Ayala-Perez, V. O., R. Carmona, N. Arce, and Y. V. Albores-Barajas. 2021. Over-summering shorebirds in Guerrero Negro, Baja California Sur, Mexico and the particular case of the Marbled Godwit. *Wader Study* 128:109-116. <https://doi.org/10.18194/ws.00229>
- Barbieri, E. 2007. Seasonal abundance of shorebirds at Aracaju, Sergipe, Brazil. *Wader Study Group Bulletin* 113:40-46.
- Bart, J., S. Brown, B. Harrington, and R. I. G. Morrison. 2007. Survey trends of North American shorebirds: population declines or shifting distributions? *Journal of Avian Biology* 38:73-82. <https://doi.org/10.1111/j.0908-8857.2007.03698.x>
- Battley, P. F., J. R. Conklin, A. M. Parody-Merino, P. A. Langlands, I. Southey, T. Burns, D. S. Melville, R. Schuckard, A. C. Riegen, and M. A. Potter. 2020. Interacting roles of breeding geography and early-life settlement in Godwit migration timing. *Frontiers in Ecology and Evolution* 8:52. <https://doi.org/10.3389/fevo.2020.00052>
- Creel, S., M. Becker, E. Dröge, J. M'soka, W. Matandiko, E. Rosenblatt, T. Mweetwa, H. Mwape, M. Vinks, B. Goodheart, J. Merkle, T. Mukula, D. Smit, C. Sanguinetti, C. Dart, D. Christianson, and P. Schuette. 2019. What explains variation in the strength of behavioral responses to predation risk? A standardized test with large carnivore and ungulate guilds in three ecosystems. *Biological Conservation* 232:164-172. <https://doi.org/10.1016/j.biocon.2019.02.012>
- Dekker, D., I. Dekker, D. Christie, and R. Ydenberg. 2011. Do staging Semipalmated Sandpipers spend the high-tide period in flight over the ocean to avoid falcon attacks along shore? *Waterbirds* 34:195-201. <https://doi.org/10.1675/063.034.0208>
- Dekker, D., M. Out, M. Tabak, and R. Ydenberg. 2012. The effect of kleptoparasitic Bald Eagles and Gyrfalcons on the kill rate of Peregrine Falcons hunting Dunlins wintering in British Columbia. *Condor* 114:290-294. <https://doi.org/10.1525/cond.2012.110110>
- DeWitt, P. D., D. R. Visscher, M. S. Schuler, and R. P. Thiel. 2019. Predation risks suppress lifetime fitness in a wild mammal. *Oikos* 128:790-797. <https://doi.org/10.1111/oik.05935>
- Eisenmann, E. 1951. Northern birds summering in Panama. *Wilson Bulletin* 63:181-185.
- Fedrizzi, C. E., S. Júnior, and M. Larrazábal. 2004. Body mass and acquisition of breeding plumage of wintering *Calidris pusilla* (Linnaeus) (Aves, Scolopacidae) in the coast of Pernambuco, north-eastern Brazil. *Revista Brasileira de Zoologia* 21(Suppl 2):249-252. <https://doi.org/10.1590/S0101-81752004000200013>
- Fernández, G., P. D. O'Hara, and D. B. Lank. 2004. Tropical and subtropical Western Sandpipers (*Calidris mauri*) differ in life history strategies. *Ornitología Neotropical* 15:385-394.
- Gratto, C. L., F. Cooke, and R. I. G. Morrison. 1983. Nesting success of yearling and older breeders in the Semipalmated Sandpiper, *Calidris pusilla*. *Canadian Journal of Zoology* 61:1133-1137. <https://doi.org/10.1139/z83-149>
- Haverschmidt, F. 1955. North American shore birds in Surinam. *Condor* 57:366-368. <https://doi.org/10.2307/1364795>
- Hicklin, P. W., and J. W. Chardine. 2012. The morphometrics of migrant Semipalmated Sandpipers in the bay of Fundy: evidence for declines in the eastern breeding population. *Waterbirds* 35:74-82. <https://doi.org/10.1675/063.035.0108>
- Hitchcock, C. L., and C. Gratto-Trevor. 1997. Diagnosing a shorebird local population declines with a stage-structured population model. *Ecology* 78:522-534. [https://doi.org/10.1890/0012-9658\(1997\)078\[0522:DASLPD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[0522:DASLPD]2.0.CO;2)
- Hockey, P. A. R., J. K. Turpie, and C. R. Velasquez. 1998. What selective pressures have driven the evolution of deferred northward migration by juvenile waders? *Journal of Avian Biology* 29:325-300. <https://doi.org/10.2307/3677117>
- Hope, D. D., D. B. Lank, P. A. Smith, J. Paquet, and R. C. Ydenberg. 2020. Migrant Semipalmated Sandpipers (*Calidris pusilla*) have over four decades steadily shifted towards safer stopover locations. *Frontiers in Ecology and Evolution* 8:3. <https://doi.org/10.3389/fevo.2020.00003>

- Johnson, O. W., and P. M. Johnson. 1983. Plumage-molt-age relationships in “over-summering” and migratory Lesser Golden Plovers. *Condor* 85:406-419. <https://doi.org/10.2307/1367979>
- Lee, A. M., J. M. Reid, and S. R. Beissinger. 2017. Modelling effects of nonbreeders on population growth estimates. *Journal of Animal Ecology* 86:75-87. <https://doi.org/10.1111/1365-2656.12592>
- Martínez-Curci, N. S., J. P. Isacch, V. I. D’Amico, P. Rojas, and G. J. Castresana. 2020. To migrate or not: drivers of over-summering in a long-distance migratory shorebird. *Journal of Avian Biology* 2020:e02401. <https://doi.org/10.1111/jav.02401>
- McNeil, R. 1970. Hivernage et estivage d’oiseaux aquatiques Nord-Américains dans le nord-est du Venezuela (mue, accumulation de graisse, capacité de vol et route de migration). *L’Oiseau et la Revue française d’ornithologie* 40:185-302.
- McNeil, R., M. T. Díaz, and A. Villeneuve. 1994. The mystery of shorebird over-summering: a new hypothesis. *Ardea* 82:143-152.
- Morrison, R. I. G., D. S. Mizrahi, R. K. Ross, O. H. Ottema, N. de Pracontal, and A. Narine. 2012. Dramatic declines of Semipalmated Sandpipers on their major wintering areas in the Guianas, northern South America. *Waterbirds* 35:120-134. <https://doi.org/10.1675/063.035.0112>
- Navedo, J. G., and J. Ruiz. 2020. Over-summering in the southern hemisphere by long-distance migratory shorebirds calls for reappraisal of wetland conservation policies. *Global Ecology and Conservation* 23:e01189. <https://doi.org/10.1016/j.gecco.2020.e01189>
- O’Hara, P. D., G. Fernández, F. Becerril, H. De La Cueva, and D. B. Lank. 2005. Life history varies with migratory distance in western sandpipers *Calidris mauri*. *Journal of Avian Biology* 36:191-202. <https://doi.org/10.1111/j.0908-8857.2005.03368.x>
- O’Hara, P. D., D. B. Lank, and F. S. Delgado. 2002. Is the timing of moult altered by migration? Evidence from a comparison of age and residency classes of Western Sandpipers (*Calidris mauri*) in Panamá. *Ardea* 90:61-70.
- Öst, M., A. Lindén, P. Karell, S. Ramula and M. Kilpi. 2018. To breed or not to breed: drivers of intermittent breeding in a seabird under increasing predation risk and male bias. *Oecologia* 188:129-138. <https://doi.org/10.1007/s00442-018-4176-5>
- Page, G., and D. F. Whitacre. 1975. Raptor predation on wintering shorebirds. *Condor* 77:73-83. <https://doi.org/10.2307/1366760>
- Piersma, T. 2019. Ornithology from the flatlands. *Ardea* 107:115-117. <https://doi.org/10.5253/arde.v107i2.a9>
- Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501-509. <https://doi.org/10.1890/04-0719>
- Puttick, G. M. 1979. Foraging behaviour and activity budgets of Curlew Sandpipers. *Ardea* 67:111-122.
- Rice, S. M., J. A. Collazo, M. W. Alldredge, B. A. Harrington, and A. R. Lewis. 2007. Local annual survival and seasonal residency rates of Semipalmated Sandpipers (*Calidris pusilla*) in Puerto Rico. *Auk* 124:1397-1406. <https://doi.org/10.1093/auk/124.4.1397>
- Shaw, A. K., and S. A. Levin. 2011. To breed or not to breed: a model of partial migration. *Oikos* 120:1871-1879. <https://doi.org/10.1111/j.1600-0706.2011.19443.x>
- Shaw, A. K. and S. A. Levin. 2013. The evolution of intermittent breeding. *Journal of Mathematical Biology* 66:685-703. <https://doi.org/10.1007/s00285-012-0603-0>
- Sheehy, J., C. M. Taylor, K. S. McCann, and D. R. Norris. 2010. Optimal conservation planning for migratory animals: integrating demographic information across seasons. *Conservation Letters* 3:192-202. <https://doi.org/10.1111/j.1755-263X.2010.00100.x>
- Smith, P. A., A. C. Smith, B. Andres, C. M. Francis, B. Harrington, C. Friis, R. I. G. Morrison, J. Paquet, B. Winn, and S. Brown. 2023. Accelerating declines of North America’s shorebirds signal the need for urgent conservation action. *Ornithological Applications* 125:duad003. <https://doi.org/10.1093/ornithapp/duad003>
- Soto-Montoya, E., R. Carmona, M. Gomez, V. Ayala-Perez, N. Arce, and G. D. Danemann. 2009. Oversummering and migrant red knots at Golfo de Santa Clara, Gulf of California, Mexico. *Wader Study Group Bulletin* 116:191-194.
- Spaans, A. L. 1984. Waterbird studies in coastal Suriname: a contribution to wetland conservation in northeastern South America. Annual Report 1983. Netherlands Research Institute for Nature Management Annual Report 1983:63-76.
- Summers, R. W., L. G. Underhill, and R. P. Prys-Jones. 1995. Why do young waders in southern Africa delay their first return migration to the breeding grounds? *Ardea* 83:351-357.
- Tavera, E. A. 2020. Survivorship and life history strategies in relation to migration distance in Western and Semipalmated Sandpipers in Perú. Dissertation. Simon Fraser University, Burnaby, British Columbia, Canada.
- Tavera, E. A., D. B. Lank, and P. M. González. 2016. Effects of migration distance on life history strategies of Western and Semipalmated Sandpipers in Perú. *Journal of Field Ornithology* 87(3):293-308. <https://doi.org/10.1111/jofo.12164>
- Tavera, E. A., G. E. Stauffer, D. B. Lank, and R. C. Ydenberg. 2020. Over-summering juvenile and adult Semipalmated Sandpipers in Perú gain enough survival to compensate for foregone breeding opportunity. *Movement Ecology* 8:42. <https://doi.org/10.1186/s40462-020-00226-6>
- Tomkins, J. L., and W. Hazel. 2007. The status of the conditional evolutionarily stable strategy. *Trends in Ecology and Evolution* 22:522-528. <https://doi.org/10.1016/j.tree.2007.09.002>
- Watts, B. D., K. E. Clark, C. A. Koppie, G. D. Therres, M. A. Byrd, and K. A. Bennett 2015. Establishment and growth of the Peregrine Falcon breeding population within the mid-Atlantic coastal plain. *Journal of Raptor Research* 49:359-366. <https://doi.org/10.3356/rapt-49-04-359-366.1>
- Weiser, E. L., R. B. Lanctot, S. C. Brown, H. R. Gates, J. Bêty, M. L. Boldenow, R. W. Brook, G. S. Brown, W. B. English, S. A. Flemming, S. E. Franks, H. G. Gilchrist, M.-A. Giroux, A. Johnson, S. Kendall, L. V. Kennedy, L. Koloski, E. Kwon, J.-F. Lamarre, D. B. Lank, C. J. Latty, N. Lecomte, J. R. Liebezeit, R. L. McGuire, L. McKinnon, E. Nol, D. Payer, J. Perz, J. Rausch,

M. Robards, S. T. Saalfeld, N. R. Senner, P. A. Smith, M. Soloviev, D. Solovyeva, D. H. Ward, P. F. Woodard, and B. K. Sandercock. 2020. Annual adult survival drives trends in Arctic-breeding shorebirds but knowledge gaps in other vital rates remain. *Condor* 122:duaa026. <https://doi.org/10.1093/condor/duaa026>

Wetmore, A. 1927. Our migrant shorebirds in southern South America. U.S. Department of Agricultural Technology Bulletin 26:1-24.

Wille, M., and M. Klaassen. 2022. Should I stay, should I go, or something in between? The potential for parasite-mediated and age-related differential migration strategies. *Evolutionary Ecology* 37:189-202. <https://doi.org/10.1007/s10682-022-10190-9>

Ydenberg, R. C. In press. Partial migration, over-summering, and intermittent breeding by shorebirds. *American Naturalist*.

Ydenberg, R. C., J. Barrett, D. B. Lank, C. Xu, and M. Faber. 2017. The redistribution of non-breeding Dunlins in response to the post-DDT recovery of falcons. *Oecologia* 183:1101-1110. <https://doi.org/10.1007/s00442-017-3835-2>

Ydenberg, R. C., R. W. Butler, D. B. Lank, B. D. Smith, and J. Ireland. 2004. Western Sandpipers have altered migration tactics as Peregrine Falcon populations have recovered. *Proceedings of the Royal Society B: Biological Sciences* 271:1263-1269. <https://doi.org/10.1098/rspb.2004.2713>

Ydenberg, R. C., G. Fernández, G., E. Ortiz Lopez, and D. B. Lank. 2023. Avian wings can lengthen rather than shorten in response to increased migratory predation danger. *Ecology and Evolution* 13:e10325. <https://doi.org/10.1002/ece3.10325>

Ydenberg, R. C., E. A. Tavera, and D. B. Lank. 2022. Danger, risk and anti-predator behavior in the life history of long-distance migratory sandpipers. *Journal of Avian Biology* 2022(6):e03002. <https://doi.org/10.1111/JAV.03002/v2/response1>



APPENDIX 1

Derivation of matrix equation (1)

In the October 1 census each semipalmated sandpiper is tallied either as a juvenile or as an adult. Adults that over-summered (denoted A_o) or those that made a breeding migration to and from the Arctic (denoted A_m) cannot be distinguished during the census, and are tracked separately in the model because their survival and reproduction differ strongly. Yearlings are not represented directly in the census, as they by definition graduate to adulthood just prior to the census.

Juveniles are born in the Arctic, and make a southward migration to non-breeding areas at ~4 months of age, arriving before the census is made. The juvenile classification extends through the following non-breeding season until April 1 (i.e. until they are ~10 months of age) when they by definition become *yearlings*. They decide on this date either to make a breeding migration to and from the Arctic, or to over-summer on the non-breeding area. During the summer (April 1 – September 30) the model tracks four classes, namely over-summering and migrating yearlings (Y_o, Y_m), and over-summering and migrating adults (A_o, A_m). Yearlings by definition become *adults* at the end of summer, and in the October 1 census are assigned to A_o if they over-summered, and to A_m if they migrated.

The census in year t is denoted by the vector

$$\begin{pmatrix} J(t) \\ A_o(t) \\ A_m(t) \end{pmatrix}$$

The matrix equation is

$$\begin{pmatrix} J(t+1) \\ A_o(t+1) \\ A_m(t+1) \end{pmatrix} = M \begin{pmatrix} J(t) \\ A_o(t) \\ A_m(t) \end{pmatrix} \quad (1)$$

The derivation of the matrix M is as follows. It is the product of four smaller matrices:

$$M = \begin{bmatrix} \textit{breeding plus} \\ \textit{southward survival to} \\ \textit{wintering grounds} \end{bmatrix} \begin{bmatrix} \textit{survival} \\ \textit{during northward} \\ \textit{migration} \end{bmatrix} \begin{bmatrix} \textit{decision to} \\ \textit{migrate} \\ \textit{on April 1} \end{bmatrix} \begin{bmatrix} \textit{survival} \\ \textit{from October 1} \\ \textit{to March 31} \end{bmatrix}$$

or

or

$$M = M_4 M_3 M_2 M_1$$

The matrix M_1 models the winter (October – March) survival of the three census classes (juveniles J , adults that over-summered A_o , adults that migrated A_m):

$$M_1 = \begin{pmatrix} S_{JN} & 0 & 0 \\ 0 & S_{AN} & 0 \\ 0 & 0 & S_{AN} \end{pmatrix}$$

At the end of winter (April 1) juveniles by definition become yearlings, and along with surviving adults are assigned to over-summering and migrating classes with the measured probabilities. Adults over-summer with probability p_{A_o} and migrate with probability $1 - p_{A_o}$. Yearlings over-summer with probability p_{Y_o} , and migrate with probability $1 - p_{Y_o}$. During the summer the model tracks these four classes of individuals in matrix M_2 :

$$M_2 = \begin{pmatrix} \textit{decision on April 1st} \\ p_{Y_o} & 0 & 0 \\ 1 - p_{Y_o} & 0 & 0 \\ 0 & p_{A_o} & p_{A_o} \\ 0 & 1 - p_{A_o} & 1 - p_{A_o} \end{pmatrix}$$

At the start of summer (indexed as $(t + 0.5)$) the numbers of these classes can be calculated as the product of M_1 and M_2 and the fall census

$$\begin{pmatrix} Y_o(t + 0.5) \\ Y_m(t + 0.5) \\ A_o(t + 0.5) \\ A_m(t + 0.5) \end{pmatrix} = M_2 M_1 \begin{pmatrix} J(t) \\ A_o(t) \\ A_m(t) \end{pmatrix}$$

Successful breeding requires that yearling migrants survive the northward migration to the Arctic. This is estimated as the square root of the survival of the return migration (S_{Ym} which was measured). The survival of over-summering yearlings and adults during this half of the summer is estimated as the square root of their (measured) over-summering survival S_{Y_o} and S_{A_o} . This step is denoted in matrix M_3 :

$$M_3 = \begin{matrix} \textit{survival during migration} \\ \begin{pmatrix} \sqrt{S_{Y_o}} & 0 & 0 & 0 \\ 0 & \sqrt{S_{Y_m}} & 0 & 0 \\ 0 & 0 & \sqrt{S_{A_o}} & 0 \\ 0 & 0 & 0 & \sqrt{S_{A_m}} \end{pmatrix} \end{matrix}$$

In the final step, the reproduction of migrants and the survival of both migrants and over-summering birds is accounted. The expected reproduction of migrant yearlings is $F_Y \sqrt{S_{Y_m}}$, and the expected reproduction of adult migrants is $F_A \sqrt{S_{A_m}}$. All birds must survive the second half of the summer, denoted in matrix M_4 :

$$M_4 = \begin{matrix} \textit{breeding and survival till October} \\ \begin{pmatrix} 0 & S_J F_Y & 0 & S_J F_A \\ \sqrt{S_{Y_o}} & 0 & \sqrt{S_{A_o}} & 0 \\ 0 & \sqrt{S_{Y_m}} & 0 & \sqrt{S_{A_m}} \end{pmatrix} \end{matrix}$$

The full matrix M is the product $M_4 M_3 M_2 M_1$ in which all periods are combined:

$$M = \begin{pmatrix} S_J F_Y \sqrt{S_{Y_m}} (1 - p_{Y_o}) S_{JN} & S_J F_A \sqrt{S_{A_m}} (1 - p_{A_o}) S_{AN} & S_J F_A \sqrt{S_{A_m}} (1 - p_{A_o}) S_{AN} \\ S_{Y_o} p_{Y_o} S_{JN} & S_{A_o} p_{A_o} S_{AN} & S_{A_o} p_{A_o} S_{AN} \\ S_{Y_m} (1 - p_{Y_o}) S_{JN} & S_{A_m} (1 - p_{A_o}) S_{AN} & S_{A_m} (1 - p_{A_o}) S_{AN} \end{pmatrix}$$

.....

APPENDIX 2

Denote a 3x3 matrix R as

$$R = \begin{pmatrix} a & d & d \\ b & e & e \\ c & f & f \end{pmatrix}$$

where a, b, c, d, e and f correspond to the terms in (1.b) and (1.c) in the text. The characteristic equation is

$$-\lambda(\lambda^2 - (a + e + f)\lambda + ae + af - bd - cd) = 0$$

and the three eigenvalues are:

$$\lambda = 0$$

$$\left(\lambda = (a + e + f) + \sqrt{(a + e + f)^2 - 4(ae + af - bd - cd)} \right)$$

$$\left(\lambda = (a + e + f) - \sqrt{(a + e + f)^2 - 4(ae + af - bd - cd)} \right)$$