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Matrix Model Analysis of a Coastal Northern California Subpopulation of the Western Snowy Plover (*Charadrius alexandrinus nivosus*)

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Matrix model analysis of a coastal northern California subpopulation of the western snowy plover (*Charadrius alexandrinus nivosus*)

A Thesis Presented

By

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Abstract

Shorebirds are increasingly threatened by introduced predators, invasive grasses, and human disturbance. Matrix models can be used to predict population growth and assess management options. The Pacific coast population of the western snowy plover, *Charadrius alexandrinus nivosus*, is listed as threatened under the Endangered Species Act, largely due to high rates of nest predation. A matrix model for the entire Pacific coast metapopulation of western snowy plovers was published in 1999 by Nur et al., but population growth has not been comprehensively reassessed since, even after development of a recovery plan (USFWS 2007) and extensive management intervention. I built and analyzed a matrix model for one subpopulation of western snowy plovers previously considered a sink habitat—Recovery Unit 2 in northern California, comprising Humboldt, Mendocino, and Del Norte counties. Based on my model, growth rate (λ) is 1.05—countering a previous finding that Recovery Unit 2 is a sink—compared to 1.036 for the Nur et al. (1999) metapopulation model. I found that sensitivities and elasticities for each vital rate were similar between the two models; adult survival had the greatest effect on λ , followed by juvenile survival, and fecundity had the least effect. Even though fecundity was lower for my model than Nur et al.'s (1999), adult survival was higher, which had a larger impact on population growth. In terms of management strategies, predator control, habitat restoration, and restriction of human activity should continue as outlined in the recovery plan, so as to continue the trend of positive growth for the coastal breeding population. Future directions involve performing population viability analyses for other recovery units to reassess the state of western snowy plovers compared to 1999.

Introduction

Shorebirds are known for extensive breeding and wintering ranges, and therefore dependence on networks of beaches, rocky shorelines, and estuaries that tend to be limited in size and distribution (Drut and Buchanan 2000). Due to this dependence on limited habitats, they are threatened by any habitat loss or degradation. Shorebirds, from plovers to oystercatchers to sandpipers, have been witnessing an increase in habitat loss and other threats to their populations in recent years, including increased nest predation by subsidized predators, the introduction of invasive grasses, and human disturbance (Hickey et al. 2003). To assess the severity of these problems and evaluate whether different management options are useful, a variety of demographic approaches could be implemented that measure and predict population growth under different conditions. One of the best tools to make such measurements and assessments is a matrix model.

Matrix Models in Conservation Ecology

Matrix models are a tool, common in conservation ecology, for predicting population growth rate and determining which demographic factors have the greatest effect on that rate. These demographic factors are referred to as vital rates, which quantify survivorship and reproduction for different life history stages—for example, juvenile survivorship, adult survivorship, and fecundity (reproductive rate). Vital rates are the parameters comprising matrix models. Using a matrix model, one can determine the contribution of each age or stage class to the persistence of the population, by characterizing a population's growth rate—generally referred to as lambda, λ —as a function of individual vital rates for each age or stage class (Stearns 1992). A matrix model is an ideal method for studies of population

viability because it allows one to determine a multitude of information about a population. While one could use a series of population counts over time to determine growth rate and to project future population sizes, this method cannot inform the researcher of the relative contribution of different age or stage classes. Matrix models, on the other hand, use age-specific survival and fecundities, and so allow one to determine how particular life history stages and processes contribute to population growth.

After a matrix model has been developed, the stable age distribution and reproductive values can be determined. An age or stage distribution represents the distribution of individuals among the various life stages within a population—the *stable* age distribution represents the convergence on a stable proportion of individuals in each age class once the population reaches exponential growth (Stearns 1992). Reproductive values represent an individual's (or entire age class's) expected contribution to population growth, both through current and future reproduction (Stearns 1992). In addition, sensitivity and elasticity analyses can be performed to determine which vital rates have the largest influence on population growth. Sensitivity (equation a) is the absolute change in lambda given an absolute change in a vital rate, while elasticity (equation b) is the proportional change in lambda given a proportional change in a vital rate (Stearns 1992).

$$(a) \textit{Sensitivity} = \frac{\partial \lambda}{\partial a_{ij}} \qquad (b) \textit{Elasticity} = \frac{\frac{\partial \lambda}{\lambda}}{\frac{\partial a_{ij}}{a_{ij}}}$$

The stable age distribution, reproductive values, sensitivities, and elasticities are useful for informing management decisions about endangered and threatened species because they indicate which life history stage should contain the greatest proportion of individuals, which stages produce the most offspring, and how a change in a single vital rate could

influence population trajectory. Matrix model analysis has been used for a variety of shorebirds (Hitchcock and Gratto-Trevor 1997; Nur et al. 1999). In this thesis, I describe a matrix model I created to analyze a currently threatened population of the western snowy plover (*Charadrius alexandrinus nivosus*).

Study Species: Western Snowy Plover



Figure 1. Western snowy plovers on Morro Strand State Beach, Morro Bay, CA (Photo: Mike Baird, flickr.bairdphotos.com).

The western snowy plover (WSP), *Charadrius alexandrinus nivosus*, is a small shorebird with populations extending from Washington to Baja California (USFWS 2007). The Pacific coast population, defined as the birds that nest adjacent to tidal waters of the Pacific Ocean, was federally listed by the United States Fish and Wildlife Service as threatened under the Endangered Species Act in 1993 (U.S. Dept. of Interior 1993), and remains listed currently (USFWS 2007). Regionally, it is designated as a California Species of Special Concern, it is listed as endangered in Washington, and it is listed as threatened in Oregon (USFWS 2007). This subspecies is threatened particularly because nesting season extends from March through September, which corresponds to the greatest human use of beaches during the year, putting plover breeding sites at higher risk (USFWS 2007). Other

causes of habitat degradation, and therefore threat to the species, include human disturbance along beaches, urban development, introduced beachgrass, and expanding predator populations (Hickey et al. 2003; USFWS 2007). As birds that nest primarily along sandy, dune-backed beaches, the introduction of European beachgrass (*Ammophila arenaria*) is contributing to a loss in dune habitat (Hickey et al. 2003). Natural predators to WSP include falcons, raccoons, coyotes, and owls (Audubon). In addition, human activity has led to greater predation by gulls, crows, ravens, red foxes, coyotes, feral cats, skunks, raccoons, and domestic dogs—generalist species whose populations are subsidized by human disturbance, such as food left on beaches (Audubon; National Park Service). Predation lowers nesting success by causing adults to abandon nests and expend energy that could have been used to maintain nests (Audubon).

Critical habitat for the Pacific coast population has been designated and a recovery plan was published, which separates this population into six subpopulations, referred to as recovery units (USFWS 2007). The recovery plan's criteria for delisting include a target of at least 3000 breeding adults for 10 years for the entire Pacific coast with specifications for each recovery unit, a yearly average productivity of at least 1 fledged chick per male in each recovery unit for 5 consecutive years, and mechanisms developed to maintain the specified population sizes and average productivity. In general, adult survival is considered the vital rate that has the strongest influence on population growth (Hitchcock and Gratto-Trevor 1997, Saether and Bakke 2000, Sandercock 2003; cited in Colwell et al. 2013). However, the recovery plan issued by USFWS focuses largely on increasing reproductive success, which has in some cases been found to decrease adult survival, potentially due to increased energetic stress (Colwell et al. 2013).

Predator management has been identified as a key strategy to recover the Pacific coast population. Particularly in Humboldt County, a suggested management action is ameliorating the effects of predation by ravens to increase plover productivity (Burrell 2010). Thus far, attempts at predator management have had mixed results, particularly the use of nest enclosures. Nest enclosures are defined as mesh fences that surround a snowy plover nest and act to keep away predators, both mammalian and avian (Lauten et al. 2015). Nest enclosures on the Pacific coast have been effective by increasing hatching success; however, they have also resulted in increased adult mortality. In particular, the reproductive success of a population was monitored in Monterey Bay with and without predator management from 1984-1999. The predator management was shown to increase hatching success and number of chicks hatched per male, but not fledging success or number of chicks fledged per male (Neuman et al. 2004). Similarly, plover nests were monitored in coastal Oregon from 1990–2009 to examine the effectiveness of a variety of nest enclosures, as well as removal of invasive grasses; the authors found that these strategies resulted in the short-term benefit of increased nesting success, but they could not determine how improved nest success contributes to population growth (Dinsmore et al. 2014). According to life history theory, a tradeoff exists between reproductive effort and survival (Stearns 1992), so any management efforts to increase productivity might actually compromise population growth. However, Colwell et al. (2013) studied a 10-year plover data set which indicated that nest enclosures would not compromise survival in the following year. The authors warned, however, that such predator management practices may still be detrimental if higher productivity does not result in higher per capita fledging success, or if the practice directly results in adult mortality.

My analysis focused on Recovery Unit 2 (RU2), a coastal northern California subpopulation comprising Humboldt, Del Norte, and Mendocino counties (Colwell et al. 2013) (Figure 2). Out of the 3000 breeding adults needed from the entire Pacific coast population to de-list the species, 150 individuals are needed from RU2 specifically. The recovery plan outlines management activities needed in WSP breeding and wintering locations, such as management of vegetation, restriction of vehicles and pets, and addition of exclosures and fencing when breeding is observed (USFWS 2007). Subsidized predation by the Common Raven (*Corvus corax*) is the most important ecological factor limiting the Humboldt County portion of the population (where the majority of nesting takes place) (Burrell 2010). Previous studies indicate this subpopulation is a sink ($\lambda < 1$) if the rest of the recovery units are considered source populations as part of a greater Pacific coast metapopulation (Eberhart-Phillips et al. 2014; Mullin et al. 2010). Eberhart-Phillips et al. (2014) conducted a population viability analysis by simulating stochastic growth rate of the northern California population. They argue that the WSP recovery objectives do not take source-sink dynamics into account, leading to unrealistic criteria for the sink population so that the entire metapopulation is restricted from being delisted, even if the source populations were to meet delisting requirements. RU2 has been considered a sink due to its reliance on immigration, though Eberhart-Phillips et al. (2014) found that lethal predator removal and reduction of human disturbance may reduce reliance on immigration by increasing permanent resident numbers. However, they were cautionary about use of nest exclosures as a management strategy due to their potential to compromise adult survival. The current status of RU2 WSP, according to a recent report by Feucht et al. (2016), is a population of around 72 breeding adults, roughly halfway to the recovery objective of 150 breeding adults in RU2.

However, it is unclear whether continued increases toward the recovery goals are likely. If RU2 is actually a sink, then immigration from other populations is the only factor allowing increased numbers; this would make it difficult to ever meet the recovery objectives, as Eberhart-Phillips argue. If previous conclusions about the sink status of RU2 are not correct, then this would suggest a greater potential for recovery.

The goals of this paper are to (1) estimate λ for RU2 of the Pacific coast population of WSP, to (2) compare sensitivities and elasticities of the RU2 model to the Nur et al. (1999) model of the entire Pacific coast metapopulation, to (3) determine how uncertainty in vital rates plays a role in model output and predictions, and to (4) in light of these analyses, evaluate the existing USFWS recovery plan for the northern California subpopulation.

Methods

Study Site

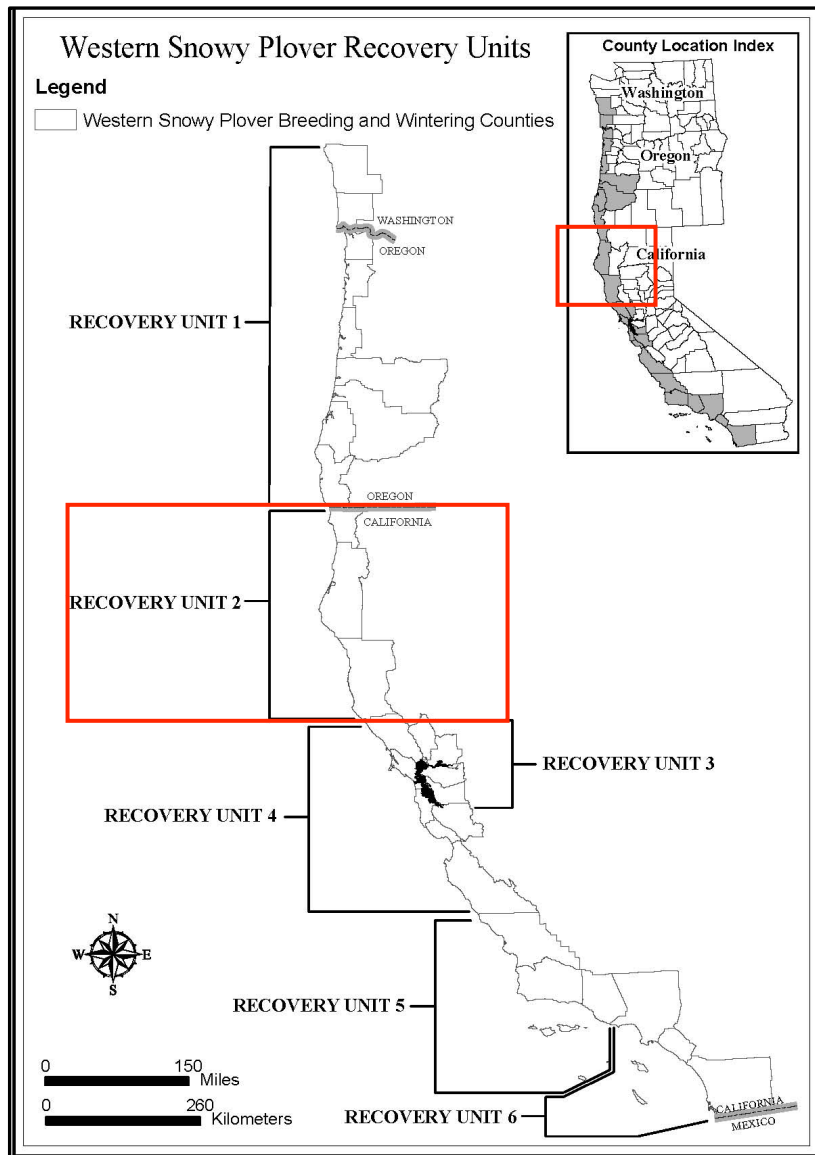


Figure 2. Distribution of WSP recovery units (baseline model was based on RUs 1–6; my model was based on RU2, highlighted above) (USFWS 2007).

Data Collection and Matrix Construction

My matrix follows the construction of the model used in a previous population viability analysis conducted by Nur et al. (1999) (hereafter “baseline model”). This study was

a metapopulation analysis of the entire Pacific coast population of WSP, in which the authors simulated a variety of scenarios and simulations that incorporated dispersal and catastrophic stochasticity. I have included the vital rates used for their deterministic model in Table 1. In this model, a Leslie matrix is divided into age classes from years 1 to 20—this technique seeks to eliminate the probability of adult survival past an age feasible for this species. The model also follows a pre-breeding census and assumes that all individuals one year of age and older are breeders. In effect, the matrix itself is structured by age, while the vital rate inputs are stage-based—specified for juveniles and adults. Following the convention of previous snowy plover studies, the vital rates are presented in terms of males. According to Nur et al. (1999) and Warriner et al. (1986), demographic parameters can be estimated with greater certainty for males than females, and male availability is considered to limit reproductive success since they are responsible for the majority of post-hatching parental care.

Table 1. Vital rates used to produce the baseline matrix from Nur et al. (1999).

| Vital Rate | Value |
|-----------------------|--------------|
| Juvenile Survivorship | 0.5 |
| Fecundity | 1.105 |
| Adult Survivorship | 0.76 |

The vital rates for my matrix came from a variety of sources, including a Colwell et al. (2013) study of a 10-year data set of the northern California population, Feucht et al. (2016), and Nur et al. (1999). The exact values for the vital rates implemented in the model are outlined in Table 2. Juvenile survivorship, which represents survival from fledging to one year (breeding age), was given a value identical to the Nur et al. (1999) model because no

estimates were available in the more recent studies. Fecundity, which represents the number of fledglings per male, was determined using an appendix on plover breeding from Feucht et al. (2016)—by dividing the average number of chicks fledged in RU2 from 2001-2016 by the average number of males in the population for those years. Adult survivorship was determined by extracting points from the apparent survival graph for adults from the Colwell et al. (2013) study. I used WebPlotDigitizer (Rohatgi 2016) to extract the values of the points representing apparent survival of males from 2001–2010, and then I averaged these values for use in my matrix. Table 2 presents fecundity and adult survival with 95% confidence intervals.

Table 2. Vital rates used to produce my age matrix.

| Vital Rate | Value | Source |
|-----------------------|------------------|----------------------|
| Juvenile Survivorship | 0.50 | Nur et al., 1999 |
| Fecundity | 0.85 ± 0.15 | Feucht et al., 2016 |
| Adult Survivorship | 0.84 ± 0.069 | Colwell et al., 2013 |

As the framework by which I structured my own matrix, the baseline model served as a source to which I could compare my resulting lambda values and sensitivity analyses. The results of this study also served as the basis for the recovery criteria proposed by USFWS, so in this respect it is a useful tool to explore how management strategies have affected subpopulations in the past 15 or so years.

Moving across the matrix rows (Figure 3), the adult (1–20) to one-year-old transition is a function of fecundity (chicks fledged per male) multiplied by juvenile survivorship (survival from the point of fledging to one year), multiplied by a 0.5 sex ratio (equation c).

$$(c) \quad \text{Adult to one year transition} = S_j * F * \text{sex ratio}$$

Adult survival is the only other value included in the matrix, accounting for the transition from one year to the next (1–2, 2–3, ..., 19–20). As mentioned above, the matrix is divided by years up to 20 to reduce the possibility of adults surviving past a feasible age in the model.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|----|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| 1 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 | 0.21 |
| 2 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 7 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 | 0 |
| 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 | 0 |
| 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 | 0 |
| 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 | 0 |
| 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.84 | 0 |

Figure 3. Age matrix for Recovery Unit 2 of the western snowy plover.

Calculating Lambda, Sensitivity, and Elasticity

After the matrices were constructed, the dominant eigenvalue and eigenvectors were calculated in order to determine lambda, reproductive values of each age class, and the stable age distribution for the RU2 population. The lambda value from my matrix was compared with lambda from the baseline model to determine how much they differed. Then, to simply compare the sensitivities of the three vital rates in my model to the sensitivities in the baseline model, I ran simulations in R version 3.2.3 in which each rate was altered, one at a time, by a fixed value of 0.01. The corresponding absolute change in lambda was determined, and the sensitivities of each vital rate were compared. I conducted the same comparison with elasticities of the three vital rates in both models by running simulations in which each rate was lowered, one at a time, by one percent. The corresponding proportional change in

lambda was determined, and the elasticities of each vital rate were compared. By doing so, I could determine how my prediction of population growth rate might change given a slightly different value for juvenile or adult survival.

The Full Relationship Between Vital Rates and Lambda

Next, because there was uncertainty surrounding my values both for adult survival and especially juvenile survival, I examined the full relationship between vital rates and lambda. To do so, I ran simulations in R that systematically varied a single vital rate, either juvenile survival or adult survival, from 0.05–1 by increments of 0.05 while holding the other rates constant (see Appendix B for R code). Fecundity was varied from 0.1–2 by increments of 0.1, which is more in line with the potential range of reproductive rate. Based on these simulations, I determined the full impact of each individual vital rate on lambda, since sensitivities and elasticities only indicate the effects of very small changes in vital rates.

Results

Lambda, Reproductive Values, and Stable Age Distribution

The initial vital rates used to construct the WSP RU2 matrix resulted in a positive population growth rate (Table 3).

Table 3. Comparison of lambda for my matrix, the baseline, and a stable population.

| Population | Lambda |
|-------------------|---------------|
| RU2 Model | 1.050 |
| Baseline Model | 1.036 |
| Stable | 1.000 |

Reproductive values for the RU2 model decreased as life stages progressed, in line with the adult-only matrix in which every age class is capable of reproduction—0.26 for one-year-olds, and 0.057 for 20-year-olds (Figure 4).

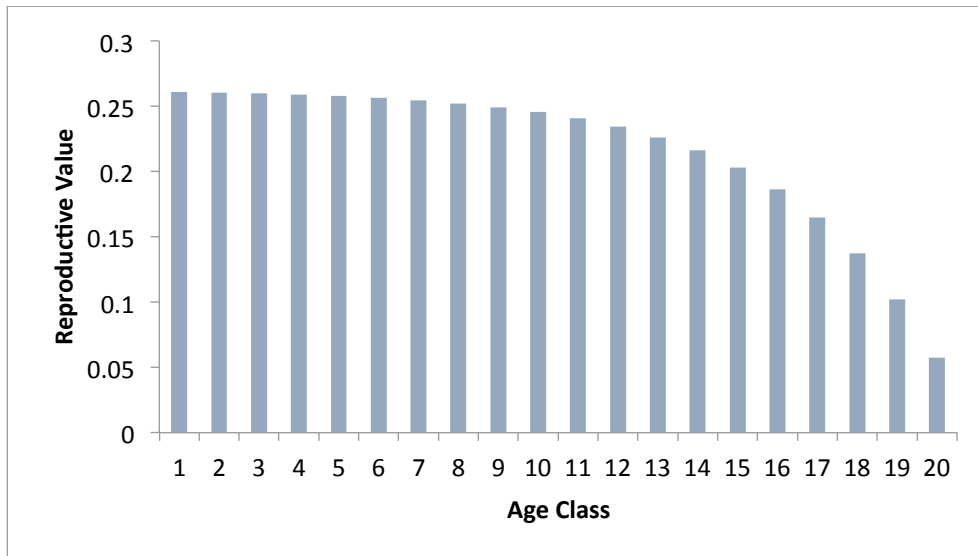


Figure 4. Reproductive values by age class for WSP in RU2 (values shown are absolute values).

The stable age distribution, based on my matrix parameters, indicates one-year-olds as the highest proportion of the population, with proportion decreasing exponentially as adults age (Figure 5).

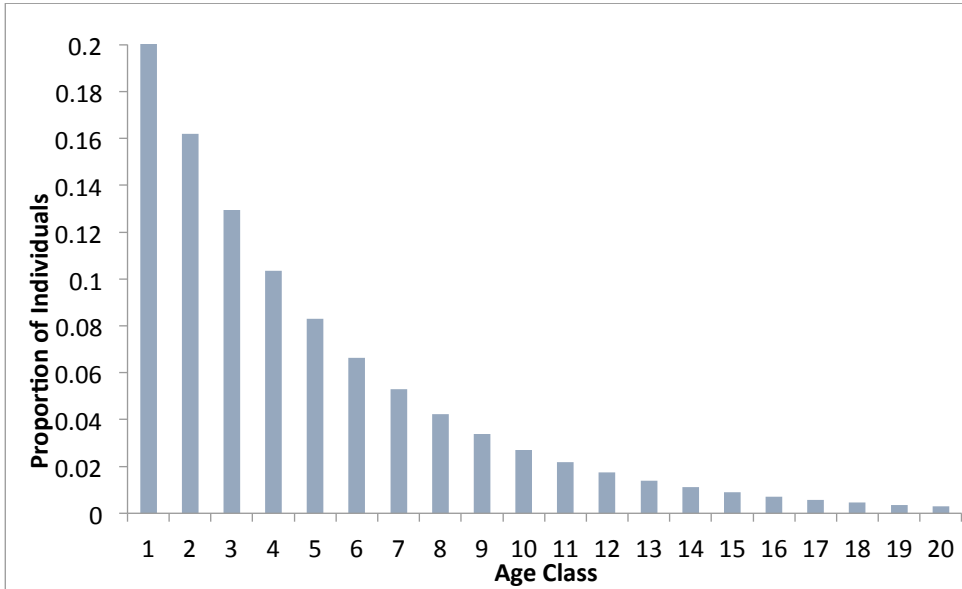


Figure 5. Stable age distribution for WSP RU2 adults.

Sensitivities and Elasticities

The sensitivities followed the same general trend for my model and the baseline model. That is, an absolute change in adult survival produced the largest absolute change in lambda, followed by juvenile survival, and fecundity had the lowest sensitivity (Figures 6, A-1–A-3).

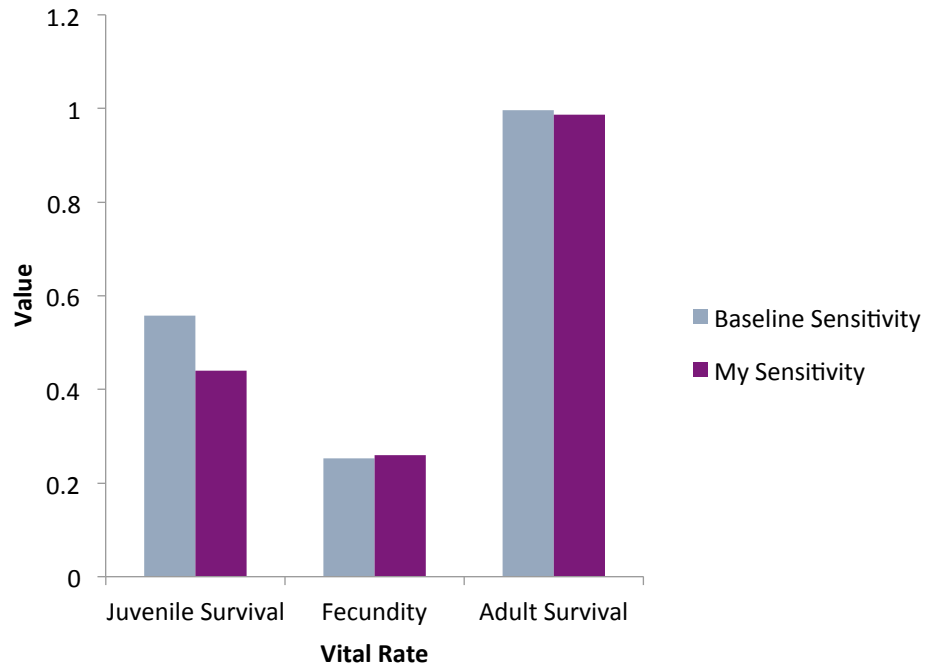


Figure 6. Sensitivities for juvenile survival, fecundity, and adult survival of RU2 compared to the baseline model when each vital rate is altered by 0.01.

In terms of elasticity, juvenile survival and fecundity were identical to each other, both in my model and the baseline, due to the structure of the matrix. Because juvenile survival and fecundity are parameters in the same matrix transitions (adult to one year), a proportional change in this transition means that both vital rates produce the same proportional change in λ . Adult survival had an elasticity roughly three times larger than the other two vital rates, in line with the general understanding that adult survival is the vital rate with the largest influence on population growth (Colwell et al. 2013). In addition, for each vital rate, elasticity was slightly lower in my model than in the baseline (Figures 7, A-4–A-6).

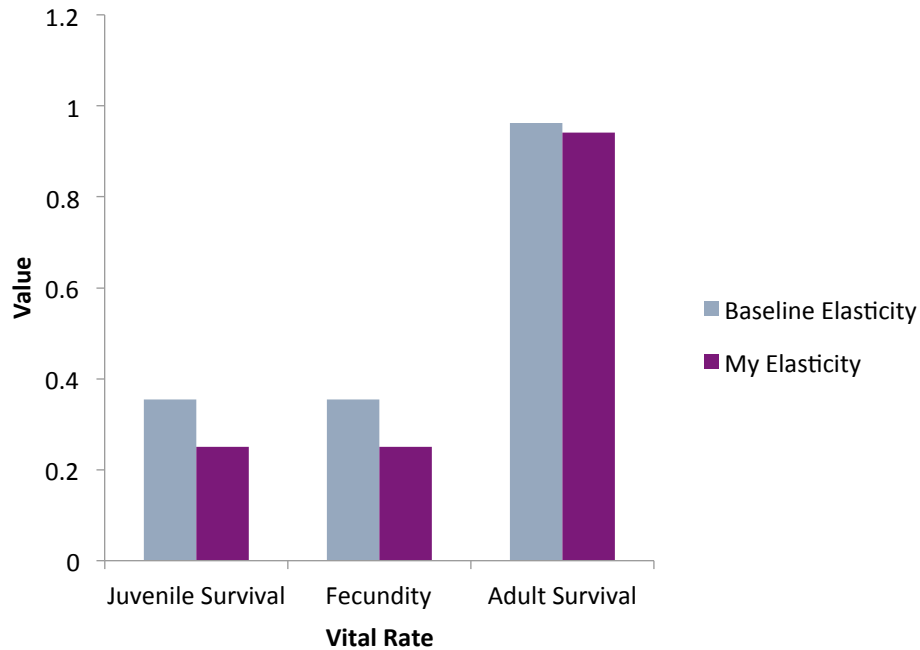


Figure 7. Elasticities for juvenile survival, fecundity, and adult survival of RU2 compared to the baseline model when each vital rate is lowered by one percent.

The Full Relationship Between Vital Rates and Lambda

For my WSP RU2 model, varying juvenile survivorship from 0.05 to 1 resulted in lambda ranging from 0.79 to 1.27. Juvenile survivorship was the most uncertain vital rate in the model because data was not available for my population. While I used 0.5 as juvenile survival for my matrix, this vital rate could decrease to at least 0.39 before lambda would fall below 1 (Figure 8).

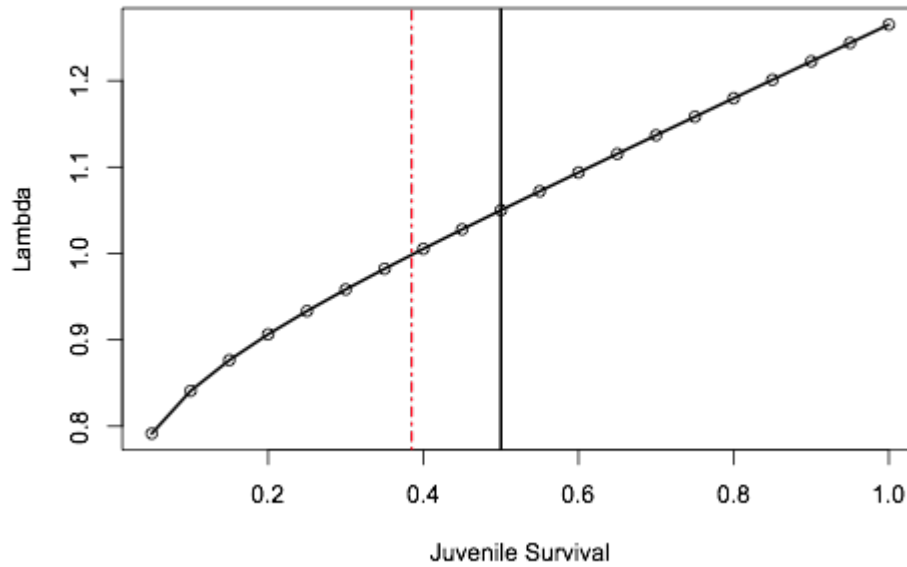


Figure 8. The effect of varying juvenile survival on lambda (black=0.5, the value used in my matrix and the baseline; red=0.39, the lowest value juvenile survival could reach and maintain a stable lambda).

Varying fecundity from 0.1 to 2 resulted in lambda ranging from 0.80 to 1.34. While this vital rate is lower in my model than the baseline, even the value for the lower 95% confidence interval results in a lambda greater than 1 (Figure 9).

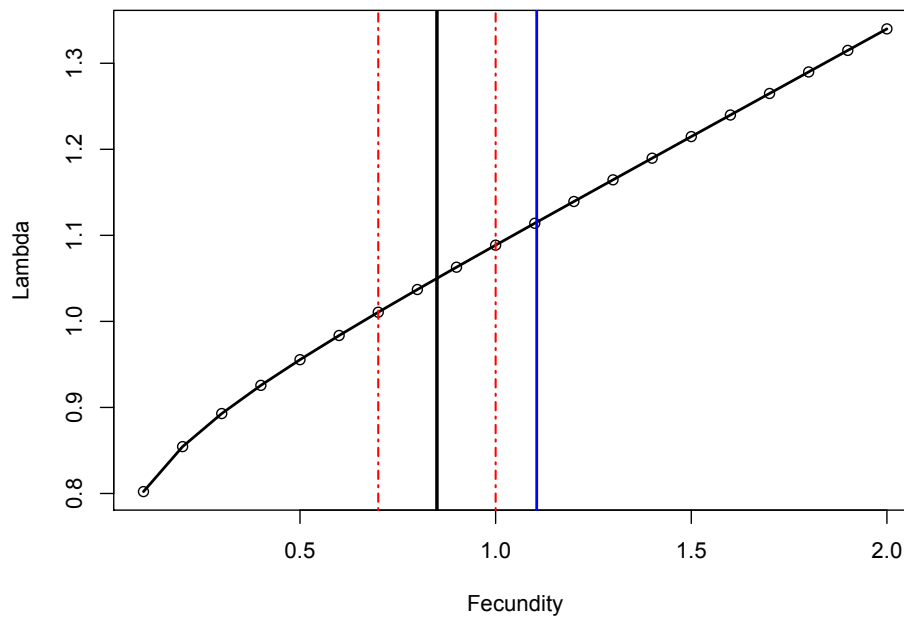


Figure 9. The effect of varying fecundity on lambda (black=0.85, the value used in my matrix; red=95% confidence intervals surrounding the value used in my matrix; blue=1.105, the value used in the baseline matrix).

Varying adult survival from 0.05 to 1 while the other rates were held constant resulted in lambda ranging from 0.26 (when adult survival was 0.05) to 1.21 (when adult survival was 1). The lower 95% CI of adult survival for my matrix was larger than adult survival in the baseline matrix. This low estimate of adult survival resulted in a negative growth rate (lambda=0.98), while the average and high estimate of adult survival resulted in lambda greater than 1 (Figure 10). It is interesting to note that the value for adult survival in the baseline matrix results in a negative growth rate when paired with the other vital rates from the RU2 model, whereas the same value for adult survival resulted in positive growth when paired with the other vital rates from the baseline matrix.

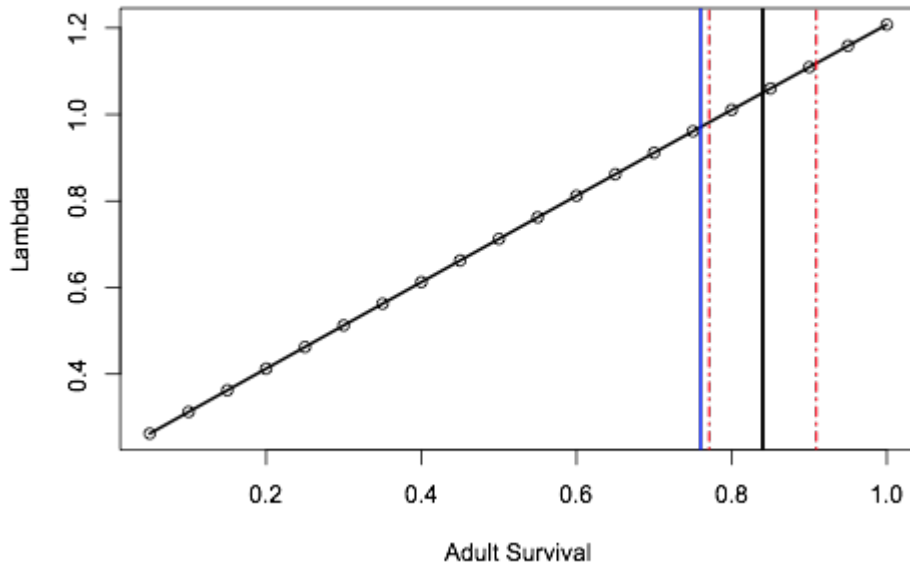


Figure 10. The effect of varying adult survival on lambda (black=0.84, the value used in my matrix; red=95% confidence intervals surrounding the value used in my matrix; blue=0.76, the value used in the baseline matrix).

Discussion

Lambda, Reproductive Values, and Stable Age Distribution

The projected population growth rate of WSP in RU2 was estimated at 1.05, so the population is slightly increasing. In fact, my model output counters previous findings that RU2 is a sink habitat. There is still the possibility that this subpopulation could be a sink habitat, however, based on the reasoning of Mullin et al. (2010); they stated that RU2 is sustained by immigration (a parameter I did not include in my model), which is similar to the most recent findings about RU2 by Eberhart-Phillips et al. (2014) and Feucht et al. (2016). In the population viability analysis by Eberhart-Phillips et al. (2014), they used a juvenile survivorship with a mean of 0.23, which explains their resulting $\lambda < 1$. My model

produced similar results, since juvenile survival could not drop below 0.39 and maintain a stable population. Interestingly, the authors of the 2014 model stated that 0.23 was probably too pessimistic. When they used a juvenile survival closer to 0.5, they also found a positive population growth rate, though not as fast as my prediction. Their model made a lot more assumptions as well, such as stochasticity and source-sink dynamics, so it is interesting that even though my model is simpler and makes less assumptions, it still produced similar results. This uncertainty in juvenile survival leads to an uncertainty concerning the classification of RU2 as a sink or not.

In addition, because my model excluded immigration, its outcomes have the potential to be overly optimistic. For example, it is possible that some birds recruiting as adults are not actually survivors from chicks that fledged in the RU2 area, but are instead new immigrants. However, if my vital rates are correct, excluding immigration from the model should not alter the results, because I am still able to determine if net local growth without immigrants is >1 .

Reproductive values for the RU2 subpopulation decreased slightly with each passing year. While one might be surprised that reproductive values did not increase over time, my result is expected due to the structure of my matrix, in which all inputs represent adults capable of breeding. Once maturity is reached, it is expected that reproductive values decline (Stearns 1992). The stable age distribution had the greatest proportion of one-year-olds, then the proportion of all age classes afterward decreased rapidly, following a trend of exponential decay with time. Because the average life span of WSP is very short, around three years (USFWS 2001), this sharp drop-off is expected.

Sensitivities and Elasticities

Sensitivities and elasticities for RU2 and the baseline were very similar. For both models, adult survival was the most influential vital rate on lambda, followed by juvenile survival, and fecundity was the least influential rate. In addition, for each vital rate, elasticity was slightly lower in my model than in the baseline. Because my initial lambda was higher than the baseline's, any percent change in lambda in response to a vital rate altered by a fixed amount would end up being a smaller percentage of lambda compared to the baseline, which had a lower initial lambda. Even though fecundity in my model was lower than the baseline's, adult survival was higher, which can explain the higher lambda compared to the baseline.

Limitations

My analysis faced some shortcomings by using the deterministic, average vital rates and lambda values of the baseline matrix as the basis for comparison with my own matrix. I also did not consider stochasticity or dispersal in my model. Another limiting factor was the need to use vital rates from other populations and years in the RU2 matrix because estimates for those rates were not available from the RU2 study on which I based the majority of the matrix. Because juvenile survival was not available for the 2013 or 2016 northern California population, I decided to use the juvenile survival value from Nur et al. (1999), but this estimate may have been too high. Mullin et al. (2010) observed apparent juvenile survival around 0.4 for the time span 2001-2007, and as mentioned above, Eberhart-Phillips (2014) estimated juvenile survival at merely 0.23. In addition, my value for adult survival may not

have been an accurate representation of the whole RU2 population, simply because the data represented annual variation in *apparent* survival of males from 2001–2010 in Humboldt County (the county in which the majority of breeding and nesting occurs). Apparent survival is a slightly different measure than true survival; it is most likely an underestimate because it cannot distinguish between mortality and permanent emigration. Therefore, if a large portion of birds migrated to a different site in a following year, the apparent survival measurement would count that emigration as a death. Countering this possible underestimation, however, is the fact that the matrix was constructed in terms of males, who overall displayed a higher adult survival rate than females (which could be a source of potential overestimation).

The Full Relationship Between Vital Rates and Lambda

Due to these uncertainties in vital rates, I explored the full relationship between vital rates and lambda. Juvenile survival could drop below 0.39 before growth rate became negative. Adult survival produced a positive growth rate in all scenarios except the lower 95% confidence interval, in which lambda was 0.98. These results depict the importance of focusing efforts on adult survival and juvenile survival. Recovery plan stipulations are focused on increasing productivity, but according to my model, these efforts toward increasing number of offspring will only be helpful if juvenile survival also increases (so that more plovers reach maturation and eventually increase the adult population). The rate for fecundity (including 95% confidence intervals) always returned lambda greater than 1. However, the fledging rate itself has not yet reached recovery plan objectives.

One of the stipulations of the recovery plan is an annual average productivity of at least 1 fledged chick per male in each recovery unit for 5 consecutive years (USFWS 2007). Based on the data used to construct my model, RU2 has not yet reached the point of 1 fledged chick per male on average (the fledge rate for my model was based on average fledging rate in northern California from 2001–2016). While there were periods within that time span in which the yearly average productivity was 1 or greater, the overall trend in this time span has been a productivity of 0.85 fledglings per male. Because of this, recovery efforts geared toward productivity should continue, but the recovery method should not put adult survival at risk. The direction of this population is a positive one, however, because in 2016, per capita productivity reached 1.21 ± 1.29 fledglings per male, which is the highest productivity for RU2 since 2001, and the first time since 2004 that it has exceeded the 1.0 fledglings per male delisting requirement (Feucht et al. 2016). In addition, the number of breeding adults in RU2 exceeds 70 individuals, almost halfway to the recovery plan objective of 150 breeding individuals.

Based on my results, efforts to restore habitat, restrict human activity, and control predator populations should continue, in order to further the positive trend in growth for RU2. Particular attention should be paid to adult survival and juvenile survival, and future analyses can incorporate more certain data on these vital rates to more accurately assess the state of RU2. Another way to build on the results of this study is to perform population viability analyses for the other recovery units in order to assess how population growth has changed from 1999 to the present. The most accurate models will incorporate data from the same populations and time periods, and will incorporate dynamics such as source-sink populations, stochasticity, and dispersal.

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Literature Cited

- Audubon California. About the Western Snowy Plover. National Audubon Society. Accessed December 2, 2016. ca.audubon.org/about-western-snowy-plover
- Baird, M., 2010. "Western Snowy Plover (*Charadrius alexandrinus nivosus*) birds on Morro Strand State Beach, opposite the Cloisters City Park or the Morro Bay, CA High School, 23 April 2010," flickr.bairdphotos.com. Retrieved from <https://www.flickr.com/photos/mikebaird/4546865553/in/photostream/>
- Burrell, N.S. 2010. Breeding patch dynamics of the western snowy plover (*Charadrius alexandrinus nivosus*) in Humboldt County, California. Humboldt State University, Natural Resources: Wildlife.
- Colwell, M. A., Pearson, W. J., Eberhart-Phillips, L. J., Dinsmore, S. J., 2013. Apparent survival of snowy plovers (*Charadrius nivosus*) varies with reproductive effort and year and between sexes. *The Auk* 130, 725-732. DOI: 10.1525/auk.2013.13147
- Dinsmore S.J., Lauten, D.J., Castelein, K.A., Gaines, E.P., Stern, M.A., 2014. Predator exclosures, predator removal, and habitat improvement increase nest success of Snowy Plovers in Oregon, USA. *The Condor* 116, 619-628. DOI: <http://dx.doi.org/10.1650/CONDOR-14-7.1>
- Drut, M.S. and Buchanan, J. B., 2000. U.S. National Shorebird Management Plan: Northern Pacific Coast Working Group Regional Management Plan. U.S. Fish and Wildlife Service and Cascadia Research Collective.
- Eberhart-Phillips, L. J., Colwell, M. A., 2014. Conservation challenges of a sink: the viability of an isolated population of the snowy plover. *Bird Conservation International* 24, 327-341. DOI:10.1017/S0959270913000506
- Feucht, E.J., Colwell, M.A., King, T.R., Murphy, S.E., Orluck, D.J., Papian, N.C., McAllister, S.E., 2016. Final Report: 2016 Snowy Plover Breeding in Coastal Northern California, Recovery Unit 2. U.S. Fish and Wildlife Service.
- Hickey, C., Shuford, W.D., Page, G.W., Warnock, S., 2003. Version 1.1. The Southern Pacific Shorebird Conservation Plan: A strategy for supporting California's Central Valley and coastal shorebird populations. PRBO Conservation Science, Stinson Beach, CA.
- Hitchcock, C.L. and Gratto-Trevor, C., 1997. Diagnosing a shorebird local population decline with a stage-structured population model. *Ecology* 78, 522-534. DOI: 10.1890/0012-9658(1997)078[0522:DASLPD]2.0.CO;2

- Lauten, D.J., Castelein, K.A., Farrar, D.J., Kotaich, A.A., Gaines, E.P., 2015. The distribution and reproductive success of the western snowy plover along the Oregon Coast – 2015. Oregon Biodiversity Information Center, Institute for Natural Resources, Portland State University.
- Mullin, S. M., Colwell, M. A., McAllister, S. E., Dinsmore, S. J., 2010. Apparent survival and population growth of snowy plovers in coastal northern California. *Journal of Wildlife Management* 74, 1792-1798. DOI: 10.2193/2009-503
- National Park Service. Snowy Plovers at Point Reyes. U.S. Department of the Interior. Accessed December 2, 2016.
https://www.nps.gov/pore/learn/nature/birds_snowyplover.htm.
- Neuman, K. K., Page, G. W., Stenzel, L. E., Warriner, J. C., Warriner J. S., 2004. Effect of mammalian predator management on snowy plover breeding Success. *Waterbirds* 27, 257-263.
- Nur, N., Page, G. W., Stenzel, L. E., 1999. Population viability analysis for Pacific Coast western snowy plovers. In *Western Snowy Plover (Charadrius alexandrinus nivosus) Pacific Coast population recovery plan*. U.S. Fish and Wildlife Service. Vol. 2. Pp. D1-D40.
- Rohatgi, A., 2016. WebPlotDigitizer. Version 3.10. <http://arohatgi.info/WebPlotDigitizer/>
- Saether, B.E. and Bakke, O., 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81, 642-653.
- Sandercock, B.K., 2003. Estimation of survival rates for wader populations: A review of mark-recapture methods. *Wader Study Group Bulletin* 100, 163-173.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. New York (NY): Oxford University Press.
- U.S. Department of Interior. 1993. Threatened status for the Pacific Coast population of the Western Snowy Plover. *Federal Register* 58:2864–12874.
- U.S. Fish and Wildlife Service. 2001. Western snowy plover natural history and population trends. Adapted from Western Snowy Plover Pacific Coast Population Draft Recovery Plan.
- U.S. Fish and Wildlife Service. 2007. Recovery Plan for the Pacific Coast Population of the Western Snowy Plover (*Charadrius alexandrinus nivosus*). In 2 volumes. Sacramento, California. xiv + 751 pages.
- Warriner, J.S., Warriner, J.C., Page, G.W., Stenzel, L.E., 1986. Mating system and reproductive success of a small population of polygamous snowy plovers. *Wilson Bulletin* 98, 15-37.

Appendix A

Sensitivity and elasticity graphs for juvenile survival, fecundity, and adult survival of western snowy plovers in RU2.

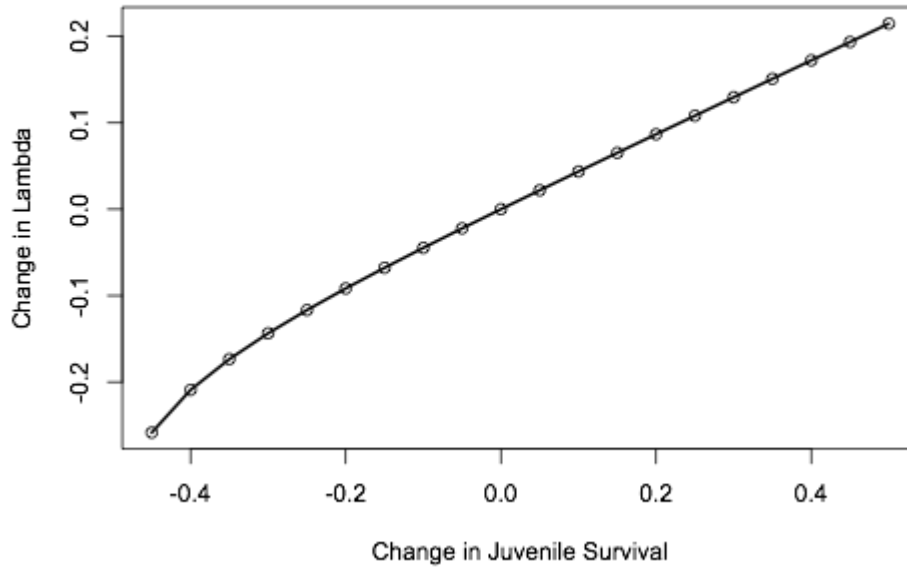


Figure A-1. Sensitivity of lambda to variations in juvenile survival.

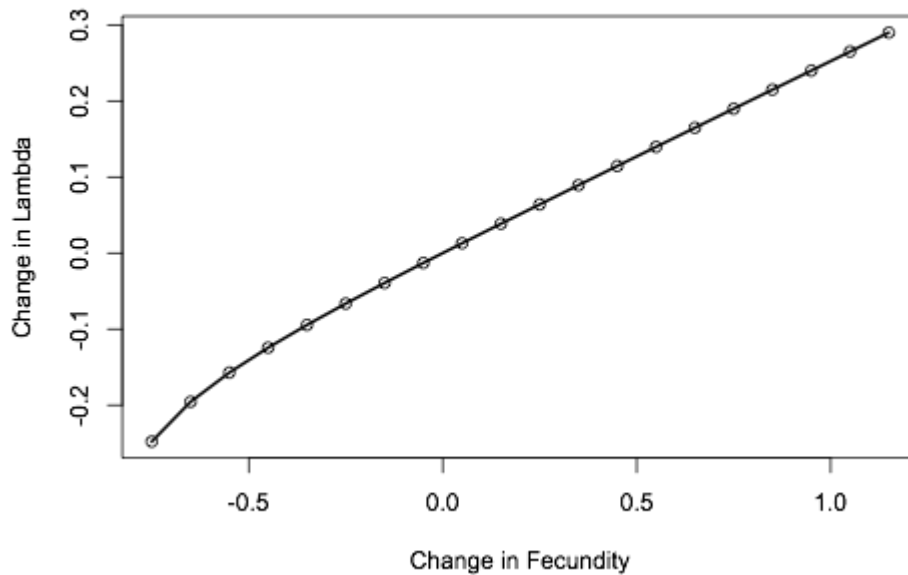


Figure A-2. Sensitivity of lambda to variations in fecundity.

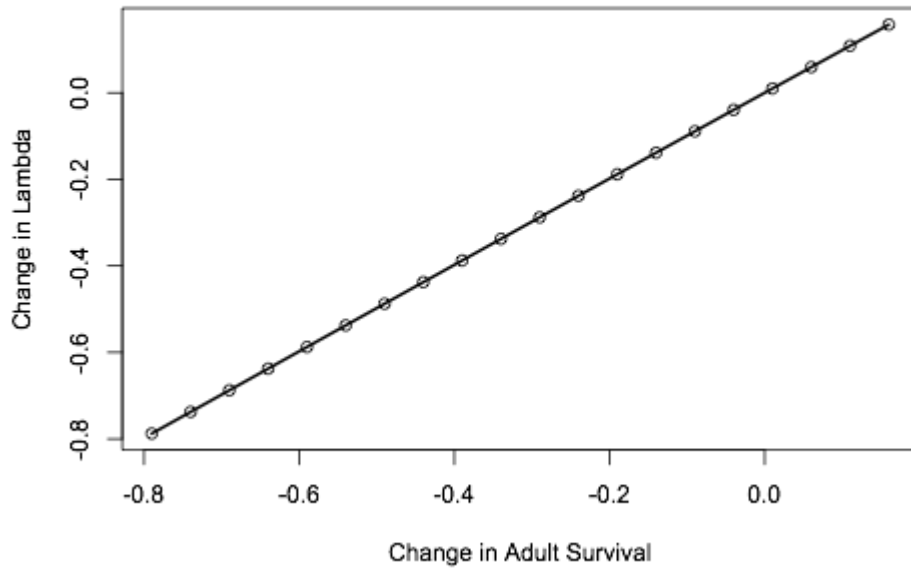


Figure A-3. Sensitivity of lambda to variations in adult survival.

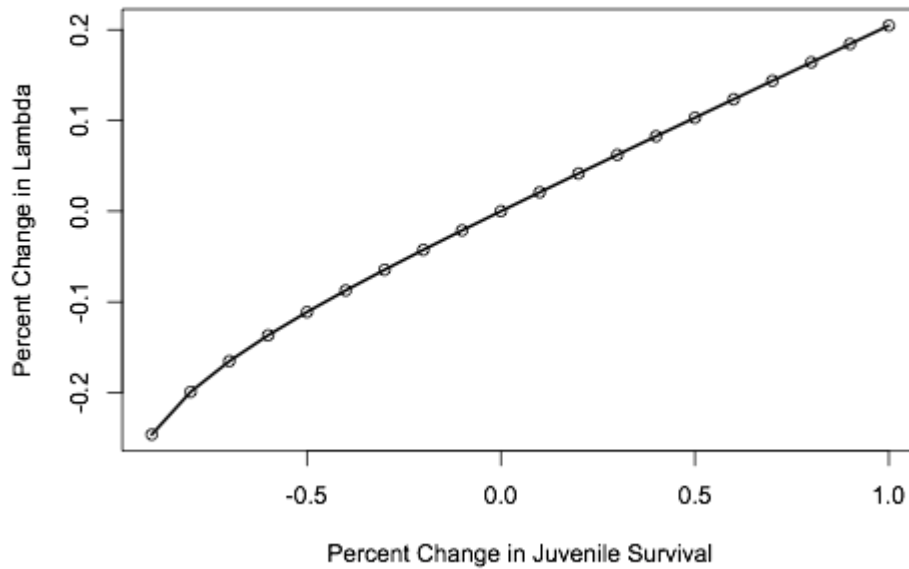


Figure A-4. Elasticity of lambda given proportional changes in juvenile survival.

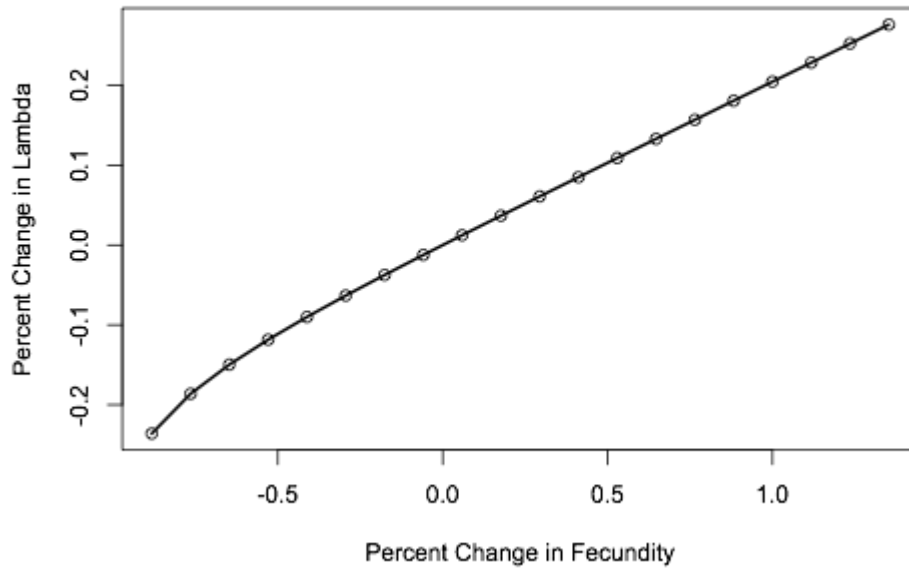


Figure A-5. Elasticity of lambda given proportional changes in fecundity.

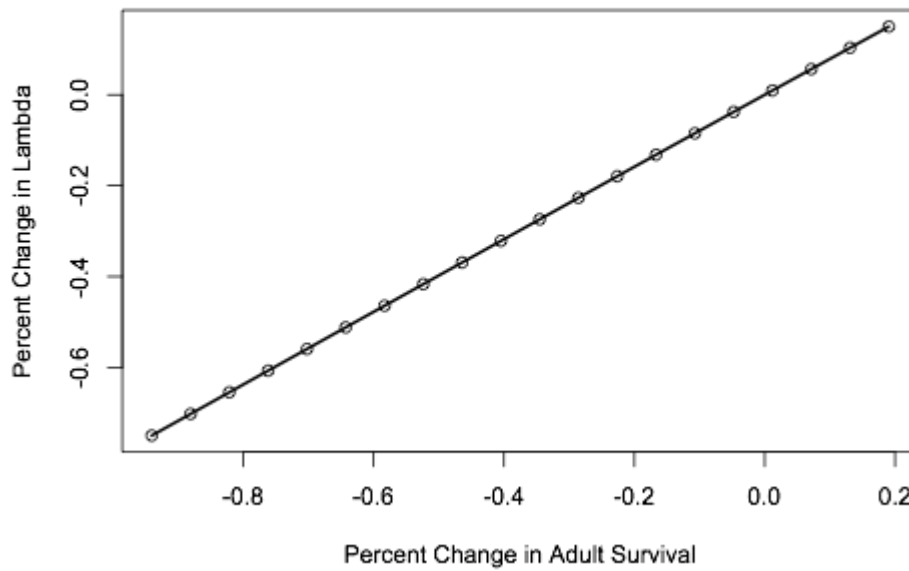


Figure A-6. Elasticity of lambda given proportional changes in adult survival.

Appendix B

R code for matrix model analysis of the baseline and RU2 plover populations

```
# Baseline matrix from Nur et al. (1999)
sa=0.76
sj=0.5
f=1.105
sexratio=0.5

plover=rep(sj*f*sexratio,20)
plover=rbind(plover,c(sa,rep(0,19)))

for (i in 1:18){
  plover=rbind(plover,c(rep(0,i),sa,rep(0,19-i)))
}

modell=eigen(plover)
modell$values
lambda0 = modell$values[1]
lambda0

# Comparison of vital rate elasticities: decrease by 1%
vars=c(sj,f,sa)
lambda=numeric(0)

for(vr in 1:3) {

  vars[vr]=vars[vr]*.99
  plover=rep(vars[1]*vars[2]*sexratio,20)
  plover=rbind(plover,c(vars[3],rep(0,19)))

  for (i in 1:18){
    plover=rbind(plover,c(rep(0,i),vars[3],rep(0,19-i)))
  }
  y=eigen(plover)
  lambda=c(lambda,y$values[1])
  vars=c(sj,f,sa)
}

changelambda=(lambda-lambda0)/lambda0
elast=changelambda/(.01*vars[vr])
elast

# Comparison of vital rate sensitivities: change by 0.01
vars=c(sj,f,sa)
lambda=numeric(0)

for(vr in 1:3) {

  vars[vr]=vars[vr]+0.01
  plover=rep(vars[1]*vars[2]*sexratio,20)
  plover=rbind(plover,c(vars[3],rep(0,19)))

  for (i in 1:18){
    plover=rbind(plover,c(rep(0,i),vars[3],rep(0,19-i)))
  }
}
```

```

}
y=eigen(plover)
lambda=c(lambda,y$values[1])
vars=c(sj,f,sa)
}

sensitivity=(lambda-lambda0)/(0.01)
sensitivity

# MY MODEL: RU2
f=0.85 # average fledge rate from 2001-2016 in Feucht et al. (2016)
sa=0.84 # average apparent male survival found by digitizing graph in Colwell et al. (2013)
sj=0.5 # no data on this, for 2013 or 2016, used Nur et al. (1999) value
sexratio=0.5

plover=rep(sj*f*sexratio,20)
plover=rbind(plover,c(sa,rep(0,19)))

for (i in 1:18){
  plover=rbind(plover,c(rep(0,i),sa,rep(0,19-i)))
}

y=eigen(plover)
lambda1=y$values[1]
lambda1
ssd=y$vectors[,1]
ssd
sum(ssd)
ssd=ssd/(sum(ssd))
ssd
z=eigen(t(plover))
rv=z$vectors[,1]
rv

# VARYING VITAL RATES:

# 1. VARYING JUVENILE SURVIVAL

vars=c(sj,f,sa)
juvsurvival=seq(0.05,1,0.05)
lambda=numeric(0)

for(percent in 1:20) {

  vars[1]=juvsurvival[percent]
  plover=rep(vars[1]*f*sexratio,20)
  plover=rbind(plover,c(sa,rep(0,19)))

  for (i in 1:18){
    plover=rbind(plover,c(rep(0,i),sa,rep(0,19-i)))
  }
  y=eigen(plover)
  lambda=c(lambda,y$values[1])
  vars=c(sj,f,sa)
}

```

```

lambda
plot(juvsurvival, lambda, xlab="Juvenile Survival", ylab="Lambda")
lines(juvsurvival, lambda, type="l", lwd=2)
abline(v=0.5, lwd=2)
abline(v=0.385, col="red", lty=4, lwd=1.5)

# SENSITIVITY ANALYSIS on juvenile survival
sensitivity=(lambda-lambda1)/(juvsurvival-sj)
sensitivity
plot(juvsurvival-sj, lambda-lambda1, xlab="Change in Juvenile Survival", ylab="Change in
Lambda")
lines(juvsurvival-sj, lambda-lambda1, lwd=2)

# ELASTICITY ANALYSIS
elasticity=((lambda-lambda1)/lambda1)/((juvsurvival-sj)/sj)
elasticity
plot((juvsurvival-sj)/sj, (lambda-lambda1)/lambda1, xlab="Percent Change in Juvenile
Survival", ylab="Percent Change in Lambda")
lines((juvsurvival-sj)/sj, (lambda-lambda1)/lambda1, lwd=2)

# 2. VARYING FECUNDITY

vars=c(sj, f, sa)
fecundity=seq(0.1, 2, 0.1)
lambda=numeric(0)

for(percent in 1:20) {

vars[2]=fecundity[percent]
plover=rep(sj*vars[2]*sexratio, 20)
plover=rbind(plover, c(sa, rep(0, 19)))

for (i in 1:18){
plover=rbind(plover, c(rep(0, i), sa, rep(0, 19-i)))
}
y=eigen(plover)
lambda=c(lambda, y$values[1])
vars=c(sj, f, sa)
}
lambda
plot(fecundity, lambda, xlab="Fecundity", ylab="Lambda")
lines(fecundity, lambda, type="l", lwd=2)
abline(v=0.85, lwd=2.5)
abline(v=1.105, col="blue", lwd=2)
abline(v=0.85+0.15, col="red", lty=4, lwd=1.5)
abline(v=0.85-0.15, col="red", lty=4, lwd=1.5)

# SENSITIVITY ANALYSIS on fecundity
sensitivity=(lambda-lambda1)/(fecundity-f)
sensitivity
plot(fecundity-f, lambda-lambda1, xlab="Change in Fecundity", ylab="Change in Lambda")
lines(fecundity-f, lambda-lambda1, lwd=2)

# ELASTICITY ANALYSIS
elasticity=((lambda-lambda1)/lambda1)/((fecundity-f)/f)
elasticity
plot((fecundity-f)/f, (lambda-lambda1)/lambda1, xlab="Percent Change in
Fecundity", ylab="Percent Change in Lambda")
lines((fecundity-f)/f, (lambda-lambda1)/lambda1, lwd=2)

```

```

# 3. VARYING ADULT SURVIVORSHIP

vars=c(sj,f,sa)
adultsurvival=seq(0.05,1,0.05)
lambda=numeric(0)

for(percent in 1:20) {

  vars[3]=adultsurvival[percent]
  plover=rep(sj*f*sexratio,20)
  plover=rbind(plover,c(vars[3],rep(0,19)))

  for (i in 1:18){
    plover=rbind(plover,c(rep(0,i),vars[3],rep(0,19-i)))
  }
  y=eigen(plover)
  lambda=c(lambda,y$values[1])
  vars=c(sj,f,sa)
}
lambda
plot(adultsurvival,lambda,xlab="Adult Survival",ylab="Lambda")
lines(adultsurvival,lambda,type="l",lwd=2)
abline(v=0.84,lwd=2.5)
abline(v=0.76,col="blue",lwd=2)
abline(v=0.84+0.069,col="red",lty=4,lwd=1.5)
abline(v=0.84-0.069,col="red",lty=4,lwd=1.5)

# SENSITIVITY ANALYSIS on adult survival
sensitivity=(lambda-lambda1)/(adultsurvival-sa)
sensitivity
plot(adultsurvival-sa,lambda-lambda1,xlab="Change in Adult Survival",ylab="Change in Lambda")
lines(adultsurvival-sa,lambda-lambda1,lwd=2)

# ELASTICITY ANALYSIS
elasticity=((lambda-lambda1)/lambda1)/((adultsurvival-sa)/sa)
elasticity
plot((adultsurvival-sa)/sa,(lambda-lambda1)/lambda1,xlab="Percent Change in Adult
Survival",ylab="Percent Change in Lambda")
lines((adultsurvival-sa)/sa,(lambda-lambda1)/lambda1,lwd=2)

# MY MATRIX Comparison of vital rate elasticities: decrease by 1%
vars=c(sj,f,sa)
lambda=numeric(0)

for(vr in 1:3) {

  vars[vr]=vars[vr]*.99
  plover=rep(vars[1]*vars[2]*sexratio,20)
  plover=rbind(plover,c(vars[3],rep(0,19)))

  for (i in 1:18){
    plover=rbind(plover,c(rep(0,i),vars[3],rep(0,19-i)))
  }
  y=eigen(plover)
  lambda=c(lambda,y$values[1])
  vars=c(sj,f,sa)
}

```

```

changelambda=(lambda-lambda1)/lambda1
elast=changelambda/(0.01*vars[vr])
elast

# Comparison of vital rate sensitivities: change by 0.01
vars=c(sj,f,sa)
lambda=numeric(0)

for(vr in 1:3) {

vars[vr]=vars[vr]+0.01
plover=rep(vars[1]*vars[2]*sexratio,20)
plover=rbind(plover,c(vars[3],rep(0,19)))

for (i in 1:18){
    plover=rbind(plover,c(rep(0,i),vars[3],rep(0,19-i)))
}
y=eigen(plover)
lambda=c(lambda,y$values[1])
vars=c(sj,f,sa)
}

sensitivity=(lambda-lambda1)/(0.01)
sensitivity

```