POPULATION VIABILITY OF SNOWY PLOVERS IN COASTAL NORTHERN CALIFORNIA

By

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ABSTRACT

Population Viability of Snowy Plovers in Coastal Northern California.

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For endangered metapopulations, the roles of source-sink dynamics are easily overlooked or not fully understood when formulating delisting requirements. This could lead to unrealistic recovery criteria imposed on sink populations, which in turn might restrict the entire metapopulation from being delisted. Therefore, an understanding of the viability of sink populations within the context of source populations is needed to develop appropriate conservation objectives. Consequently, I conducted a population viability analysis on the small geographically isolated northern California population of the snowy plover (*Charadrius nivosus*), a shorebird that is listed as threatened under the federal Endangered Species Act. The threatened status of the plover results from three factors that limit population recovery: 1) predation by native and introduced vertebrates, 2) encroachment of invasive vegetation in breeding habitats, and 3) human disturbance. I utilized 11 years of mark-recapture, productivity, and movement data to explore population viability under various management scenarios that addressed the three limiting factors within the framework of surrounding source populations. I also investigated how viability is influenced by periodic over-winter catastrophes that reduce survival. Simulations confirmed that the northern California population is a sink that relies upon immigrants originating from surrounding populations such as Oregon, San Francisco Bay, and Monterey Bay. Within the next 50 years, simulations revealed that these source populations will increase and are likely to achieve the delisting requirements. However, the northern California population is unlikely to reach the delisting criteria given the current vital rate estimations. Management scenarios demonstrated that reducing human disturbance through the use of symbolic fencing and the restriction of recreational vehicle use on beaches occupied by plovers provides benefits to the local population that may partially alleviate the reliance upon immigration. Lethal predator management was also found to be effective at growing the population; however the use of nest exclosures reduced current population growth because they are known to compromise the survival of incubating adults, the most "elastic" vital rate in northern California. The dependence of northern California upon immigration highlights the importance of continued plover management in source populations. A cold winter weather catastrophe was an influential phenomenon affecting population growth in northern California, and is likely a major factor contributing to its status as a sink because these catastrophes trigger large stochastic shifts in adult and juvenile survival. Sink populations such as northern California may be important for the viability of the greater metapopulation. Therefore I recommend that the protection and maintenance of productive source populations should be a priority for snowy plover management, however the preservation of the northern California population should be part of a revised conservation plan that formulates delisting criteria based upon the active source-sink processes of the Pacific coast metapopulation.

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INTRODUCTION

Formulating a recovery plan for an endangered metapopulation requires a thorough understanding of source-sink dynamics because unidentified sink populations may delude management into imposing unachievable delisting requirements (Pulliam 1988). This could ultimately lead to sink populations preventing the species from being delisted even if surrounding source populations have met the recovery requirements and are viable. Therefore an understanding of the viability of sink populations within the context of source populations is needed to develop appropriate conservation objectives (Harveson et al. 2004). However, an accurate assessment of viability requires long-term data capturing the environmental variation of all life history stages (White 2000). In the past, this data requirement had been lacking for many endangered species, but recent efforts to collect vital rate data and improve databases offer the opportunity to evaluate the recovery potential and viability of populations with greater confidence. This is especially the case for shorebirds (suborder Charadrii), which can be banded and monitored relatively easily to estimate survival, reproductive success, and dispersal using mark-recapture methods (Sandercock 2003).

In order to meet the recovery objectives of a threatened or endangered species, management strategies and efforts must be tailored to maximize the benefit of the entire population of concern. However, due to economic limitations (Baur et al. 2009) and pressures from the public to keep critical habitat open for recreational or commercial use (Baldwin 2003), recovery objectives can be seriously compromised. Population viability analysis (PVA) has become a popular method used by management agencies to evaluate recovery objectives and demographic requirements that would support the delisting of threatened or endangered species (Morris et al. 2002). PVA is a powerful tool that can evaluate population extinction risk and the relative importance of stage, age, or sex specific demographic processes to the long-term viability of a population (Morris et al. 2002). With this technique, management is able to evaluate alternative strategies that maximize the recovery of the species while acknowledging socioeconomic concerns.

In this study, I conducted a PVA on a small, geographically isolated population of the snowy plover (*Charadrius nivosus*) in coastal northern California. The United States Fish and Wildlife Service (hereafter USFWS) listed the Pacific coast metapopulation of the snowy plover (hereafter plover) as threatened under the United States Endangered Species Act in 1993. The species' Recovery Plan (USFWS 2007) identified three factors that are thought to limit population recovery: 1) predation of eggs, chicks, and adults by native and introduced vertebrates, 2) encroachment of invasive vegetation such as European beachgrass (*Ammophila arenaria*), which degrades breeding habitats, and 3) human activity, which causes direct mortality of eggs, chicks, and adults or indirectly affects the distribution of plovers.

In 1999, Nur et al. produced a coast-wide PVA that assessed the demographic response of the plover metapopulation to 19 scenarios that perturbed vital rates such as adult and juvenile survival, reproductive success, and dispersal. The results of this PVA provided guidance for the formulation of delisting criteria published in the USFWS Recovery Plan (2007). The Recovery Plan states that to delist the plover the following requirements must be met: 1) a population of 3,000 breeding adults for 10 years distributed disproportionally among six recovery units along the Pacific coast of the United States, 2) maintenance of an average annual productivity of one (1.0) fledged chick per male in each recovery unit for five years prior to delisting, and 3) development and implementation of useful mechanisms that assure the long-term protection and management of the first two criteria (USFWS 2007).

The plover's distribution along the Pacific coast of the United States extends from the beaches of southern Washington to the Mexican border in southern California (USFWS 2007). Of the 3,000 breeding adults required to delist the plover, Recovery Unit 2 of coastal northern California (which includes Mendocino, Humboldt, and Del Norte counties) must maintain 150 breeding adults over 10 years (USFWS 2007). I utilized 11 years of survival and productivity data collected from northern California and elsewhere along the Pacific coast to assess the viability of the northern California population within the context of surrounding source populations. My study had two main objectives pertaining to the viability of the northern California population: 1) to evaluate the relative importance of specific aspects of plover life history, and 2) to explore various management strategies that address the limiting factors of predation, habitat loss, and human disturbance. The findings of a survival analysis prompted a third objective, which was to investigate the influence of periodic over-winter catastrophes on population viability. With the results of this study, I evaluated the likelihood of population recovery given the current delisting requirements and made management recommendations specific to the northern California population that highlighted the importance of source-sink dynamics operating in the Pacific coast metapopulation.

METHODS

Study Species

The snowy plover is a small shorebird that weighs between 34 to 58 grams and belongs to the family Charadriidae (USFWS 2007). Most individuals first breed as yearlings (Page et al. 1995). Breeding begins in mid-March and finishes by mid-September (Page et al. 1995). The plover mating system has been described as serial polyandry, because both sexes acquire new mates for the second brood (Warriner et al. 1986). Female plovers lay up to three eggs per clutch, and can produce a maximum of three broods per breeding season (Warriner et al. 1986). Upon hatching, females usually desert males, which are then solely responsible for parental care of broods; consequently males father a maximum of two broods per season (Warriner et al. 1986). Plovers are partial migrants, with a proportion of a subpopulation residing year-round and another proportion either wintering or breeding (Colwell et al. 2007). Permanent emigration has been documented to occur as far as 790 km from natal sites (Stenzel et al. 2007).

Study Area

Over the past decade, nearly all plovers breeding in Recovery Unit 2 of coastal northern California have occurred in Humboldt County (Colwell et al. 2010). The study area consisted of gravel bars along the Eel River and several ocean-fronting sandy beaches within Humboldt County. On beaches, plovers occupied habitat composed of fine homogeneous substrates littered with natural and human debris, and vegetated with large expanses of introduced European beachgrass or small restored tracts of native flora. On gravel bars, plovers utilized habitat characterized by large, heterogeneous substrates littered with driftwood and vegetated with sparse stands of willow (*Salix spp.*) and sweet white clover (*Meliolotus alba*). Colwell et al. (2010) provided a detailed description of the study area and the distribution of plovers within habitats over the past decade.

Field Methods

Since 2001 biologists have monitored the northern California population of plovers intensively each year, banding nearly every adult and chick with a unique combination of UV-stable color bands and a USFWS metal band (Colwell et al. 2010, Mullin et al. 2010). Observers also captured and banded unmarked immigrants breeding in the study area each year. Between mid-March and mid-August, observers surveyed the study area weekly by visiting known breeding sites and suitable breeding habitats; survey frequency increased when observers detected plovers at a site (Colwell et al. 2010). Observers walked slowly along beaches and gravel bars, scanning for plovers with spotting scopes and binoculars. When observers detected banded plovers at a site, they recorded color band combinations. Observers monitored nests during surveys and determined parenthood based on multiple observations of banded plovers near the nest, adults incubating eggs, or brooding chicks (Colwell et al. 2010). Observers conducted research under federal, state, and university permits (USFWS permit TE-823807-3; California Department of Fish and Game collecting permit #801059-03; State Parks Collecting Permit #09-635-002; Humboldt State University IACUC #11/12.W.12-A; USFWS Federal banding permit #22971).

Modeling Population Viability

I assessed population viability using VORTEX, version 9.99b (Lacy et al. 2003), a stochastic simulation software package. To investigate source-sink dynamics, I modeled northern California population viability within the context of the rest of the listed population segment by defining two subpopulations (Figure 1). I defined the focal population as Recovery Unit 2 of coastal northern California (hereafter “northern California”). I grouped the populations of Oregon, San Francisco Bay, and Monterey Bay into a single source population (hereafter “Pacific coast”) from which the majority of immigration to northern California is known to occur (unpublished data, M. A. Colwell 2011. Humboldt State University, 1 Harpst Street, Arcata, CA 95521). Using two subpopulations allowed me to target population-specific processes pertaining to viability and quantify the importance of movement between the two populations. Because VORTEX is an individual-based model, it tracked the simulated fate of an individual through its lifetime (birth, survival, reproduction, movement, and death; Figure 2). VORTEX simulated population dynamics stochastically by randomly drawing the annual success and fate of each individual from vital rate distributions I estimated and provided in the model. In addition to distributions of survival, productivity, and movement, VORTEX required fundamental plover life history information such as clutch size, mating system, longevity, etc., which I obtained from published literature (Appendix A). I chose to use $N = 5$ as the quasi-extinction threshold (Ginzburg et al. 1982) for simulations because in 2011 there were only 36 breeding plovers, and therefore the population is already well below a typical quasi-extinction threshold of 50, for example. Therefore, I assumed that if the population declined to five individuals it would result in a major change in management practices (e.g., captive breeding). I ran 1000 iterations per simulation to obtain accurate measures of stochastic population dynamics as recommended by Caswell (2001). I ran simulations for 50 years because it is unrealistic

Figure 1. Map of the snowy plover distribution along the Pacific coast of the United States with the delineation of the two populations used in the stochastic model. Where NCA is the northern California focal population and PAC is a source population consisting of surrounding recovery units contributing immigrants to NCA.

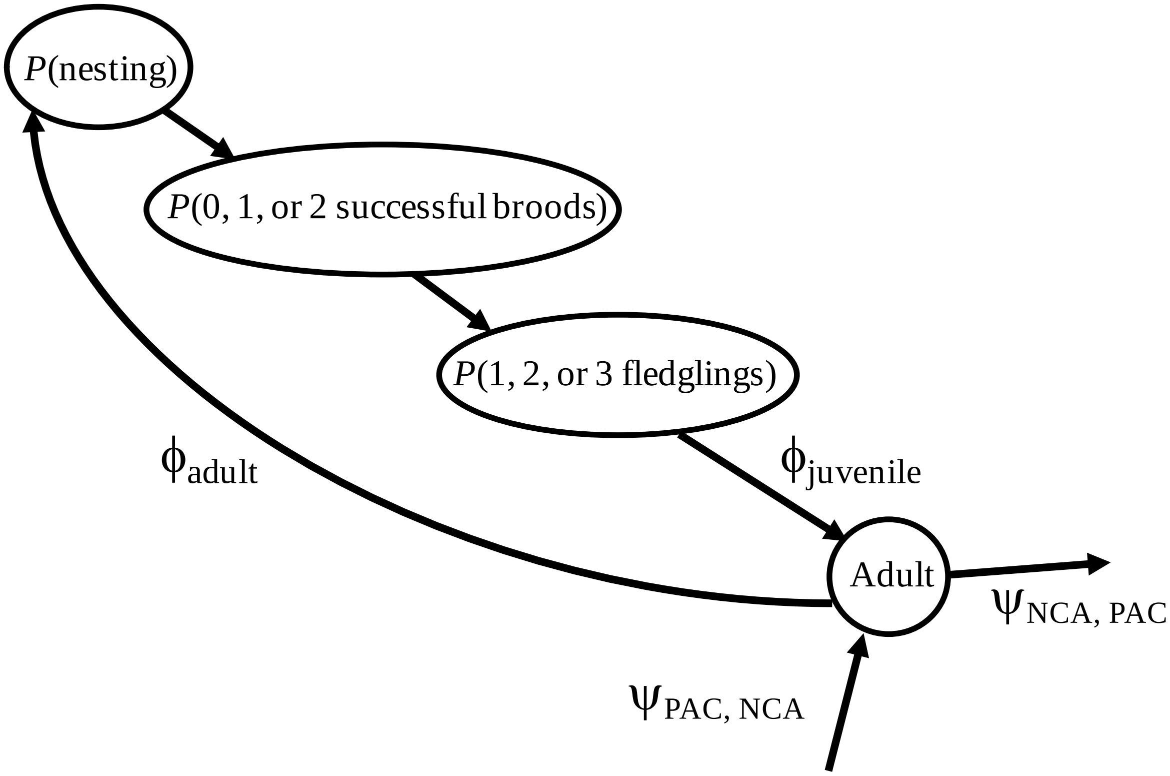

Figure 2. Sequence of life-history events and probabilities (*P*) used by VORTEX to model population growth of male snowy plovers in northern California (NCA) in the context of the Pacific coast population (PAC), where ϕ_i is the survival of age class *i* and $\psi_{j,k}$ is the movement between population *j* and population *k*.

to foresee beyond 50 years given the data available and the time frame that legislative bodies are capable of managing (Mace and Lande 1991).

Vital Rate Estimation

I used an 11-year (2001 to 2011) dataset containing mark-resight and individual lifetime reproductive success data from northern California to estimate annual apparent survival, productivity, and movement parameters (Figure 2). At the end of the 2011 breeding season, the dataset included 224 males and 244 females; 176 were immigrants originating from the Pacific coast, 64 were recruited locally within northern California, and 228 were individuals that hatched in northern California but did not return in subsequent breeding seasons. I defined the resighting interval as the breeding season (i.e., interval over which pairs initiated clutches), a period of approximately 125 days between 15 March and 20 July; however, some adults occasionally tended broods into mid-August or early September (Colwell et al. 2011). I provide detailed methods for estimating vital rates in the Appendices (survival: Appendix B; movement: Appendix E; productivity: Appendix F). In the VORTEX simulation, I assumed constant survival for adults of all ages after the juvenile age class, but I constrained the longevity of adults to 15 years, which is the oldest known age for snowy plovers (Page et al. 1995).

Evaluating Population Viability

Long-term population growth is best predicted by the arithmetic mean of the population growth rates of many simulated iterations, known as the stochastic growth rate ($\hat{r}_S$; Morris and Doak 2002). To quantify the viability of the northern California plover population, I evaluated the $\hat{r}_S$ of 1000 iterations each simulated for 50 years. The units of $\hat{r}_S$ are the number of individuals gained or lost per individual per year, with positive values describing population increase and negative values describing population decline. I used $\hat{r}_S$ because it is a useful population metric that is easily understood by management agencies, which can evaluate differences in the predicted $\hat{r}_S$ of various management scenarios to promote the recovery of a species while considering socioeconomic constraints.

Density dependent population growth is a complex issue that is not well understood for snowy plovers, and thus it was difficult to confidently consider its role in population viability. However, Nur et al. (1999), assumed a carrying capacity of 200 for Recovery Unit 2 in their coast-wide PVA. Biologically this value may not be realistic, as plovers breed at low density (Page et al. 1983) and there appears to be plenty of unoccupied breeding and wintering habitat available in northern California (Burrell 2010, Brindock and Colwell 2011). In addition, there have been no studies assessing carrying capacity or density dependence across the study area. Inbreeding between close relatives has been observed in the northern California population on four occasions with one of these events resulting in an infertile clutch (Colwell and Pearson 2011). Inbreeding depression is especially a threat to the viability of small isolated populations (Hagen et al. 2011), thus it was valid to consider its role in the viability of plovers in northern California (Appendix K). To address these issues I tested the influence of perturbing the carrying capacity and the inbreeding parameters in an elasticity analysis.

The baseline model included all of the averaged vital rates and their distributions observed in both populations between 2001 and 2011 (Appendix H). I evaluated the accuracy of the baseline model by comparing the observed coefficient of variation in the two populations between 2001 and 2011 with the 95 percent confidence interval of the average coefficient of variation across 30 iterations that ran for 10 years, using the 2001 counts as the initial population sizes (N_{NCA} = 57, N_{PAC} = 437).

Elasticity analysis for stochastic population growth

A common approach to determine the extent at which various vital rates affect population dynamics is to conduct an elasticity analysis, which quantifies the relative change in stochastic population growth resulting from a change in a vital rate (Morris and Doak 2002). To estimate the elasticity of vital rates, I perturbed the vital rates of the baseline model by 10, 20, and 50 percent in the direction that would most likely increase $\hat{r}_{s_{\mathrm{NCA}}}$ (Appendix H). I calculated elasticities as the proportional increase in $\hat{r}_{s_{\mathrm{NCA}}}$ divided by the proportional change in the vital rate (Morris and Doak 2002), a method commonly used to calculate elasticities in PVAs (Benton and Grant 1999, Finkelstein et al. 2010, Hudgens et al. 2011).

Assessment of Limiting Factors

I used the results of the elasticity analysis to develop hypothetical scenarios that evaluated the effectiveness of methods managing one or a combination of the three limiting factors affecting plover viability identified by the Recovery Plan (USFWS 2007). Additionally, I assessed the influence of prolonged cold winter weather on population viability and recovery.

Nest and brood predation

Predation of eggs and chicks by corvids (*Corvus brachyrhynchos* and *C. corax*) is the most influential factor affecting snowy plover productivity in northern California (Burrell and Colwell in review). Lethal predator removal and nest exclosures are two methods used to increase productivity that have been implemented at recovery units along the entire Pacific coast (Lauten et al. 2010, Knapp and Peterson 2010, Page et al. 2010, Pearson et al. 2010, Hardy and Colwell 2008, Robinson-Nilsen et al. 2011). Currently there is no lethal predator management in northern California, nor was it practiced in northern California between 2001 and 2011. Nest exclosures were used in northern California between 2001 and 2006, and are designed to keep predators out of nests while allowing incubating adults to freely move to and from the nest. I simulated two scenarios that utilized lethal predator removal or nest exclosures in northern California to evaluate how an increase in reproductive success using these two methods may influence population viability and the likelihood of reaching the delisting requirements. I implemented this by changing the productivity distributions of northern California to those reported elsewhere on the Pacific coast (see Appendix F) where lethal predator removal has been practiced and predator exclosures were used to protect eggs and enhance hatching success since 2002 (Lauten et al. 2010, Page et al. 2010, Robinson-Nilson et al. 2011). Likewise, to assess the use of only nest exclosures, I used productivity distributions estimated from 2001 to 2006 productivity data in northern California, when local management used nest exclosures. Exclosure management is known to compromise the survival of incubating adults in northern California (Hardy and Colwell 2008), and to acknowledge this I used the survivorship distribution estimated for the population between 2001 to 2006 (Appendix B). I evaluated the results of these stochastic simulations by comparing the $\hat{r}_{s_{\mathrm{NCA}}}$ to that of the baseline model.

Habitat loss

The invasion of European beachgrass has decreased the amount and quality of plover nesting habitat by increasing beach slope and creating less open space (Wiedemann 1987, Muir and Colwell 2010). Agencies commonly restore plover habitat by removing European beachgrass, which enhances recovery of the native dune ecosystem. With the creation of open habitat, it is assumed that the carrying capacity of nesting plovers increases (USFWS 2007). To assess the influence of habitat restoration on population viability in northern California, I ran six management scenarios of the stochastic simulation that perturbed the baseline carrying capacity ($K = 200$) in both directions by 10, 20, and 50 percent (see Appendix H).

Human activity

Human activity compromises plover productivity (Ruhlen et al. 2003, Lafferty et al. 2006, Wilson and Colwell 2010) and survival (Brindock and Colwell 2011), and affects the distribution of plovers on a beach (Lafferty et al. 2006). Symbolic fencing, consisting of a roped boundary that delineates an area where access by pedestrians and vehicles is restricted, is commonly used to reduce human disturbance (USFWS 2007). Wilson and Colwell (2010) found that plover productivity in northern California was almost two times higher within a symbolic fence than outside the fence. Additionally, Lafferty et al. (2006) observed more than a 50 percent reduction in disturbance events after installation of a symbolic fence. It has also been suggested that survival can be negatively impacted by human activities, such as driving vehicles through wintering flocks and occasionally killing plovers (Brindock and Colwell 2011).

I assessed how a reduction in human disturbance influenced population viability by simulating scenarios in which I matched productivity distributions to those observed inside symbolic fencing (Wilson and Colwell 2010) and increased the survival of adults and juveniles by two, five, or ten percent. There are no data to quantitatively assess the reduction in the average survival of the plover population exposed to varying levels of vehicle use on beaches, therefore I used a range of values that I believe is conservative given accounts by Buchanan (2011) who documented the direct mortality of 468 shorebirds in a single incident involving a vehicle on a beach in Washington.

Catastrophic severe winter weather

Severe weather can reduce over-winter survival of shorebirds (Parr 1992, Yalden and Pearce-Higgins 1997, Durell et al. 2006, Roche et al. 2010). The results of an *a priori* survival analysis demonstrated dramatic annual variation in apparent survival (see Appendix B) and subsequently prompted a *post hoc* analysis investigating the influence of prolonged cold winter weather on apparent survival in northern California (see Appendix L for details). Estimates of juvenile and adult survival in the vicinity of Monterey Bay indicate marked declines in 1987 and 1998 (Stenzel et al. 2007, Stenzel et al. 2011); this could be related to climatic events like the winter of 1998 during which there were seven consecutive days with a minimum temperature at or below freezing. If similar phenomena are observed at regular intervals elsewhere along the Pacific coast, these declines in survival will affect the recovery of the species.

I used the severity and frequency statistics of the winter weather survival analysis (Appendix L) as parameters in VORTEX to simulate the influence of a catastrophe on the viability of the northern California plover population. I used an elasticity analysis to evaluate the sensitivity of stochastic population growth to perturbations in the severity and frequency of the catastrophe.

RESULTS

The observed coefficient of variation of both populations between 2001 and 2011 (NCA = 0.366, PAC = 0.207) fell within the 95 percent confidence intervals of the coefficient of variation of the 2001 to 2011 baseline model ($\widehat{\mathrm{CV}}_{\mathrm{NCA}} = 0.377, 95\%\ \mathrm{CI} = 0.310$ to 0.443; $\widehat{\mathrm{CV}}_{\mathrm{PAC}} = 0.229, 95\%\ \mathrm{CI} = 0.200$ to 0.258), demonstrating that the structure of the baseline model accurately predicted the observed stochasticity. The observed trend of northern California deviated positively from the simulated projection between 2001 and 2006 when nest exclosures were used in northern California, but between 2007 and 2011 the model effectively predicted the observed (Figure 3a). Between 2001 and 2011, the simulated projection of the Pacific coast population slightly underestimated the observed population size, but the observed trend fell within one standard deviation of the simulation's average projection for all years except 2004 (Figure 3b).

When I used the 2011 observed population as the initial population size (N_{NCA} = 36), the baseline model experienced slightly positive growth ($\hat{r}_{s_{\mathrm{NCA}}} = 0.008 \pm 0.248$ SD) such that by the fiftieth year, northern California had an average of 59 individuals with a 0.2 percent probability of quasi-extinction (Appendix O, Figure 4a). Similarly, the baseline model of the Pacific coast exhibited positive growth ($\hat{r}_{s_{\mathrm{PAC}}} = 0.035 \pm 0.147$ SD; Figure 4b) and increased to an average of 1054 individuals after 50 years with a zero percent probability of quasi-extinction.

The elasticity of $\hat{r}_{s_{\mathrm{NCA}}}$ was greater for perturbations of Pacific coast vital rates than to perturbations in the vital rates of northern California (Appendix O, Figure 5), with

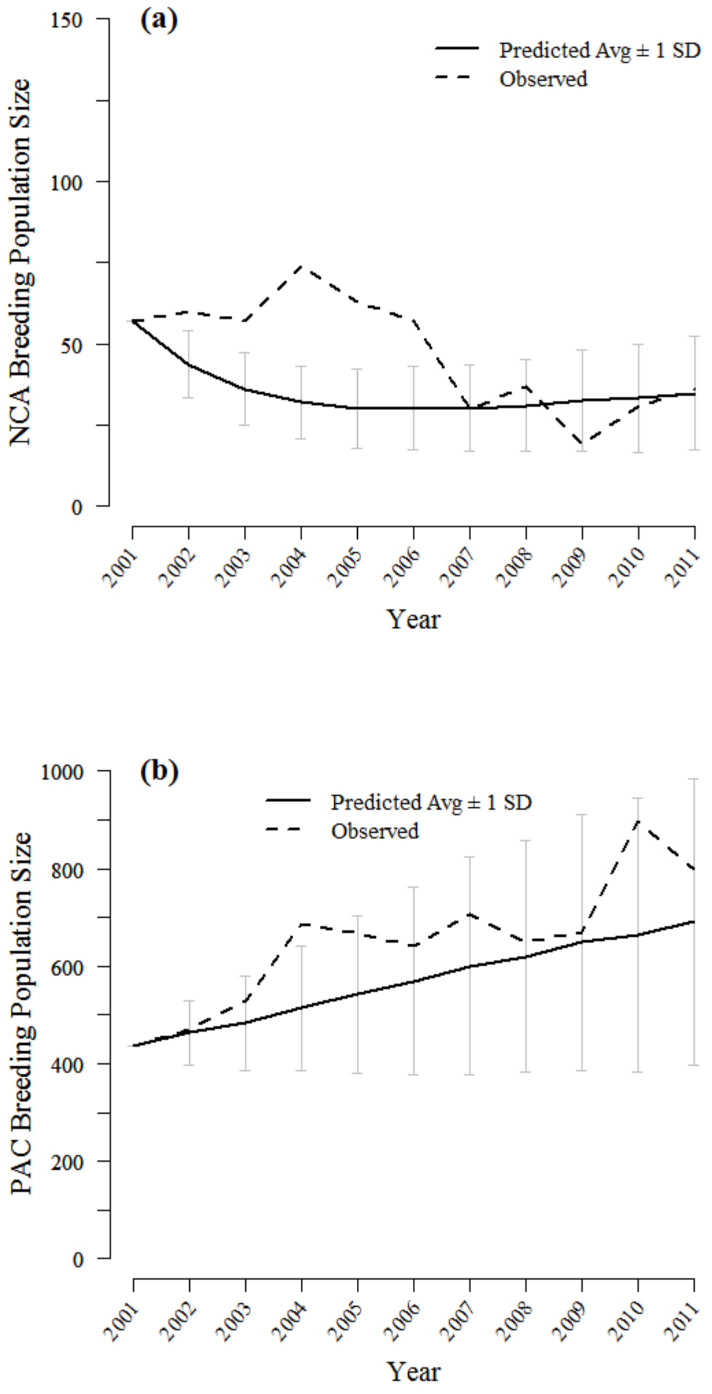

Figure 3. Comparison of observed and predicted population projections for (a) northern California and (b) the Pacific coast between 2001 and 2011 using the 2001 initial population sizes and the baseline vital rates. Error bars represent one standard deviation around the average population size of 1000 iterations.

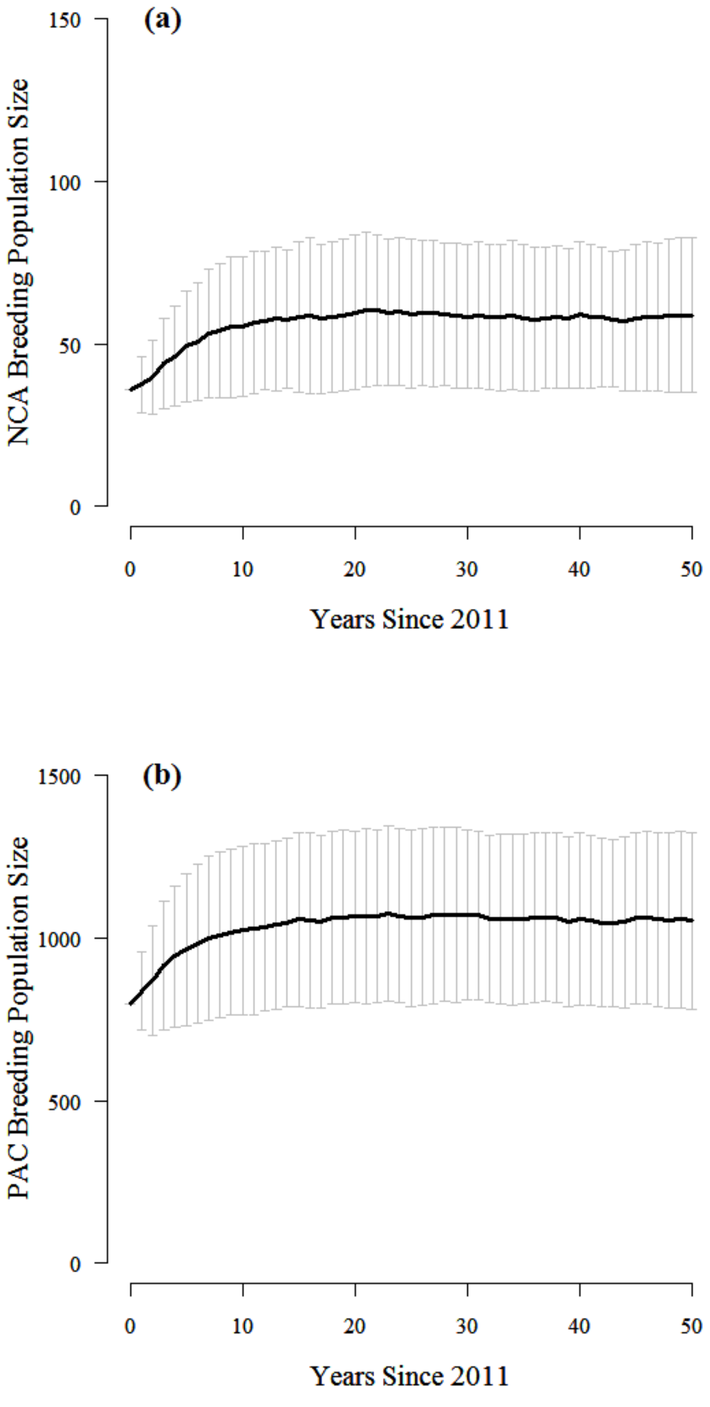

Figure 4. Baseline model population projections for (a) northern California and (b) the Pacific coast. Error bars represent one standard deviation around the average population size of 1000 iterations.

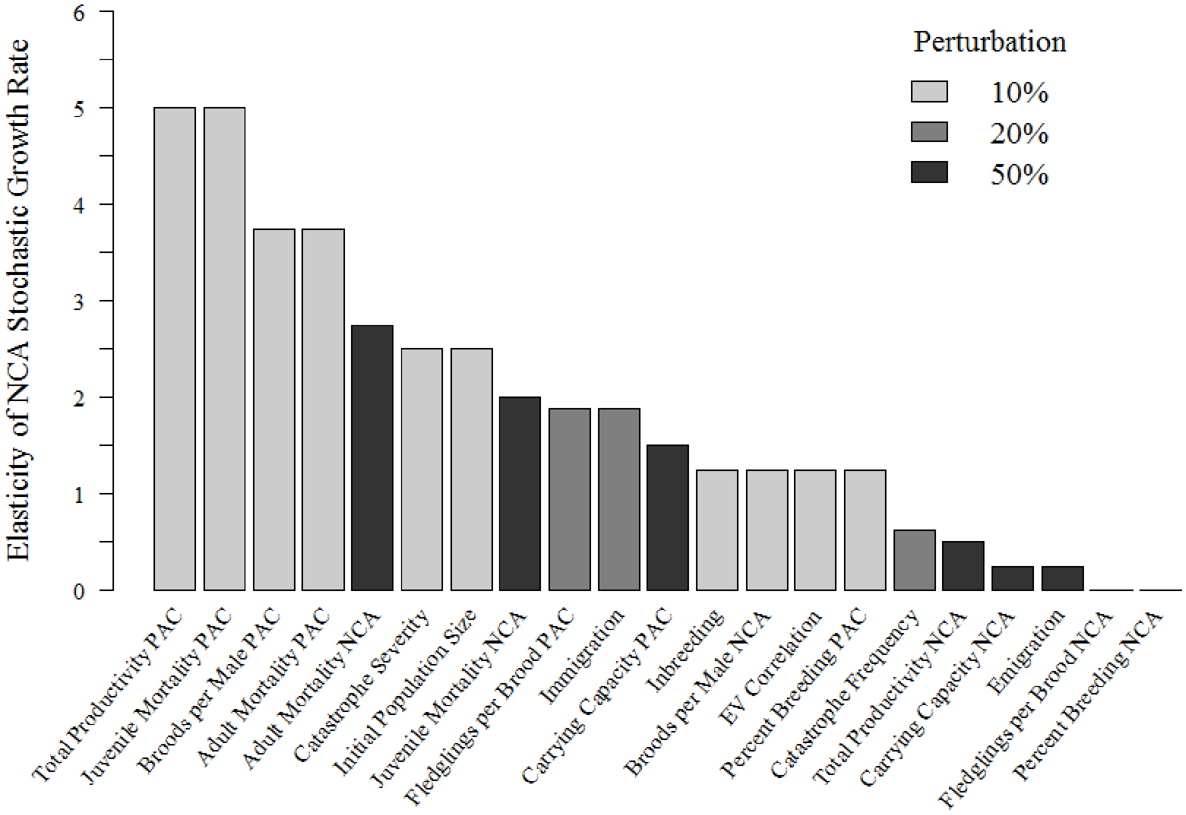

Figure 5. Elasticity of the stochastic growth rate of the northern California population for 21 model components specific to northern California (NCA), the Pacific coast (PAC), or globally effecting both populations simultaneously (immigration, emigration, the winter cold weather catastrophe, and inbreeding). Total productivity represents a perturbation of both the broods per male and fledglings per brood distributions. All perturbations were made in the direction that would hypothetically favor growth in northern California.

the productivity of the Pacific coast having the largest influence on $\hat{r}_{s_{\mathrm{NCA}}}$ (Appendix O, Figure 5). For example, a 10 percent increase in two parameters describing productivity of the Pacific coast increased the $\hat{r}_{s_{\mathrm{NCA}}}$ 1.81 times more than a 50 percent increase in northern California adult survival, 10 times more than a 50 percent increase in northern California successful broods per male and fledglings per brood parameters, and 20 times more than a 50 percent increase in the carrying capacity of northern California.

Immigration was an important component of the model. A 20 percent increase in the immigration rate had a greater effect on northern California growth than all other northern California productivity vital rates (Figure 5). A scenario in which no movement occurred between the two populations resulted in 100 percent probability of quasi-extinction of northern California after an average of five years (Figure 6a). Interestingly, the Pacific coast population responded positively to the no movement scenario with a 46 percent increase in growth ($\hat{r}_{s_{\mathrm{PAC}}} = 0.051 \pm 0.146$ SD).

The estimate of juvenile apparent survival ($\widehat{\phi}_{\mathrm{Juvenile}} = 0.23 \pm 0.09$; Appendix B) was 50 percent of the true survival estimated in Monterey Bay ($\phi_{\mathrm{Juvenile}} = 0.46 \pm 0.07$) by Stenzel et al. (2007). This suggests the estimate of juvenile apparent survival in northern California was probably biased low because it is confounded with permanent emigration (Sandercock 2003). To evaluate the relative difference in the two estimates of juvenile survival, I simulated the baseline model with the northern California juvenile survival and variation equal to that of the Pacific coast. This resulted in a 50 percent increase in the growth of northern California ($\hat{r}_{s_{\mathrm{NCA}}} = 0.012 \pm 0.23$ SD$, N_{50} = 72$; Appendix O, Figure 6b); however, the delisting criteria of 150 breeding adults was not achieved within the 50 year simulation.

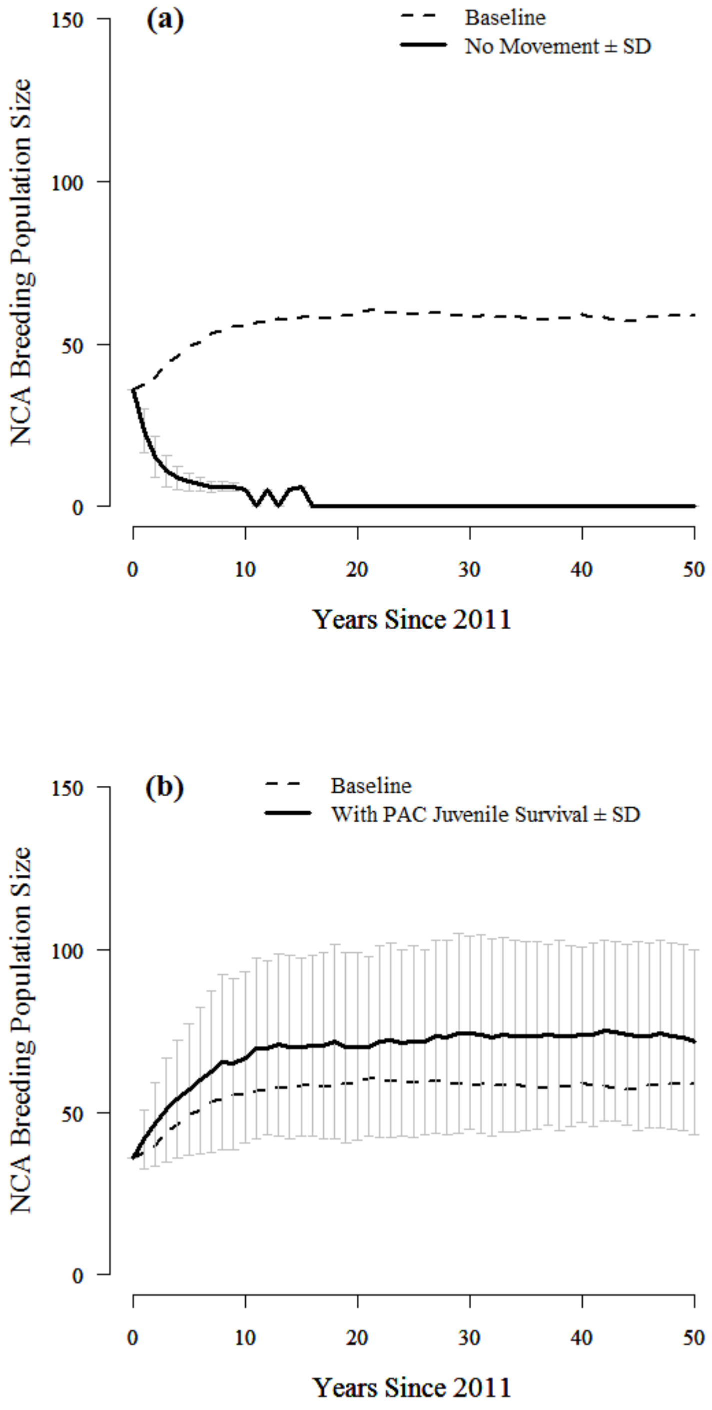

Figure 6. Northern California population projections for (a) a no movement scenario and (b) a scenario using estimated juvenile survival in the Pacific coast. Error bars represent one standard deviation around the average population size of 1000 iterations.

Assessment of Limiting Factors

Nest and brood predation

To simulate the use of lethal predator removal in northern California, I increased the expected successful broods per breeding male from 0.44 to 0.84 and the expected fledglings per successful brood from 1.82 to 1.87, which were the productivity rates observed across the Pacific coast where such management is practiced. This simulation resulted in a 25 percent increase in the growth of northern California over the baseline model. However the population did not reach the recovery objective of 150 individuals ($\hat{r}_{s_{\mathrm{NCA}}} = 0.01 \pm 0.262$ SD, $N_{50} = 68$; Appendix O, Figure 7a).

Likewise, to simulate the use of nest exclosures I increased the expected successful broods per breeding male from 0.44 to 0.54 and decreased adult survival from 0.62 to 0.57, which was the brood distribution and survival observed and estimated in northern California between 2001 and 2006 when nest exclosures were used. This simulation resulted in a 12.5 percent decrease in the growth of northern California ($\hat{r}_{s_{\mathrm{NCA}}} = 0.007 \pm 0.255$ SD) over the baseline model (Appendix O, Figure 7b).

Habitat loss

All perturbations of carrying capacity in northern California that simulated habitat restoration did not result in a change in $\hat{r}_{s_{\mathrm{NCA}}}$ from that of the baseline model (Appendix O). However, increasing the carrying capacity of the Pacific coast by 10 percent from 1300 to 1450 individuals resulted in a 12.5 percent increase in the growth of northern California (Appendix O).

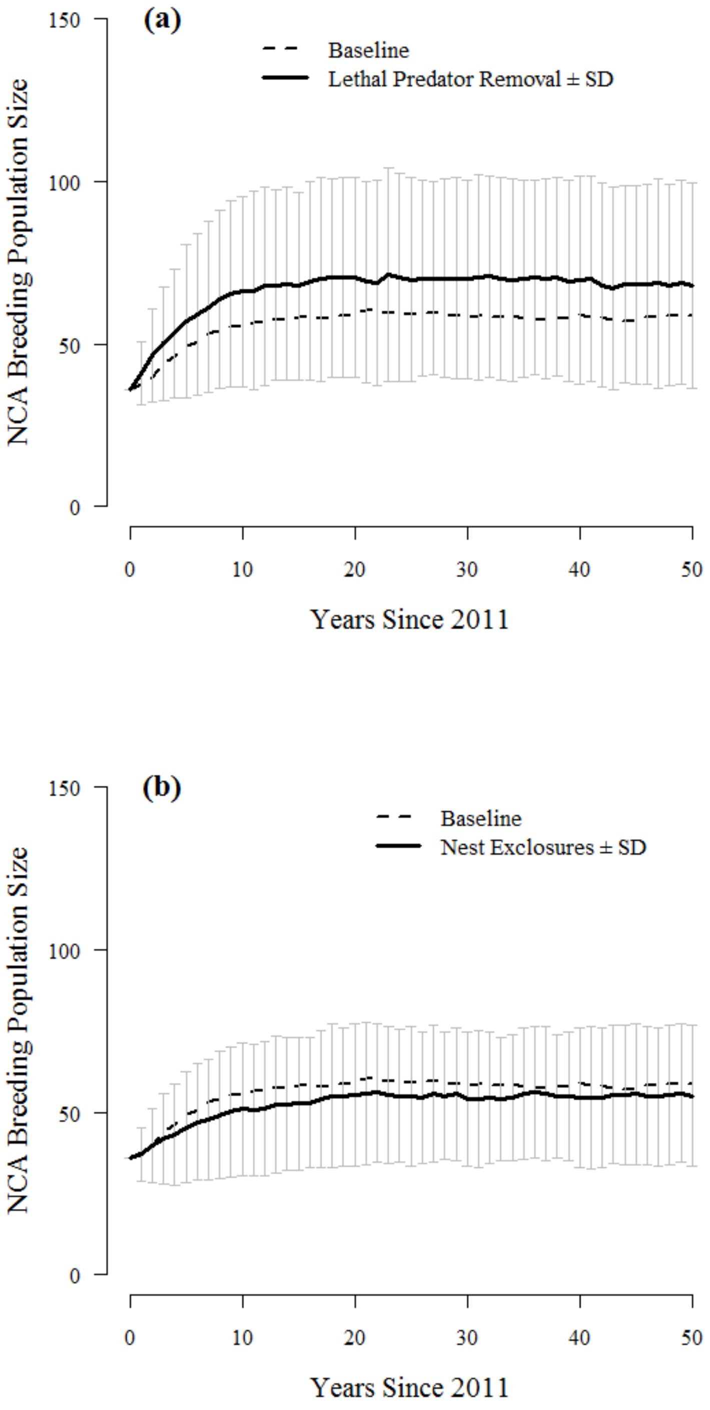

Figure 7. Population projections of northern California under two different management approaches, (a) lethal predator removal and (b) the use of nest exclosures. Error bars represent one standard deviation around the average population size of 1000 iterations.

Human disturbance

I assessed management of human disturbance using two models. The first model simulated a doubling in productivity (0.68 to 1.36 fledglings per male) through the use of symbolic fencing throughout suitable breeding habitat in northern California. This model differed from the current management regime, which has used symbolic fencing sparingly at a few sites. I iteratively solved for the appropriate productivity distributions using a productivity correction formula (see Appendix F). This resulted in increasing the successful broods per nesting male in northern California from 0.46 to 0.76, and increasing the fledglings per successful brood in northern California from 1.82 to 2.12. This simulation resulted in a 50 percent increase in the growth of northern California ($\hat{r}_{S_{\text{NCA}}} = 0.012 \pm 0.257$ SD) from that of the baseline model (Appendix O, Figure 8a).

The second model simulated the use of symbolic fencing and prohibition of recreational vehicle use near known plover habitat. I simulated this management scenario by using the productivity distributions of the first model and by increasing adult and juvenile survival by two, five, or ten percent. With symbolic fencing and a two percent increase in survival, there was a 50 percent increase in the growth of northern California ($\hat{r}_{S_{\text{NCA}}} = 0.012 \pm 0.255$ SD) over the baseline model (Appendix O, Figure 8b). However with symbolic fencing and a ten percent increase in survival, there was a 140 percent increase in the baseline growth of northern California ($\hat{r}_{S_{\text{NCA}}} = 0.019 \pm 0.244$ SD; Appendix O, Figure 8b).

Catastrophic severe winter weather

The severity of the cold winter catastrophe was an important component of the model. A 10 percent reduction in the severity had a greater elasticity than all

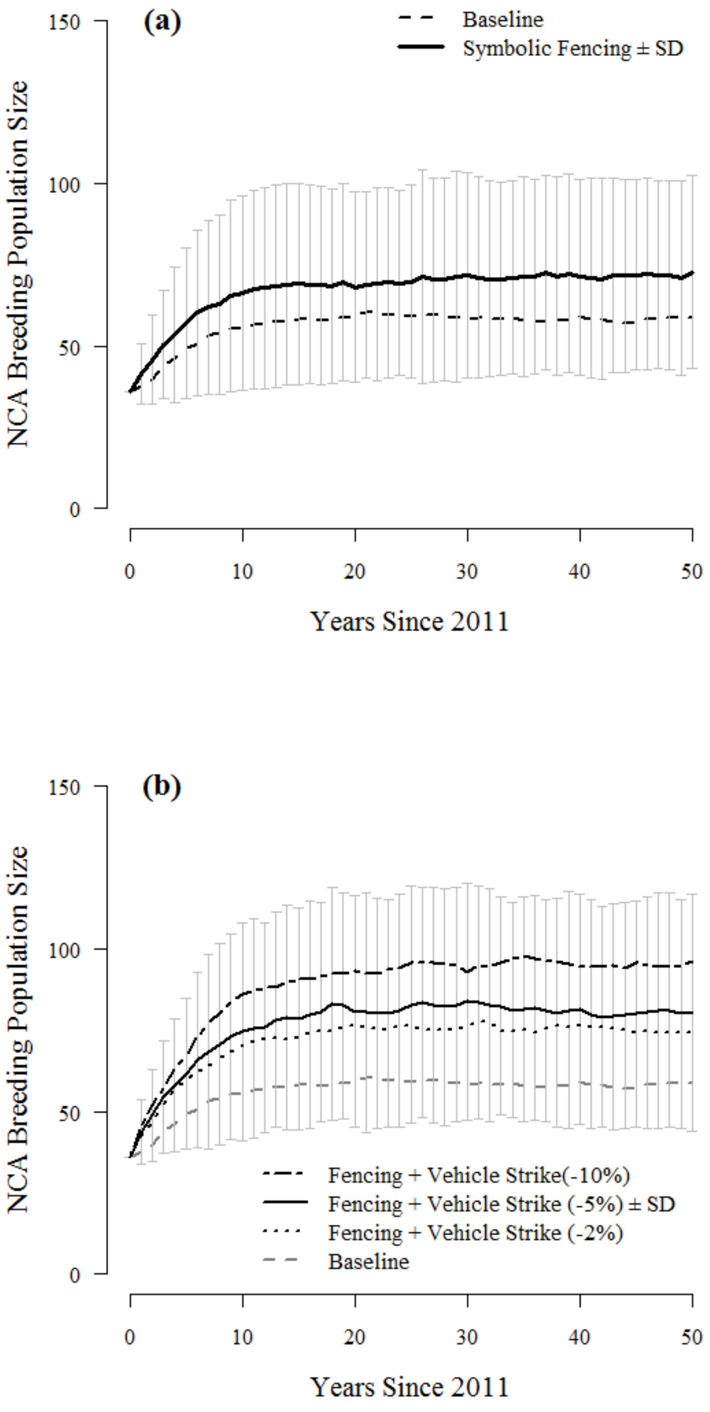

Figure 8. Population projections of northern California for two management methods addressing human disturbance: (a) symbolic fencing and (b) symbolic fencing with three levels of hypothetical reductions in mortality related to vehicle strike. Error bars represent one standard deviation around the average population size of 1000 iterations of the five percent reduction in mortality scenario.

perturbations of northern California vital rates, except a 50 percent reduction in adult mortality (Figure 5). Reducing the catastrophe severity by 10 percent resulted in a 25 percent increase in the growth of northern California ($\hat{r}_{s_{\mathrm{NCA}}} = 0.01 \pm 0.239$ SD; Appendix O). The elasticities of northern California growth to perturbations in the catastrophe frequency were not as important as those of the severity (Figure 5). A 50 percent reduction in the frequency resulted in a 12.5 percent increase in growth over the baseline model ($\hat{r}_{s_{\mathrm{NCA}}} = 0.009 \pm 0.246$ SD; Appendix O). Removing the catastrophe from the model resulted in a 37.5 percent increase in population growth in northern California ($\hat{r}_{s_{\mathrm{NCA}}} = 0.011 \pm 0.230$ SD; Appendix O).

DISCUSSION

Four main findings emerged regarding the viability of the plover subpopulation in Recovery Unit 2 of northern California: 1) the population is a sink that relies upon immigrants originating from surrounding populations such as Oregon, San Francisco Bay, and Monterey Bay; 2) population persistence depends upon continued management aimed at increasing plover productivity at source populations elsewhere on the Pacific coast; 3) local management should consider the risks associated with the use of nest exclosures and acknowledge the benefits of reducing human disturbance and enforcing predator removal; 4) decreased survival associated with cold winter weather was an influential phenomenon affecting local population growth.

Model Performance

The baseline projections over the next 50 years indicated that both the northern California and Pacific coast populations will increase and stabilize after 20 years ($N_{\mathrm{NCA}} \approx 60 \pm 23$ SD, $N_{\mathrm{PAC}} \approx 1060 \pm 269$ SD; Figure 4). The structure of the baseline model reflected the observed stochasticity accurately, however the simulated trajectory of northern California underestimated the observed between 2001 and 2006. The shortfall of the model between 2001 and 2006 probably resulted from two things. First, the 2001 to 2006 interval did not experience winters with prolonged cold weather (see Appendix L for details); whereas on average, simulations included one or more catastrophic winters during this interval which consequently depressed simulated growth rates. Second, the productivity parameters of the baseline model were based upon productivity data averaged over the entire 11-year period; whereas between 2001 and 2006, nest exclosures were used to manage nest predators which resulted in higher nest success during that interval. The model was not robust to perturbations in the initial population size, with the average stochastic growth rate of northern California increasing with a smaller initial population and decreasing with a larger initial population (Figure 5, Appendix O). This is most likely a consequence of using the average growth rate statistic, which will be positively biased for those simulations that start with smaller population sizes because there is a longer period of time needed to reach the point at which the average annual growth is stable at zero.

Population Viability

The productivity and survival distributions used in the model do not support a self-sustaining plover population in northern California. Consequently, immigration from source populations elsewhere along the Pacific coast is necessary to maintain a breeding population in northern California (Figure 6a). The significance of immigration for plovers in northern California is not a new finding. Mullin et al. (2010) classified the northern California population as a sink based on an algebraic assessment of population growth using estimates of productivity and survival. And in the PVA by Nur et al. (1999), when dispersal was reduced to zero, the northern California population became extinct. Plissner and Haig (2000) made similar conclusions from their PVA of the Atlantic Coast breeding metapopulation of piping plovers (*Charadrius melodus*): persistence time increased with increased movement rates and greater connectivity increased the total size of the metapopulation. For snowy plovers, this emphasizes the importance of dispersal to counterbalance regional low productivity or survival, such as that experienced in northern California (USFWS 2007).

The influence of inbreeding on population growth was relatively low compared to other components of the model (Figure 5). This suggests that during simulations, immigration of individuals from the Pacific coast replenished genetic variation in northern California, subsequently reducing the impact of inbreeding depression. This phenomenon, known as ‘genetic rescue’ (Ingvarsson 2001), highlights another reason why immigration is crucial for the viability of the northern California population.

The estimated standard errors of adult and juvenile survival in northern California were large compared to those of the Pacific coast (Adults: $SE_{NCA} = 0.13$, $SE_{PAC\ Males} = 0.02$, $SE_{PAC\ Females} = 0.03$; Juveniles: $SE_{NCA} = 0.09$, $SE_{PAC} = 0.07$; Appendix B), which meant that simulations of northern California experienced large fluctuations in population growth given the high elasticity of adult and juvenile mortality (Figure 5). In addition to its low productivity, the large stochasticity of influential vital rates (e.g., survival) characterizes the northern California population as a sink. This was further supported by the “no movement” scenario, which demonstrated that the growth of the Pacific coast population increased by 46 percent when immigration to northern California ceased. Viewed another way, the northern California population is a burden to the recovery of the rest of the Pacific coast metapopulation.

The delisting requirements of the plover is the maintenance of 3,000 breeding adults for 10 years distributed disproportionately among the recovery units and an average annual productivity of one fledged chick per breeding male for five years (USFWS 2007). Recovery Unit 2 of northern California requires 150 breeding adults and Recovery Units 1, 3, and 4 (which make up the Pacific coast population in this study) collectively require 1150 breeding adults (USFWS 2007). The Pacific coast population will likely achieve the delisting requirement within the next 30 years given that the population currently produces an annual average of 1.32 fledged chicks per breeding male (Appendix F) and the baseline simulation stabilized at an average of 1060 ± 269 SD individuals after 20 years (Figure 4). However, the northern California population is unlikely to reach the recovery objectives given that the population currently produces an annual average of 0.68 fledged chicks per male (Appendix F) and the baseline simulation stabilized at an average of 60 ± 23 SD individuals after 20 years (Figure 4). Even those simulations with 50 percent reductions in the mortality of adults or juveniles in northern California resulted in insufficient population growth needed to achieve 150 breeding adults (Appendix O). This finding highlights that the delisting of the entire Pacific coast snowy plover metapopulation will likely be precluded by sink populations such as northern California considering the current delisting requirements.

Although northern California is a sink, its persistence may be important for the viability of the entire metapopulation. Howe and Davis (1991) argued that a metapopulation with a large proportion of individuals residing in sinks can still be viable. Furthermore, Howe and Davis (1991) found that in many cases sink populations can 1) increase the overall size of a metapopulation, 2) increase the size of source populations, and 3) extend the persistence of metapopulations in decline. Therefore, the protection and maintenance of productive populations such as those in Oregon and Monterey Bay needs to be a priority for snowy plover management, but the preservation of marginal populations such as northern California should be part of the conservation plan. The 4(d) rule proposed by the U.S. Department of the Interior (2006) would have allowed regions to relax management if they had met the recovery criteria. However, without a productive source population, the northern California population would likely be pushed to extinction within the next 20 years.

Management of Limiting Factors

The management scenarios addressing human disturbance were the most beneficial for the growth of the northern California population. Population growth increased by 50 percent through the use of symbolic fencing and a further 25 percent with the prohibition of recreational vehicle use on beaches (assuming a five percent reduction in mortality; Appendix O). Wilson and Colwell (2010) found that symbolic fencing in northern California increased productivity through a reduction in brood movement. Because of human disturbance, chicks that were raised outside of the fenced area traveled greater distances than those raised in it, potentially exposing broods to higher risks of predation (Wilson and Colwell 2010). The influence of human disturbance on plover productivity in northern California is almost certainly augmented by corvid predation of broods, which coincides with areas of human activity (Marzluff and Neatherlin 2006).

Recreational vehicle use in plover habitat is a complicated issue considering that there is only anecdotal evidence to support its negative influence on survival in northern California (Brindock and Colwell 2011). However, the potential effects of vehicle use on population growth in northern California must be acknowledged by management because survival, especially that of adults, had the highest effect on plover population growth (Figure 5), which is a common finding for other shorebirds (Sandercock 2003). This may be especially important during the nonbreeding season, when plover survival is compromised by severe winter weather (Yalden and Pearce-Higgins 1997, Appendix L).

It is politically infeasible to enforce a coast-wide prohibition of recreational vehicle use on the beaches in northern California, but regional prohibition at locations where plovers predictably over-winter (see Brindock and Colwell 2010) could be an alternative. After a regional ban of vehicle use on beaches in South Africa, Williams et al. (2004) observed a doubling of the populations of crowned plovers (*Vanellus coronatus*), blacksmith plovers (*V. armatus*), and sanderlings (*Calidris alba*), suggesting that such management is effective.

Predation of eggs and chicks, mainly by corvids, is the most important factor limiting productivity in northern California (Burrell and Colwell in review). The simulations demonstrated that managing predation with lethal methods was 43 percent more effective at improving population growth in northern California than the use of nest exclosures (Figure 7, Appendix O). The elasticity analysis revealed that the expected number of successful broods per nesting male was the most influential productivity vital rate of northern California affecting growth (Figure 5). This provides support for the use of lethal predator removal in northern California because lethal methods improve both egg and chick survival, whereas exclosures only protect nests and are known to compromise the survival of incubating adults (Hardy and Colwell 2008), the most elastic vital rate (Figure 5). However, public resistance may prevent the application of lethal predator management (Liebezeit and George 2002). But when non-lethal predator management is more costly than lethal methods, the public could respond positively (Isaksson 2009). For example, it costs approximately $1000 to erect and monitor one snowy plover nest exclosure during the incubation period in northern California (Liebezeit and George 2002), which can quickly become expensive and labor intensive in remote areas. Thus, management in northern California must balance economic feasibility and public approval while maximizing the benefit to snowy plover population growth.

The habitat restoration scenarios revealed that for the current population size of northern California (N_{2011} = 36), the assumed carrying capacity (K = 200) is not restricting population growth. All simulations that perturbed carrying capacity (positively or negatively) did not strongly affect population growth (Appendix O). This finding relies upon the assumption of the model that habitat restoration only increases carrying capacity and not the averages of vital rates such as survival and productivity. There is no evidence to suggest an increase in survival associated with habitat restoration; however, restoration may indirectly enhance nest survival through the creation of open habitat which facilitates an early detection of predators by incubating plovers (Koivula and Rönkä 1998). Muir and Colwell (2010) found that breeding plovers selected nest sites that were more open than random sites; however there was no evidence to suggest that restored habitat was of higher quality because measures of enhanced productivity associated with open habitat were not evaluated. Although these findings suggest that habitat restoration is currently not a priority for the recovery of plovers in northern California, it is important to stress that plovers are not the only species using the native dune ecosystem. Restoration is vital for the reestablishment of native species that are restricted to the dune ecosystem such as solitary bees (e.g. *Megachile spp.* and *Emphoropsis spp.*) and two federally listed endangered plant species: the Humboldt Bay wallflower (*Erysimum menziesii eurekensii*), and the beach layia (*Layia carnosa*; USFWS 2007). Therefore, results of this study should not be misinterpreted as an argument against dune restoration in northern California.

The cold winter weather catastrophe was an influential phenomenon affecting population growth in northern California (Figure 5), and is likely a major factor contributing to its status as a sink. Evidence suggests that significantly colder winters caused decreased survival (see Appendix L for details), a vital rate with the highest elasticity in northern California (Figure 5). Winter weather severity was highly variable between 2001 and 2011 and is thus a probable source for the large variation in both adult and juvenile survival observed over the 11 year period (Appendix N). Stochastic weather events make small isolated populations like northern California especially vulnerable to extinction (Crick 2004). When the productivity of northern California was increased to that of the Pacific coast source population, the local reproductive success still failed to compensate local mortality (see lethal predator removal scenario, Appendix O), demonstrating that the sink habitat in northern California is part of the plover's realized niche (Pulliam 1988). The influence of climate highlighted by this study provides evidence that there are limiting factors at work across the Pacific coast metapopulation that are beyond the control of management.

Pulliam (1988) argued that sink populations could easily mislead management into formulating unrealistic population size expectations if the underlying source-sink dynamics of the metapopulation are not fully understood. The delisting criteria for plovers in northern California was formulated based upon a metapopulation viability analysis by Nur et al. (1999), who were forced to make large assumptions pertaining to population-specific vital rates because of data limitations at the time of analysis. For example, in their model, Nur et al. (1999) included 1) higher estimates of adult ($\phi_{\mathrm{Adult}} =$

0.76 ± 0.05) and juvenile ($\phi_{\text{Juvenile}} = 0.5 \pm 0.07$) survival with less variation, and 2) a catastrophe that reduced productivity by 50 percent every 20 years. Nur et al. (1999) also concluded that northern California is a sink. However, the differences between the parameters used in their model and those of this study are a likely source for the differing conclusions regarding an achievable recovery population size in northern California.

The results of this study draw attention to active source-sink processes working within the Pacific coast snowy plover metapopulation. However, because this study focused specifically upon northern California, the model was limited to a simple source-sink structure and thus I cannot definitively draw inference about the status of other subpopulations and their relationship to surrounding sinks or sources. Therefore, given the coast-wide efforts by plover biologists to collect ample vital rate data since the analysis by Nur et al. (1999), I recommend that future work should be focused on a thorough reassessment of metapopulation structure and viability of snowy plovers across the Pacific coast. This will provide valuable information pertaining to the recovery potential of the species given the current delisting requirements.

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APPENDICES

Appendix A. Model components and life history parameters used in the stochastic VORTEX model to simulate snowy plover population viability in northern California.

Parameter	Description	Source of Information	Value
Number of iterations	Number of times simulation was run	NA	1000
Number of years	Number of years population was simulated	NA	50
Extinction definition	How extinction is defined in model (quasi-extinction)	NA	Population size (*N*) = 5.0
Number of populations	Number of populations in the model	NA	2 (NCA and PAC)
Inbreeding depression	The effect and level of inbreeding depression	Ralls et al. 1988, Lacy et al. 1996	Lethal equivalents = 3.14 Percent due to recessive alleles = 50%
Environmental variation (EV) correlation among populations	The level of correlation between the annual vital rates of each population	Estimated with data from Page et al. 2010, Lauten et al. 2010	0.728
Reproductive system	Mating system	Warriner et al. 1986	Serial Polyandry
Age of 1st reproduction in females	Age that females start breeding	Warriner et al. 1986	1
Age of 1st reproduction in males	Age that males start breeding	Warriner et al. 1986	1
Maximum age of life	Maximum age that females and males live	Page et al. 1995	15
Maximum number of broods per year	Maximum number of successful nests fathered by a male each year	Warriner et al. 1986	2
Maximum number of progeny per brood	Maximum number of eggs fathered in each nest	Warriner et al. 1986	3
Sex ratio at birth	Sex ratio of offspring at hatching	Székely et al. 2004	1:1
Percent adult males nesting	Proportion of adult males that establish at least one nest each year	Estimated with NCA data and assumed to be comparable	NCA = 97.22%, PAC = 97.22%
Environmental variability in percent adult males nesting	Annual variation in the proportion of nesting adult males	Estimated with NCA data and assumed to be comparable	NCA = 4.04%, PAC = 4.04%
Distribution of successful broods per year	Discrete probability distribution of nesting males fathering 0, 1, or 2 broods per year that successfully produce at least one fledgling	NCA: Estimated in this study; PAC: Estimated with data from Lauten et al. 2010	NCA: 0 = 64.40%, 1 = 28.34%, 2 = 7.26% PAC: 0 = 43.37%, 1 = 36.23%, 2 = 20.40%

Appendix A. Model components and life history parameters used in the stochastic VORTEX model to simulate snowy plover population viability in northern California (continued).

Parameter	Description	Source of Information	Value
Distribution of the number of fledglings produced per male per brood per year	Discrete probability distribution of males fathering 1, 2, or 3 fledglings per successful brood per year	NCA: Estimated in this study; PAC: Estimated in this study using data from Lauten et al. 2010	NCA: 0 = 45.98%, 1 = 26.81%, 2 = 27.21% PAC: 0 = 33.98%, 1 = 31.84%, 2 = 34.18%
Female Juvenile Mortality	Mean and standard deviation mortality rates for juvenile females	NCA: Estimated in this study; PAC: Stenzel et al. 2007	NCA: 0.769 ± 0.094 PAC: 0.537 ± 0.072
Female Adult Mortality	Mean and standard deviation mortality rates for adult females	NCA: Estimated in this study; PAC: Stenzel et al. 2011	NCA: 0.375 ± 0.119 PAC: 0.307 ± 0.089
Male Juvenile Mortality	Mean and standard deviation mortality rates for juvenile males	NCA: Estimated in this study; PAC: Stenzel et al. 2007	NCA: 0.769 ± 0.094 PAC: 0.537 ± 0.072
Male Adult Mortality	Mean and standard deviation mortality rates for adult males	NCA: Estimated in this study; PAC: Stenzel et al. 2011	NCA: 0.375 ± 0.119 PAC: 0.266 ± 0.095
Dispersing classes	Ages and sexes that are able to disperse	USFWS 2007, Stenzel et al. 2007	Ages: 1 through 15 Sexes: Both
Percent Survival of Dispersers	Additive mortality risk associated with dispersing	Unknown	Assumed no additive risk (100%)
Immigration	Probability of annual movement of individuals from PAC to NCA (%)	Estimated using Unpublished USFWS Breeding Window Survey Data	2.07 ± 1.42
Emigration	Probability of annual movement of individuals from NCA to PAC (%)	Estimated in this study using Lauten et al. 2010	10.32 ± 4.08
Catastrophe frequency	Average length of the interval between cold snaps (years)	Estimated in this study	14.75
Catastrophe severity	The proportional change in the baseline survival when a cold snap catastrophe occurs	Estimated in this study	NCA: 0.738 PAC: 0.931
Initial population size	Number of individuals at the start of the simulation (2001)	NCA: Colwell et al. 2011; PAC: Unpublished USFWS Breeding Window Survey Report	NCA= 36 PAC = 799
Carrying capacity	The baseline carrying capacity of the environment of each population	Nur et al. 1999	NCA = 200 PAC = 1300
Carrying capacity EV	Variation in carrying capacity	Unknown	Assumed none (0)

Appendix B. Estimation of juvenile and adult survival in northern California between 2001 and 2011.

I used an 11-year (2001-2011) mark-resight dataset to estimate adult and juvenile survival with a Cormack-Jolly Seber model in Program MARK (White and Burnham 1999) for the demographically open northern California population. I used the R (R Development Core Team 2007) package RMark (Laake and Rexstad 2008) to build and compare a set of *a priori* models that included covariates such as sex, age, and year to predict variation in apparent survival and detection probability. I ranked competitive models based on Akaike information criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002). To remove sampling variance, I estimated process variance using the variance components procedure in Program MARK (White et al. 2001). For a few individuals that permanently emigrated to Oregon, band combinations were resighted and reported. However there was a severe lack of reported northern California emigrants that bred elsewhere on the Pacific coast, therefore I only included mark-resight data collected within northern California and the few cases of those reported in Oregon. Because of this limitation, survival estimates are likely biased low because of permanent emigration. For the Pacific coast, I used published estimates of juvenile and adult sex-specific true survival of plovers in Monterey Bay corrected for process variance (Stenzel et al. 2007, Stenzel et al. 2011).

While keeping apparent survival constant, I tested four model structures of detection probability that included constant, year, linear across time, and quadratic across time. I ranked these models according to AICc and determined that the linear across time was the best structure. I then built models to explain variation in apparent survival as a

Appendix B. Estimation of juvenile and adult survival in northern California between 2001 and 2011 (continued).

function of age (juvenile or adult), constant, year, linear across time, and quadratic across time. The global model was a good fit to the data ($\chi^2{}_{52} = 45.21,\ P = 0.736$), with no evidence of lack of fit detected by using the median ĉ estimator in Program MARK (ĉ = 1.01); thus I did not adjust ĉ. The top model was overwhelmingly competitive and included the influence of age and year on apparent survival and a linear time trend in detection probability (Appendix C). In the top model, adult survival was higher than juvenile survival ($\hat{\beta}_{\text{Adult}} = 1.69, 95\%\ \text{CI} = 1.33$ to 2.06), and annual variation in survival was highest between 2009 and 2010 ($\hat{\beta}_{2009-2010} = 1.31, 95\%\ \text{CI} =$ 0.24 to 2.37) and lowest between 2006 and 2007 ($\hat{\beta}_{2006-2007} = -1.13, 95\%\ \text{CI} =$ -1.81 to $-\ 0.45$; Appendix D). Average apparent survival estimates corrected for process variance were greater for adults ($\widehat{\phi}_{\text{Adult}} = 0.62 \pm 0.13$) than juveniles ($\widehat{\phi}_{\text{Juvenile}} = 0.23 \pm 0.09$). Apparent survival estimates for juveniles and adults were comparable to those estimated in northern California by Mullin et al. (2010).

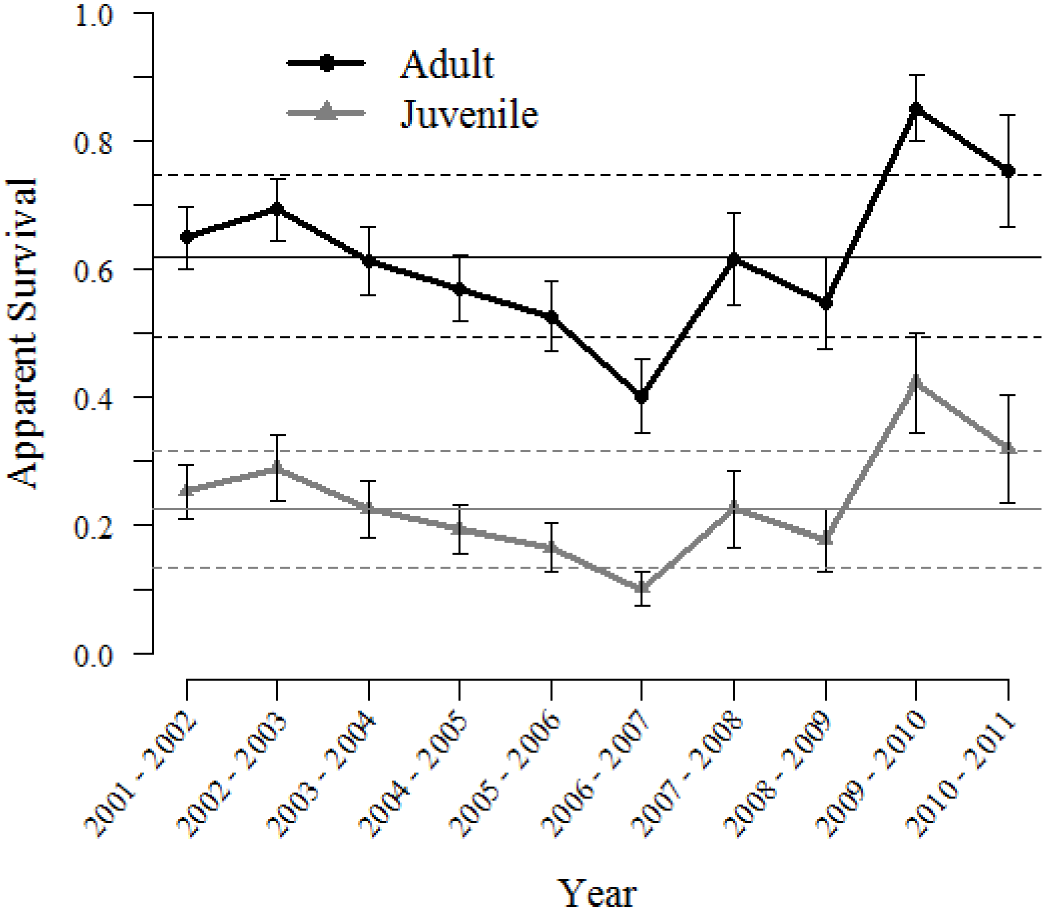
The estimates of adult and juvenile survival in Monterey Bay from Stenzel et al. (2007) and (2011) were calculated in Program MARK from mark-resight-recovery data using a Barker model and sampling variance was removed with the variance components procedure in Program MARK (White et al. 2001). Stenzel et al. (2011) found that adult survival for males ($\phi_{\text{Male}} = 0.73 \pm 0.02$) was greater than females ($\phi_{\text{Female}} = 0.69 \pm 0.03$). Similar to my survival estimates for northern California, Stenzel et al. (2007) found that juvenile survival ($\phi_{\text{Juvenile}} = 0.46 \pm 0.07$) was lower than adult survival.

Appendix C. Model selection results examining apparent survival and conditional detection probability for snowy plovers in northern California between 2001 and 2011. Model effects included constant and linear time trends (Time), and differences between years (Year), sex, and age (Age; juvenile or adult) of a bird. The table has models ranked by ΔAICc values corrected for small sample size, and also includes the model weight (w_i), number of parameters (K), and model deviance.

Model Structure		**ΔAICc**[a]	**w_i**[b]	**K**	**Deviance**
Apparent Survival	Detection Probability				
Age + Year	Time	0	0.998	13	302.542
Age	Time	17.633	0.001	4	338.617
Age + Time	Time	18.134	0.001	3	341.140

[a] The AIC value for the top model was 1093.95

[b] Only models with $w_i > 0.0001$ are shown above.



Appendix D. Apparent survival estimates of the top model in the survival analysis for snowy plovers in northern California between 2001 and 2011 corrected for process variance. Solid and dashed horizontal lines refer to average and standard errors (black: $\widehat{\phi}_{\mathrm{adults}} = 0.62 \pm 0.13$, grey: $\widehat{\phi}_{\mathrm{juveniles}} = 0.23 \pm 0.09$). Variation in apparent survival was best explained by age and year.

Appendix E. Estimation of movement between northern California and the Pacific coast.

The northern California plover population is considered a sink because productivity is consistently too low to offset mortality of adults and juveniles and thus it is maintained by immigrants originating from elsewhere along the Pacific coast (Mullin et al. 2010). Therefore to accurately assess future population viability of northern California, it was important to address the role of immigration and emigration. I obtained annual immigration rates by calculating the proportion of the Pacific coast population in year *t* – 1 that immigrated to northern California in year *t*:

$$\psi_{t_{\text{PAC,NCA}}} = \frac{\text{N}_{t_{\text{Immigrants}}}}{\text{N}_{t-1_{\text{NCA}}}}$$

where $\psi_{t_{\text{PAC,NCA}}}$ is the immigration rate from the Pacific coast to northern California in year *t*, $\text{N}_{t_{\text{Immigrants}}}$ is the number of immigrants in year *t*, and $\text{N}_{t-1_{\text{PAC}}}$ is the population size of the Pacific coast in year *t* – 1. I obtained annual Pacific coast population estimates from coast wide breeding window surveys conducted every year since 2002 over a one week period in late May (USFWS unpublished reports). The entire northern California population is banded, which allowed observers to recognize annual immigrants by color band combinations given to birds elsewhere on the Pacific coast, or by lack of bands. Likewise, I obtained annual emigration rates by calculating the proportion of northern California in year *t* – 1 that emigrated to the Pacific coast in year *t*:

$$\psi_{t_{\text{NCA,PAC}}} = \frac{\text{N}_{t_{\text{Emigrants}}}}{\text{N}_{t-1_{\text{NCA}}}}$$

Appendix E. Estimation of movement between northern California and the Pacific coast (continued).

where $\psi_{t_{\mathrm{NCA,PAC}}}$ is the emigration rate from northern California to the Pacific coast in year *t*, $\mathrm{N}_{t_{\mathrm{Emigrants}}}$ is the number of emigrants in year *t*, and $\mathrm{N}_{t-1_{\mathrm{NCA}}}$ is the population size of northern California in year *t*-1.

Reporting of northern California emigrants from along the Pacific coast was limited to Oregon, where biologists published annual reports detailing the origin of marked immigrants (Lauten et al. 2004, 2005, 2006, 2007, 2008, 2009, 2010). Although I did not have reports of northern California emigrants from elsewhere on the Pacific coast, dispersal rate declines rapidly with distance from the natal population (Stenzel et al. 2007). Oregon's beaches are the nearest sites to northern California; therefore it was valid to use only data from Oregon to evaluate movements. Furthermore, the importance of the emigration rate's precision was evaluated in an elasticity analysis.

The annual emigration rate from northern California to the Pacific coast ranged from 15.87 percent in 2006 to 5.56 percent in 2009, with an average and standard deviation of 10.32 ± 4.08 percent. Annual immigration rates from the Pacific coast to northern California were lower (2.07 ± 1.42 percent) and ranged from 5.48 percent in 2004 to 0.31 percent in 2009.

There was no significant evidence supporting density dependent movement between the northern California population and the surrounding populations of Oregon, San Fransisco Bay, and Monterey Bay. In addition to movement, all other vital rates did not have significant correlations with the size of either population.

Appendix F. Estimation of productivity distributions.

VORTEX simulates population change based, in part, on the reproductive performance of individuals, in this case male plovers. I assigned three sequential productivity probabilities each year (Figure 2) according to the following distributions: 1) probability of nesting, 2) probability of producing 0, 1, or 2 successful broods, and 3) for each successful brood, the probability of producing 1, 2, or 3 fledglings. I used data for males because they are solely responsible for the parental care of chicks and are thus the limiting sex for reproductive success (Warriner et al. 1986). I assumed a 1:1 sex birth ratio because there is no evidence to suggest otherwise (Kentish plover: Székely et al. 2004).

I used annual productivity data from northern California to estimate the distribution of the probability of nesting for each population by calculating the average and standard deviation of the proportion of the male population that nested each year between 2001 and 2011. I did not have data from the Pacific coast population that allowed me to make a similar calculation for the Pacific coast and thus I assumed nesting probability was the same as northern California. Although this is an assumption, I believe this is a conservative approach considering that Nur et al. (1999) assumed 100 percent nesting probability. All of the following productivity distributions were calculated from the nesting proportion of each population.

I calculated the successful brood distribution for northern California between 2001 and 2011 as:

Appendix F. Estimation of productivity distributions (continued).

$$P(x \text{ successful broods}) = \frac{\sum_{t=1}^{11} \sum_{x=0}^{2} \mathrm{N}_{t,x}}{\sum_{t=1}^{11} \mathrm{N}_t}$$

where $P(x$ successful broods) is the probability of having x successful broods (0, 1, or 2) and $\mathrm{N}_{t,x}$ is the number of nesting males at year t with x successful broods. Similarly, I calculated the fledgling distribution for northern California as:

$$P(y \text{ fledglings per successful brood}) = \frac{\sum_{t=1}^{11} \sum_{y=1}^{2} \mathrm{N}_{t,y}}{\sum_{t=1}^{11} \mathrm{N}_t}$$

where $P(y$ fledglings per successful brood) is the probability of having y fledglings per successful broods (1, 2, or 3) and $\mathrm{N}_{t,y}$ is the number of nesting males at year t with y number of fledglings per successful brood. To evaluate how well the two northern California productivity distributions conformed to an expected Poisson distribution, I used a chi-square goodness-of-fit test with $\alpha = 0.05$.

For the Pacific coast population, calculating the productivity distributions was more challenging because I did not have access to individual lifetime reproductive effort data. Consequently, I used annual productivity parameters that were available from Oregon's published reports to estimate the expected number of successful broods per nesting male ($\hat{\xi}_b$) between 2001 and 2010 as:

$$\hat{\xi}_b = \frac{1}{10} \sum_{t=1}^{10} \frac{\beta_t \times \mathrm{B}_t}{\mathrm{N}_t}$$

where β_t is the brood success in year t, B_t is the number of broods in year t, and N_t is the number of nesting males in year t. Then, to calculate the discrete distribution of

Appendix F. Estimation of productivity distributions (continued).

successful broods per nesting male for the Pacific coast, I used the Poisson formula:

$$f(k_b;\ \hat{\xi}_b) = \frac{\hat{\xi}_b^{\ k_b} e^{-\hat{\xi}_b}}{k_b!}$$

where k_b is the number of successful broods per nesting male per year (0, 1, or 2). Likewise, I used annual productivity parameters that were available from Oregon's published reports to first estimate the expected number of fledglings per successful brood per nesting male ($\hat{\xi}_f$) between 2001 and 2010 as:

$$\hat{\xi}_f = \frac{1}{10} \sum_{t=1}^{10} \frac{\mathrm{F}_t}{\beta_t \times \mathrm{N_t}}$$

where F_t is the total number of fledglings produced in year *t*, β_t is the brood success in year *t*, and N_t is the number of nesting males in year *t*. Then, to calculate the discrete distribution of fledglings per successful brood per nesting male for the Pacific coast, I used the Poisson formula:

$$f(k_f;\ \hat{\xi}_f) = \frac{\hat{\xi}_f^{\ k_f} e^{-\hat{\xi}_f}}{k_f!}$$

where k_f is the number of fledglings per successful brood per nesting male per year (1, 2, or 3). The right tails of both the brood and fledgling distributions of the Pacific coast were collapsed into the 2 broods and 3 fledglings categories of each distribution respectively.

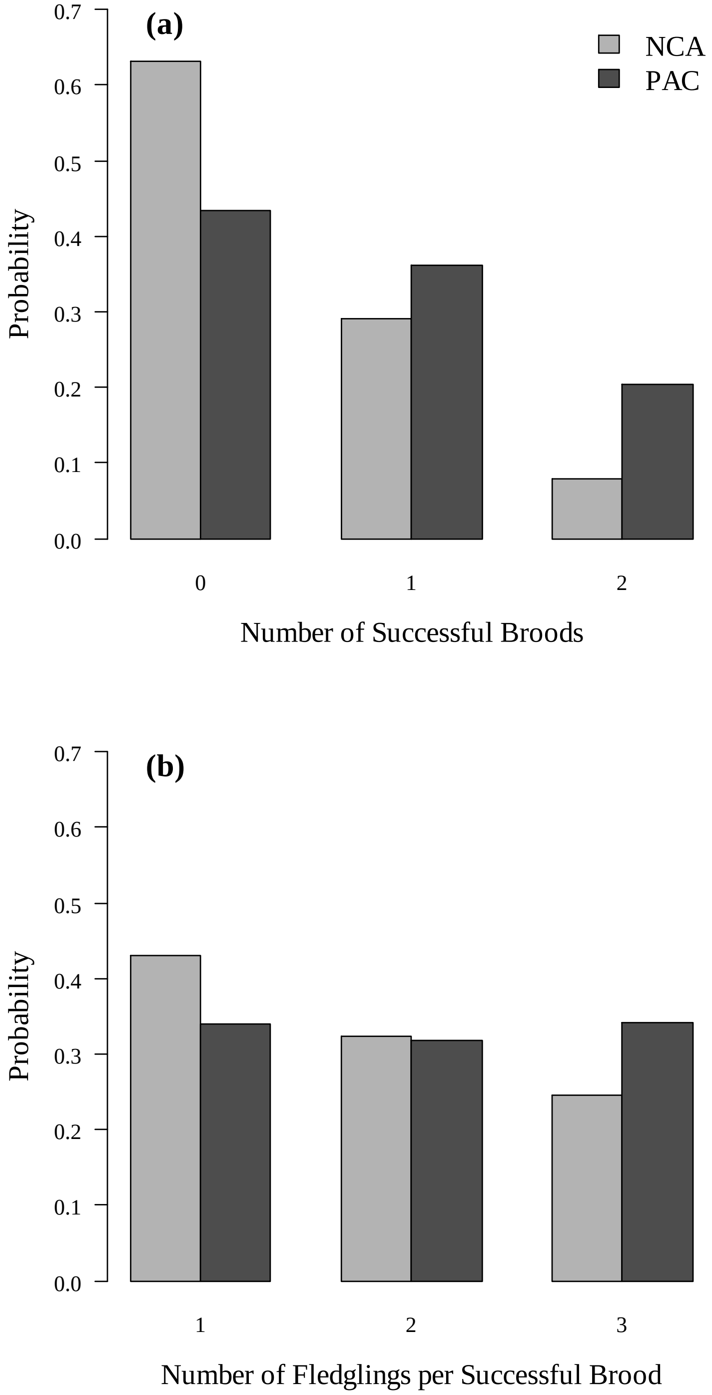
The percent of the male population nesting varied in northern California between 100 percent for most years and 90 percent in 2011, with an average and standard deviation of 97.22 ± 4.04 percent. Between 2001 and 2011 there were a total of 177 males in northern California that had zero successful broods in a year, 112 with one, and 10 with two. This translated into an expected number of successful broods per nesting male of 0.44 for northern California. In comparison, the Pacific coast had an expected number of successful broods per nesting male of 0.84 averaged between 2001 and 2010. Likewise, between 2001 and 2011 there were a total of 49 successful broods in northern California that produced one fledgling, 56 that produced two, and 25 that produced three. This translated into an expected number of fledglings per successful brood of 1.82 for northern California. In comparison, the Pacific coast had an expected number of fledglings per successful brood of 1.87 averaged between 2001 and 2010. Both productivity distributions of northern California varied significantly from the expected Poisson distribution (successful broods per nesting male: $\chi^2_{1,99} = 5.72, P = 0.017$; fledglings per successful brood: $\chi^2_{1,99} = 14.14, P \ll 0.05$). Consequently I used the expected Poisson probabilities for each distribution. The respective brood and fledgling distributions of the two populations revealed that the productivity of the Pacific coast was higher than northern California (Appendix H).

It was not surprising to find that both the brood and fledgling distributions were greater in the Pacific coast ($\hat{\xi}_b = 0.84, \hat{\xi}_f = 1.87$) than in northern California ($\hat{\xi}_b = 0.44, \hat{\xi}_f = 1.82$; Appendix H) because management throughout the Pacific coast uses various methods such as nest exclosures and lethal predator removal to boost productivity. The successful broods per nesting male of the Pacific coast was almost twice as high as that of northern California suggesting that predator management is most effective at increasing the expected number of successful broods per male, possibly because predators are most responsible for egg loss as opposed to chick loss (Page et al. 1983). However, it is important to point out that this assumes that the differences in the productivity distributions are solely due to predator management and not other environmental factors that could boost productivity in the Pacific coast population.

To translate the successful brood and fledgling productivity metrics that I calculated for the VORTEX simulation into the “fledged chicks per nesting male” productivity criteria used in the USFWS Recovery Plan, I assessed the correlation between the $\xi_b \times \xi_f$ of the Pacific coast and the reported fledged chicks per male in the Pacific coast for all years between 2004 and 2010. As expected, this regression was highly significant (Pearson’s product-moment correlation: $t_6 = 70.65, P \ll 0.001$, $r^2 = 0.999$) and produced the following productivity correction formula:

$$\text{Fledged chicks per nesting male} = 0.8544 \times \hat{\xi}_b \times \hat{\xi}_f$$

which allowed me to extrapolate fledged chicks per nesting male metrics from perturbed successful brood and fledglings vital rates for the various scenarios of management and the elasticity analysis. I did this with the intent to report my findings in a format (i.e., fledged chicks per nesting male) familiar to those who manage snowy plovers. By using the correction formula and baseline expected productivity rates of both populations, the annual average fledged chicks per nesting male in northern California was 0.68 whereas the Pacific coast was 1.32.



Appendix G. (a) Baseline successful brood distribution for nesting males of northern California (NCA) and the Pacific coast (PAC), and (b) baseline fledglings per successful brood distribution for nesting males of northern California and the Pacific coast.

Appendix H. Perturbed vital rate estimates used in the elasticity analysis.

Vital Rate	Direction of Perturbation[a]	Baseline Parameter Value	10%	20%	50%
Juvenile Mortality					
NCA	-	0.77 ± 0.09	0.69 ± 0.09	0.62 ± 0.09	0.38 ± 0.09
PAC	-	0.54 ± 0.07	0.48 ± 0.07	0.43 ± 0.07	0.27 ± 0.07
Adult Mortality					
NCA	-	0.38 ± 0.12	0.34 ± 0.12	0.30 ± 0.12	0.19 ± 0.12
$\text{PAC}_{\text{Females}}$	-	0.31 ± 0.09	0.28 ± 0.09	0.25 ± 0.09	0.15 ± 0.09
$\text{PAC}_{\text{Males}}$	-	0.27 ± 0.10	0.24 ± 0.10	0.21 ± 0.10	0.13 ± 0.10
Immigration (%)	-	2.07 ± 1.42	1.86 ± 1.42	1.66 ± 1.42	1.04 ± 1.42
	+	2.07 ± 1.42	2.28 ± 1.42	2.48 ± 1.42	3.11 ± 1.42
Emigration (%)	-	10.32 ± 4.08	9.29 ± 4.08	8.26 ± 4.08	5.16 ± 4.08
Males Breeding (%)					
NCA	+	97.2 ± 4.04	100 ± 4.04	NA	NA
PAC	+	97.2 ± 4.04	100 ± 4.04	NA	NA
Successful Broods					
$\hat{\xi}_{b_{\text{NCA}}}$	+	0.44	0.48	0.53	0.66
$\hat{\xi}_{b_{\text{PAC}}}$	+	0.84	0.92	1.01	1.26
Fledglings per Brood					
$\hat{\xi}_{f_{\text{NCA}}}$	+	1.82	2.00	2.18	2.73
$\hat{\xi}_{f_{\text{PAC}}}$	+	1.87	2.06	2.24	2.81
Environmental Variation (EV) Correlation	-	0.73	0.66	0.58	0.36
	+	0.73	0.80	0.87	1

[a] Perturbations were made in the direction that would hypothetically increase the growth of northern California, unless specified otherwise.

Appendix H. Perturbed vital rate estimates used in the elasticity analysis (continued).

Vital Rate	Direction of Perturbation[a]	Baseline Parameter Value	10%	20%	50%
Inbreeding					
Lethal Equivalents per Individual	-	3.14	2.83	2.51	1.57
Deleterious Alleles (%)	-	50	45	40	25
Catastrophe Severity					
NCA	+	0.74	0.81	0.89	1.00
PAC	+	0.93	1.00	1.00	1.00
Global Catastrophe Frequency	-	0.14	0.13	0.11	0.07
Carrying Capacity					
NCA	-	200	180	160	100
	+	200	220	240	300
PAC	-	1300	1170	1040	650
	+	1300	1430	1560	1950
Initial Population Size					
NCA	-	36	32	31	18
	+	36	40	43	54
PAC	-	799	719	639	400
	+	799	879	959	1199

[a] Perturbations were made in the direction that would hypothetically increase the growth of northern California, unless specified otherwise.

Appendix I. Correlation in environmental variation.

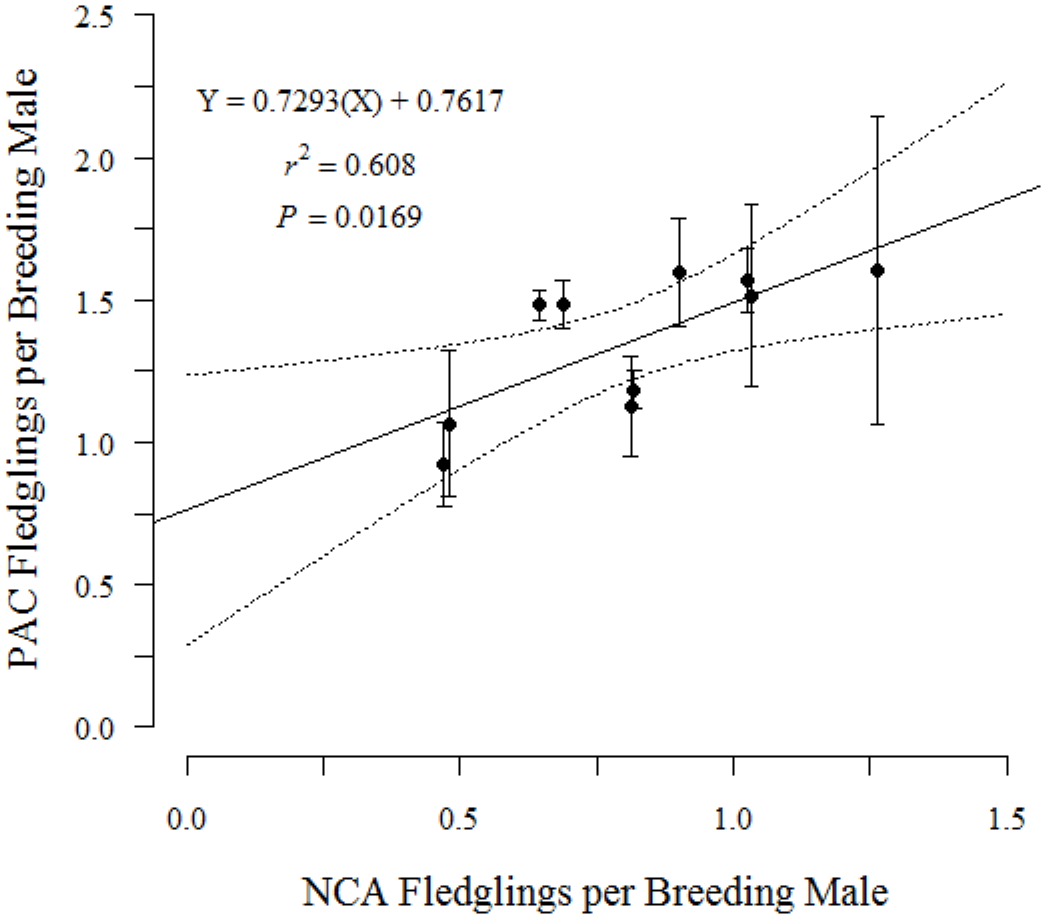
The annual productivity of subpopulations within the Pacific coast population was not correlated (Oregon and Monterey Bay: Pearson's product-moment correlation: $t_8 = -0.724, P = 0.49, r^2 = 0.061$), a similar finding to that of Nur et al. (1999). However, there was a stronger correlation between the productivity of northern California and Monterey Bay (Pearson's product-moment correlation: $t_8 = 3.57, P = 0.007$, $r^2 = 0.614$), than northern California and Oregon (Pearson's product-moment correlation: $t_8 = 0.0462, P = 0.964, r^2 = 0.000$). To find a balance between the two extremes in spatial correlation within what I defined as the Pacific coast, I used the average of Monterey Bay and Oregon's annual fledglings per male (*y*-axis of Appendix J).

There was evidence that the annual fledglings produced per breeding male was positively correlated between northern California and the Pacific coast (Pearson's product-moment correlation: $t_8 = 3.01, r^2 = 0.608, P = 0.017$; Appendix J). I included this correlation coefficient in the VORTEX model so that fate of one population's productivity was dependent upon the other population. All other vital rates did not show any significant correlations between the two populations nor with each other (i.e. survival and productivity).

The correlation in the productivity of both populations was a new finding for snowy plovers across the Pacific coast. Spatial correlation in vital rates for metapopulations has been well documented in other avian species (Kanyamibwa et al. 1993, Akçakaya and Atwood 1997, Ringsby et al. 2002, Wintle et al. 2005) because it is

Appendix I. Correlation in environmental variation.

expected that local populations are most likely exposed to similar fluctuations in the timing of management regimes or environmental pressures such as climate and predator and prey abundance.



Appendix J. Correlation in productivity between northern California (NCA) and the Pacific coast (PAC) from 2001 to 2010. Standard error bars refer to the averaged Pacific coast productivity derived from annual Monterey Bay and Oregon estimates of fledglings produced per nesting male.

Appendix K. Inbreeding.

Inbreeding has been documented in northern California in recent years and may be related to low hatchability of eggs (Colwell and Pearson 2011). Thus, it was important to consider the role of inbreeding depression for the viability of the northern California plover population. There are no published estimates of lethal equivalents per diploid individual for snowy plovers. Thus, I used the default value in VORTEX that is a summary statistic based on a survey of 40 captive vertebrate populations (3.14 *from* Ralls et al. 1988). Furthermore, there is no published information on the percent of the total genetic load that is due to recessive lethal alleles in snowy plovers. Thus I used a default value in VORTEX that is based on a few well studied species (50 percent *from* Lacy et al. 1996). To evaluate the relative importance in the precision of these assumed inbreeding statistics, I perturbed them in an elasticity analysis (see Appendix O for results).

Appendix L. Catastrophic severe winter weather.

The catastrophic effect of severe weather on the over-winter survival of shorebirds has been well documented (Parr 1992, Yalden and Pearce-Higgins 1997, Durell et al. 2006, Roche et al. 2010). The results from the *a priori* survival analysis found dramatic annual variation in apparent survival in northern California (see Appendix B). This prompted a *post hoc* analysis investigating the influence of prolonged cold winter weather on apparent survival of plovers in northern California.

I quantified cold winters by summing the total number of days that fell below one standard deviation of the 1941 to 2011 daily minimum temperature average between the winter months of December and February in northern California. Between 1951 and 2011, the average daily minimum winter temperature was 5.53 ± 3.24°C. Therefore, I counted days that were below 2.29°C as days that met the cold weather criteria. I defined winters with significant cold weather as those that had more than one standard deviation above the annual average number of days below 2.29°C between 1941 and 2011 ($\hat{x} = 12.81 \pm 7.72$). This meant that winters with more than 20 days below 2.29°C were considered significantly cold winters. Between 1941 and 2011, significant winters occurred during the winters of 1948, 1949, 1956, 1978, 1998, 2000, 2006, 2007, and 2008 resulting in a frequency of 14.75 years.

Other studies have found that broad-scale climate indices such as the El Niño-Southern Oscillation and North Atlantic Oscillation have strong relationships to the over-winter survival of avian species (Robinson et al. 2007, LaManna 2010), however Stenzel et al. (2007) found that this was not the case for snowy plovers in Monterey Bay. To acknowledge the potential effects of a broad scale climate index, I included the same metric used by Stenzel et al. (2007) as a covariate predicting annual variation in apparent survival, which was the sum of the winter monthly El Niño-Southern Oscillation indices for 2001 to 2011. I also tested two other climate covariates from northern California to acknowledge other potential unknown phenomena: the total amount of winter precipitation and the average negative deviance from 2.29°C of each winter. In addition to these climate covariates, I used the summed total number of days that fell below 2.29°C for each winter between 2001 and 2011 as a covariate predicting variation in apparent survival using the R (R Development Core Team 2007) package RMark (Laake and Rexstad 2008) to construct Cormack-Jolly Seber models in Program MARK (White and Burnham 1999). I acquired all climate data from the University of California Davis (UCD 2011).

The *a priori* analysis demonstrated that a linear time trend described variation in detection probability the best when apparent survival was held constant, thus I used this structure of detection probability for all models in the *post hoc* analysis (Lebreton et al. 1992). To be able to compare the *post hoc* analysis to that of the *a priori* survival analysis (Appendix B), I used the same constants and factors (sex, age, and year) in the candidate model set predicting variation in apparent survival and detection probability. To acknowledge the possible confounding effect of nest exclosure management on adult survival (Hardy and Colwell 2008), I included additive models that incorporated a covariate quantifying the number of exclosures used in northern California each year. I

Appendix L. Catastrophic severe winter weather (continued).

selected competitive models based on Akaike information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002) and I estimated process variance using the variance components procedure in Program MARK (White et al. 2001). The predictive covariates met assumptions of normality with all covariates having $P >> 0.05$ using the Anderson-Darling test for normality.

The global model of the *post hoc* cold winter survival analysis was a good fit to the data (${\chi^2}_{52} = 45.21,\ P = 0.736$). There was no evidence of lack of fit detected by using the median ĉ estimator in Program MARK on the global model (ĉ = 1.00). The top model included the additive effects of nest exclosures, the total days below 2.29°C, and age on apparent survival (Appendix M, Appendix N). The winter monthly El Niño-Southern Oscillation index, total precipitation, and summed negative deviance of each winter were not competitive predictors of annual variation in survival. As I found with the *a priori* analysis, adult survival was higher than juvenile survival in the top model ($\hat{\beta}_{\text{Adult}} = 1.70, 95\%\ \text{CI} = 1.27\ \text{to}\ 2.13$). There was a negative effect of exclosures and the total days below 2.29 °C ($\hat{\beta}_{\text{Exclosures}} = -0.044, 95\%\ \text{CI} = -0.070\ \text{to} -0.019;\ \hat{\beta}_{\text{Days Below}} = -0.080,\ 95\%\ \text{CI} = -0.118\ \text{to} - 0.042$). The top two models both included the number of exclosures and age (Appendix M). The only difference in the structure of the second best model was that it included the average negative deviance in temperature from 2.29°C, however this model was relatively uncompetitive (ΔAICc = 5.44, $w_i = 0.06$; Appendix M).

I used the beta coefficients of the top model to predict juvenile and adult apparent

Appendix L. Catastrophic severe winter weather (continued).

survival in northern California based on the average annual number of days below 2.29°C observed between 1941and 2011, and zero nest exclosures used (the management currently being practiced):

$$\widehat{\phi}_{\mathrm{j}} = \frac{\mathrm{e}^{\beta_0+\beta_1(\text{average 1941 to 2011 days below})+\beta_2(0)}}{1+\mathrm{e}^{\beta_0+\beta_1(\text{average 1941 to 2011 days below})+\beta_2(0)}}$$

where $\widehat{\phi}_{\mathrm{j}}$ is the baseline apparent survival of plovers in age class j, β_0 is the intercept, β_1 is the total days below 2.29°C coefficient, and β_2 is the nest exclosure coefficient.

With this baseline survival rate I was able to quantify the severity of cold winter weather by calculating the proportional change in survival when a significant cold winter occurred:

$$\hat{S}_{\mathrm{NCA}} = 1 - \left(\frac{1}{n}\sum_{t=1}^{n}\frac{\phi_{t,j}}{\widehat{\phi}_j}\right)$$

where $\hat{S}_{\mathrm{NCA}}$ is the average severity of a significant cold winter on apparent survival in northern California, *n* is the number of significant cold winters observed between 2001 and 2011, $\phi_{t,j}$ is the estimated apparent survival in year *t* for individuals of age class *j*, and $\widehat{\phi}_j$ is the baseline apparent survival of plovers in age class *j*.

The severity of cold winter weather for the Pacific coast was calculated as the proportional change in the size of the Pacific coast from the 2001 to 2010 average population size after a significant cold winter occurred. Although this underestimates the effect of cold winters on survival in the Pacific coast, it is a conservative approach and was the best I could acquire given data availability. The frequency of cold winters was simply quantified as the average length of the interval between significant cold winters in years and was assumed to be equal for both populations.

Three significantly cold winters occurred between 2001 and 2011, with the first in the winter of 2006-2007 (24 days below 2.29°C) and the second and third in the following winters of 2007-2008 (29 days below 2.29°C) and 2008-2009 (28 days below 2.29°C; Appendix N). Using these metrics and zero nest exclosures in combination with the beta coefficients of the top model, the severity of cold winter weather ($\hat{S}_{\mathrm{NCA}}$) was calculated as 0.262 in northern California. The cold winter weather severity for the Pacific coast was calculated as 0.069. The severity of a cold winter on the Pacific coast was expected to be less than that of northern California because: 1) northern California is near the northern limits of the species' range, and 2) wintering plovers are more abundant in southern areas, where 3) warmer winter weather occurs.

Adult and juvenile survival experienced large fluctuations in northern California over the 11 year period ranging from 0.47 to 0.85 for adults and from 0.14 to 0.45 for juveniles (Appendix N). This trend was well explained by variation in the use of nest exclosures and the severity of cold weather over winter months. There is reason to suspect that there is a combination of factors that cause cold winter weather to compromise survival. Firstly, cold winter weather undoubtedly increases the thermoregulatory demands of plovers to levels that are not sustainable for prolonged periods of time, which potentially makes them susceptible to hypothermia or forces them to compromise immunodefence in an effort to increase metabolic performance (Piersma

Appendix L. Catastrophic severe winter weather (continued).

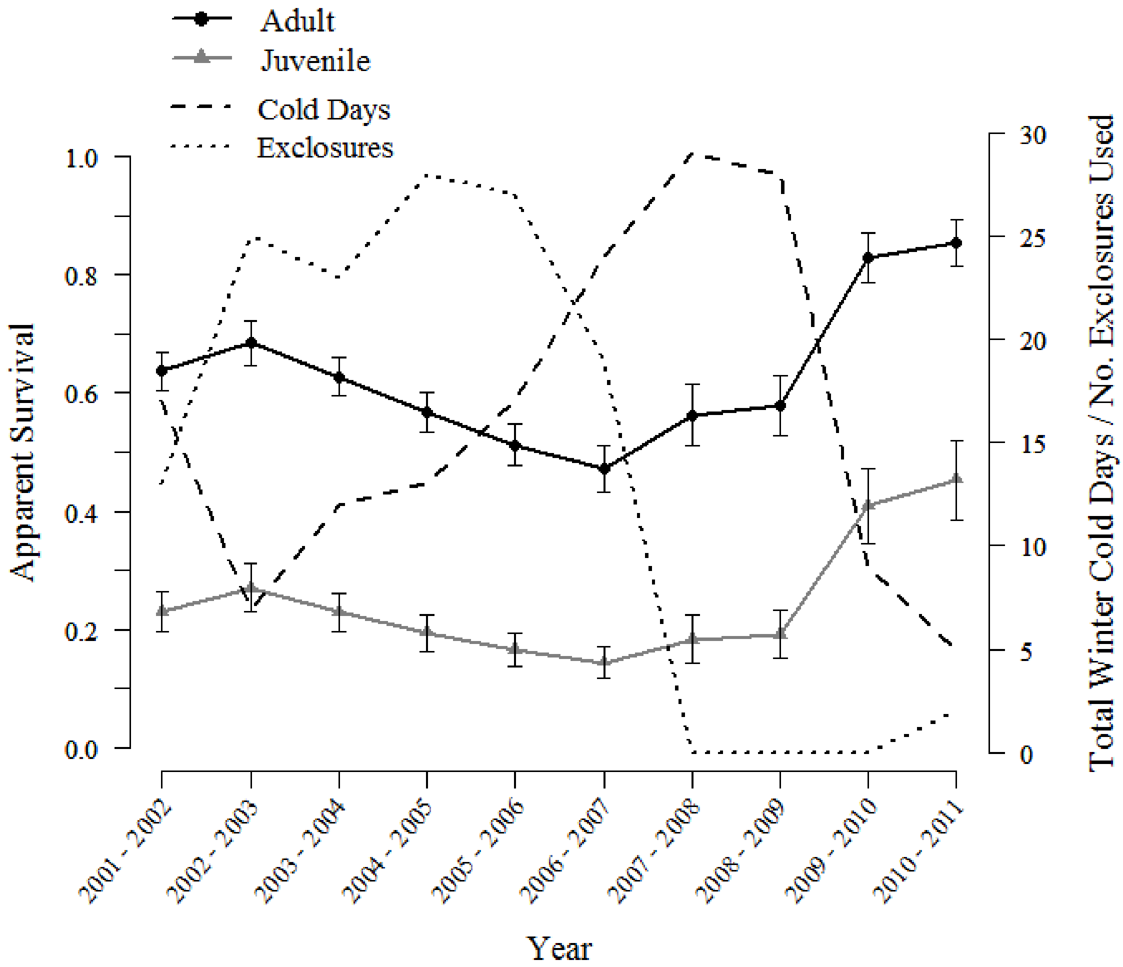
1997). Secondly, cold winter weather could reduce the availability of the plover's principal prey, amphipods (de March 1978, Pienkowski 1983, Marsden 1988, Williams 1995, Tsubokura et al. 1997, Tsoi et al. 2005).

Appendix M. Results of *post hoc* cold winter weather model selection used to explain apparent survival and conditional detection probability for snowy plovers in northern California between 2001 and 2011. Model effects included constant and linear time trends, number of exclosures used (Exclosures), number of days below 2.29°C (Σ Days Below), total winter precipitation (Precipitation), the average negative deviance from 2.29°C of outliers (AvgNegDeviance), and differences between years (Year) and age (Age) of a bird. The table has models ranked by ΔAICc values, corrected for small sample size, and also includes the model weight (w_i), number of parameters (K), and model deviance.

Model Structure		**ΔAICc**[a]	**w_i**[b]	**K**	**Deviance**
Apparent Survival	Detection Probability				
Exclosures + Σ Days Below + Age	Time	0	0.935	6	300.33
Exclosures + AvgNegDeviance + Age	Time	5.44	0.061	6	308.77
Age + Year	Time	11.63	0.003	13	300.58
AvgNegDeviance + Age	Time	16.55	0.002	5	321.90
Σ DaysBelow + Age	Time	17.23	0.002	5	322.58
$\sqrt{\Sigma \text{ Days Below} \times \text{AvgNegDeviance}} \times \text{Age}$	Time	17.48	0.002	6	320.81
Precipitation + AvgNegDeviance + Age	Time	18.33	0.001	6	321.65

[a] The AIC value for the top model was 1075.380

[b] Only models with $w_i > 0.0001$ are shown below.



Appendix N. Apparent survival estimates of the top model in the *post hoc* cold winter weather survival analysis for snowy plovers in northern California. Annual variation in apparent survival was best explained by age, the use of nest exclosures, and the total number of days below one standard deviation of the daily minimum temperature for winter months between 1941 and 2011.

Appendix O. Elasticity analysis results of the 50-year VORTEX simulation used to assess the population viability of snowy plovers in northern California. The scenario column indicates the parameter perturbed or management scenario tested, followed by the proportional change in the baseline vital rate, the stochastic growth rate of northern California ($\hat{r}_{s_{\text{NCA}}}$), the standard deviation (SD) of $\hat{r}_{s_{\text{NCA}}}$, the difference in predicted $\hat{r}_{s_{\text{NCA}}}$ and the elasticity (E) of the predicted $\hat{r}_{s_{\text{NCA}}}$ to the perturbation.

Scenario (Modified Parameter[s])	Proportional Change	$\hat{r}_{s_{\text{NCA}}}$	SD of $\hat{r}_{s_{\text{NCA}}}$	$\Delta\hat{r}_{s_{\text{NCA}}}$	E of $\hat{r}_{s_{\text{NCA}}}$[a]
Baseline	NA	0.008	0.248	NA	NA
Decreased adult mortality of NCA	0.1	0.009	0.241	0.001	1.25
	0.2	0.012	0.23	0.004	2.5
	0.5	0.019	0.205	0.011	2.75
Decreased adult mortality of PAC	0.1	0.011	0.241	0.003	3.75
	0.2	0.013	0.239	0.005	3.125
	0.5	0.015	0.234	0.007	1.75
Increased the expected number of successful broods per nesting male in NCA	0.1	0.007	0.252	-0.001	1.25
	0.2	0.008	0.25	0	0
	0.5	0.008	0.255	0	0
Increased the expected number of successful broods per nesting male in PAC	0.1	0.011	0.245	0.003	3.75
	0.2	0.012	0.242	0.004	2.5
	0.5	0.013	0.241	0.005	1.25
Increased carrying capacity of NCA	0.1	0.008	0.251	0	0
	0.2	0.008	0.251	0	0
	0.5	0.009	0.247	0	0.25
Decreased carrying capacity of NCA	0.1	0.007	0.247	-0.001	1.25
	0.2	0.008	0.244	0	0
	0.5	0.009	0.247	0.001	0.25
Increased carrying capacity of PAC	0.1	0.009	0.245	0.001	1.25
	0.2	0.01	0.246	0.002	1.25
	0.5	0.014	0.243	0.006	1.5
Decreased carrying capacity of PAC	0.1	0.005	0.252	-0.003	3.75
	0.2	0.002	0.256	-0.006	3.75
	0.5	-0.007	0.277	-0.015	3.75
Decreased the frequency of the cold weather catastrophe	0.1	0.008	0.246	0	0
	0.2	0.009	0.247	0.001	0.625
	0.5	0.009	0.241	0.001	0.25
Decreased the severity of the cold weather catastrophe	0.1	0.01	0.239	0.002	2.5
	0.2	0.01	0.232	0.002	1.25
	0.5	0.01	0.23	0.002	0.5

[a] Calculated as ($\Delta\hat{r}_{s_{\text{NCA}}}$/0.008)/(proportional change in the baseline vital rate).

Appendix O. Elasticity analysis results of the 50-year VORTEX simulation used to assess the population viability of snowy plovers in northern California. The scenario column indicates the parameter perturbed or management scenario tested, followed by the proportional change in the baseline vital rate, the stochastic growth rate of northern California ($\hat{r}_{s_{\text{NCA}}}$), the standard deviation (SD) of $\hat{r}_{s_{\text{NCA}}}$, the difference in predicted $\hat{r}_{s_{\text{NCA}}}$ and the elasticity (E) of the predicted $\hat{r}_{s_{\text{NCA}}}$ to the perturbation (continued).

Scenario (Modified Parameter[s])	Proportional Change	$\hat{r}_{s_{\text{NCA}}}$	SD of $\hat{r}_{s_{\text{NCA}}}$	$\Delta\hat{r}_{s_{\text{NCA}}}$	E of $\hat{r}_{s_{\text{NCA}}}$[a]
Baseline	NA	0.008	0.248	NA	NA
Decreased emigration from NCA	0.1	0.008	0.252	0	0
	0.2	0.008	0.251	0	0
	0.5	0.009	0.248	0.001	0.25
Increased the annual correlation in the vital rates of NCA and PAC	0.1	0.007	0.249	-0.001	1.25
	0.2	0.008	0.248	0	0
	0.5	0.008	0.249	0	0
Decreased the annual correlation in the vital rates of NCA and PAC	0.1	0.007	0.247	-0.001	1.25
	0.2	0.007	0.243	-0.001	0.625
	0.5	0.007	0.238	-0.001	0.25
Increased the expected number of fledglings per successful brood in NCA	0.1	0.008	0.249	0	0
	0.2	0.008	0.249	0	0
	0.5	0.008	0.251	0	0
Increased the expected number of fledglings per successful brood in NCA	0.1	0.009	0.248	0.001	1.25
	0.2	0.011	0.243	0.003	1.875
	0.5	0.013	0.241	0.005	1.25
Increased immigration to NCA	0.1	0.008	0.248	0	0
	0.2	0.011	0.244	0.003	1.875
	0.5	0.014	0.238	0.006	1.5
Decreased immigration to NCA	0.1	0.006	0.254	-0.002	2.5
	0.2	0.003	0.258	-0.005	3.125
	0.5	-0.006	0.287	-0.014	3.5
Increased the inbreeding depression	0.1	0.007	0.251	-0.001	1.25
	0.2	0.006	0.248	-0.002	1.25
	0.5	0.008	0.249	0	0
Decreased the inbreeding depression	0.1	0.007	0.247	-0.001	1.25
	0.2	0.008	0.248	0	0
	0.5	0.008	0.249	0	0
Increased the percent of males nesting in NCA	0.1	0.008	0.249	0	0
Increased the percent of males nesting in PAC	0.1	0.009	0.246	0.001	1.25

[a] Calculated as ($\Delta\hat{r}_{s_{\text{NCA}}}$/0.008)/(proportional change in the baseline vital rate).

Appendix O. Elasticity analysis results of the 50-year VORTEX simulation used to assess the population viability of snowy plovers in northern California. The scenario column indicates the parameter perturbed or management scenario tested, followed by the proportional change in the baseline vital rate, the stochastic growth rate of northern California ($\hat{r}_{s_{\mathrm{NCA}}}$), the standard deviation (SD) of $\hat{r}_{s_{\mathrm{NCA}}}$, the difference in predicted $\hat{r}_{s_{\mathrm{NCA}}}$ and the elasticity (E) of the predicted $\hat{r}_{s_{\mathrm{NCA}}}$ to the perturbation (continued).

Scenario (Modified Parameter[s])	Proportional Change	$\hat{r}_{s_{\mathrm{NCA}}}$	SD of $\hat{r}_{s_{\mathrm{NCA}}}$	$\Delta\hat{r}_{s_{\mathrm{NCA}}}$	E of $\hat{r}_{s_{\mathrm{NCA}}}$[a]
Baseline	NA	0.008	0.248	NA	NA
Increased the initial population size of NCA and PAC	0.1	0.006	0.247	-0.002	2.5
	0.2	0.005	0.248	-0.003	1.875
	0.5	0	0.245	-0.008	2
Decreased the initial population size of NCA and PAC	0.1	0.01	0.251	0.002	2.5
	0.2	0.012	0.252	0.004	2.5
	0.5	0.017	0.273	0.009	2.25
Decreased juvenile mortality in NCA	0.1	0.007	0.252	-0.001	1.25
	0.2	0.008	0.25	0	0
	0.5	0.008	0.255	0	0
Decreased juvenile mortality in NCA	0.1	0.009	0.244	0.001	1.25
	0.2	0.01	0.241	0.002	1.25
	0.5	0.016	0.228	0.008	2
Increased the total productivity in NCA (both broods and fledglings)	0.1	0.008	0.251	0	0
	0.2	0.008	0.251	0	0
	0.5	0.01	0.255	0.002	0.5
Increased the total productivity in PAC (both broods and fledglings)	0.1	0.012	0.244	0.004	5
	0.2	0.014	0.241	0.006	3.75
	0.5	0.016	0.241	0.008	2
2001 to 2011 baseline	NA	-0.056	0.301	NA	NA
Lethal predator removal	NA	0.01	0.262	0.002	NA
Nest exclosures	NA	0.007	0.255	-0.001	NA
No movement	NA	-0.413	0.306	-0.421	NA
Symbolic Fencing	NA	0.012	0.257	0.004	NA
Symbolic Fencing and Vehicle restriction (10%)	NA	0.019	0.244	0.011	NA
Symbolic Fencing and Vehicle restriction (5%)	NA	0.014	0.254	0.006	NA
Symbolic Fencing and Vehicle restriction (2%)	NA	0.012	0.255	0.004	NA
No cold weather catastrophe	NA	0.011	0.230	0.003	NA
NCA with same juvenile survival as PAC	NA	0.012	0.230	0.004	NA

[a] Calculated as ($\Delta\hat{r}_{s_{\mathrm{NCA}}}$/0.008)/(proportional change in the baseline vital rate).