



Assessing Vulnerability of Tidal Marsh Birds to Climate Change through the Analysis of Population Dynamics and Viability

Technical Report

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PRBO Climate Change and Tidal Marsh Bird Demograph	PRBO	Climate	Change	and Ti-	dal Mar	sh Bird	Demograph	١V
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EXECUTIVE SUMMARY

The vulnerability of species at risk from climate change is recognized as an important issue in California as well as globally. Assessing vulnerability requires information on the long-term viability of populations and understanding the influences on that viability, due to environmental drivers as well as impacts of management action. We developed population-dynamic models to assess and better understand the long-term population viability of four key, tidal marsh-dependent species, under a variety of environmental conditions, including climate change impacts. In the San Francisco Estuary, each species is represented by one or more subspecies that is entirely or mainly confined to the tidal marsh habitat in the region: California Black Rail (Laterallus jamaicensis coturniculus), a California Threatened species, California Clapper Rail (Rallus longirostris obsoletus), a Federally Endangered species, Saltmarsh Common Yellowthroat (Geothlypis trichas sinuosa), a California Species of Special Concern, and three tidal marsh subspecies of Song Sparrow, all of which are California Species of Special Concern: Alameda (Melospiza melodia pusillula), Samuel's (M. m. samuelis), and Suisun (M. m. maxillaris).

Availability of habitat is a prerequisite for long-term viability of marsh bird populations and this has been modeled in a companion California Landscape Conservation Cooperative project (Veloz et al. 2011). However, habitat alone will ensure neither resilience nor recovery of depleted and threatened populations. Two important population bottlenecks considered here are reproductive success and over-winter survival. An important component of reproductive success with respect to maximizing long-term viability and enhancing population resilience is the survival of clutches and broods from egg-laying to fledging; in particular, nest survival may be affected by flooding of nesting habitat leading to inundation of nests. The second bottleneck is overwinter survival which may be compromised when tidal marsh species are exposed to predators (e.g., herons and egrets) during the highest tides, if refugia for marsh birds are not available.

The study assessed future population trends and long-term viability due to anticipated changes in important climatic variables: precipitation, temperature, and maximum high tides. Detailed, mechanistic models were developed for one species, tidal marsh Song Sparrows. For these populations we drew on extensive, long-term field studies and our previous demographic analysis.

In this study we found that for tidal marsh Song Sparrows:

- One component of reproductive success, nest survival, decreased under cool, wet conditions. However, a second component, the number of reproductive attempts per breeding season, increased under cool, wet conditions. Field data indicated that cool, wet conditions allowed for a longer breeding season.
- Nest survival also decreased with increasing extreme tides, due to flooding of nests. One
 extreme tide during the breeding season diminished reproductive success for the entire
 season.
- Climate models suggest that, for this region, temperature will increase and precipitation will decrease in the future. In addition, some evidence suggests that the magnitude and

- frequency of extreme tides will increase, due to increased intensity and frequency of storms and sea-level rise.
- We modeled the impacts to long-term viability and trends of such climate-related effects of temperature, precipitation, and extreme tides, building on a previously developed model of marsh accretion for the San Francisco Estuary (Stralberg et al. 2011). We considered three alternatives for future sea-level rise scenarios: low (0.52 m/100 yrs), high (1.65 m/100 yrs), and an intermediate alternative. Our model incorporated assumptions of sedimentation and organic matter accumulation (Stralberg et al. 2011).
- Results indicate the most significant factor threatening long-term viability were especially high tides. Under the low sea-level rise scenario, populations are expected to increase by 5.0% or more per year from 2040 to 2060 due to high nest survival under the warm, dry conditions predicted in the future. However, under the high sea-level rise scenario, flooding risk to nests increases substantially. As a result, Song Sparrow populations are expected to decrease by 3 to 4% per year during the same time period. Under the latter scenario, populations are expected to decline, on average by 75% after 50 years.
- We quantified the risk of severe population decline, defined as an 80% decline over 50 years. Under the low sea-level rise scenario, such risk was very low (c. 2% probability) but with high sea-level rise, the risk was high (c. 60% probability).
- In addition, an extreme high tide, even if it occurred only once every 10 years, on average, is sufficient to substantially depress population growth rates, increasing the likelihood of population decline, and thus preventing population recovery and/or increasing the likelihood of local extinction. For example, under the medium sea-level rise scenario, the occurrence of infrequent extreme tides more than doubled the risk of severe population decline, from 12% probability to 28% probability.

For all four tidal marsh species:

- Relatively, short-term management actions (e.g., of a 20 year duration) can be effective in arresting and even reversing anticipated declines. A small reduction in predation on nests (by reducing predator populations or access to tidal marsh nesting habitat) can be sufficient to counteract expected population declines due to climate change.
- Improvement in nest survival represents a realistic management action that can modify current population trends, leading to, or enhancing population recovery.
- Overwinter survival is also an important bottleneck and management actions may be able to improve this parameter. Our models demonstrate changes to viability and future trends as a result of modification to this demographic parameter.

The demographic models presented here are especially valuable in that they can:

- (i) provide guidance to managers regarding which aspects of a species' ecology to focus attention on,
- (ii) demonstrate the benefits to affected species of potential management action,

- (iii) integrate the impacts of environmental influences that may have opposing effects on target species, demonstrating the long-term consequences to viability, and
- (iv) serve to identify the most important data gaps with respect to long-term viability and the efficacy of management actions. In this regard, we found that more information on the risks and consequences of extreme storm events (leading to especially high tides and impacting the habitat) is needed. In addition, more information on over-winter survival is a priority, too.

Whereas our results are of special relevance to wildlife resource managers in the San Francisco Estuary, the methods we have developed and described are applicable to estuarine bird populations anywhere, and thus the value of our approach extends beyond the specific species we have modeled. Insights from our modeling can help prioritize future action for a range of species and wetland habitats.

We are making our interactive population models available at http://data.prbo.org/apps/sfbslr/demography; in addition, our report and computer code will be freely available to others who wish to adapt our analytic and modeling approach. This study provides a valuable first stage toward our goal of integrating demographic impacts of climate change with modeling of future habitat change in the San Francisco Estuary to provide an effective decision support tool for managers, at the local and regional scales.

TABLE OF CONTENTS

EXECUTIVE SUMMARY	3				
Introduction					
Project objective and justification	9				
Overview of analysis and modeling approach	10				
Demographic parameters for population modeling of the tidal marsh species					
POPULATION DYNAMIC "MODEL 1" FOR THE FOUR TIDAL MARSH SPECIES					
Methods – Model 1	14				
Demographic Assumptions Applying to All Four Species	14				
Species-specific values of demographic parameters	15				
Results – Model 1	19				
Species-specific Results	19				
Model 2: Stochastic Model of Climate Change Impacts for a Focal Tidal Marsh Species					
Scenarios Evaluated	24				
Methods – Model 2					
Methods for Nest Monitoring	27				
Statistical Analyses of Song Sparrow Demographic Parameters	27				
Additional Details of Population Dynamic Modeling Procedure	33				
Future Scenario Models	34				
Results – Model 2	39				
Scenario Results	39				
DISCUSSION AND MANAGEMENT IMPLICATIONS OF THE POPULATION DYNAMIC MODELS					
Climate Change Impacts	60				
Impacts of Management	60				
Limitations of the Study	61				
Next Steps	63				
SUMMARY AND CONCLUSIONS					
Acknowledgments					
References	68				
Tables	73				

Introduction

Climate change is expected to have a multitude of impacts on habitats and wildlife in the next 100 years (Stenseth and Mysterud 2002). Of all habitat types, coastal and estuarine wetlands face some of the most severe threats, due to sea-level rise and the expectation of an increase in the frequency and severity of storm surges and similar events (Michener et al. 1997, Day et al. 2008, Vermeer and Rahmstorf 2009). In addition, salinity, precipitation and run-off are expected to change in the foreseeable future (Knowles et al. 2006, Day et al. 2008). Tidal marsh habitat in particular plays a critical ecological function in estuarine ecosystems, on a global, national, and regional scale (Greenberg et al. 2006a, Zedler 2010), and therefore climate-change-related impacts are of particularly great concern. Cause for concern is especially high in the San Francisco Estuary for two principal reasons. First, tidal marsh habitat supports an array of plant and animal species, many of them Threatened, Endangered or of Special Concern, including many endemic species or subspecies that have evolved adaptations to this saline environment (Greenberg et al. 2006a). Second, tidal marsh habitat has been severely altered and degraded, with more than 80% of the historic habitat in the San Francisco Estuary (Suisun, San Pablo and San Francisco Bays; Figure 1) lost since 1800 (Nichols et al. 1986, Goals Project 1999, Takekawa et al. 2006). Remaining habitat has been subject to changes in salinity, invasion by non-native species (both plants and animals), fragmentation, and encroachment by urban development (Goals Project 1999). Thus, climate change impacts can exacerbate challenges already faced by plants and animals and such impacts can mean the difference between the sustainability of populations and ecosystems, on the one hand, and extirpation and loss of ecological function by this ecosystem, on the other.

Tidal marshes occupy the zone between tidal mud flats and upland areas above the high tide line. As such these marshes are highly sensitive to changes in inundation patterns, whether due to increases in global sea level or due to storm events (Kirwan et al. 2010, Zedler 2010, Bayard and Elphick 2011). Storms, in many cases associated with El Niño events can cause water levels to exceed predicted (i.e., astronomical) tides by 33 cm, as reported by Flick & Cayan (1984) or even by 70 to 80 cm. (Thorne et al. in review).

Climate change is also expected to bring about changes in salinity in the San Francisco Estuary (Cloern et al. 2011, which will affect plant species distribution and abundance in the marsh habitat (Donnelly and Bertness 2001). Bird and wildlife populations in turn are dependent on plant species— for foraging, nesting, roosting, and, as part of the food web, supporting primary consumers (e.g., herbivorous invertebrates; Takekawa et al. 2011). Thus, birds and wildlife may be impacted by changes in tidal marsh-associated plants, reflecting changes in salinity and inundation (Veloz et al. 2011), as well as by the direct impact of changes in inundation, salinity and other physical variables, on vertebrate and invertebrate fauna.

Of all the myriad changes expected with climate change, the most dramatic may well be inundation of tidal marsh habitat, especially due to intense storms resulting in extreme storm surges (Day et al 2008), whose frequency is expected to increase, at least on the regional scale (Hamlet and

Lettenmaier 2007) and beyond (Mousavi et al. 2011). Marsh inundation is of concern, first, because major storms and extreme tides can bring about nest-failure, and, second, because inundation may cause habitat that would normally provide refuge from predators to become unavailable to at-risk marsh species, thus enhancing predation (Evens and Page 1986, Takekawa et al. in press). These potential impacts are considered in this study.

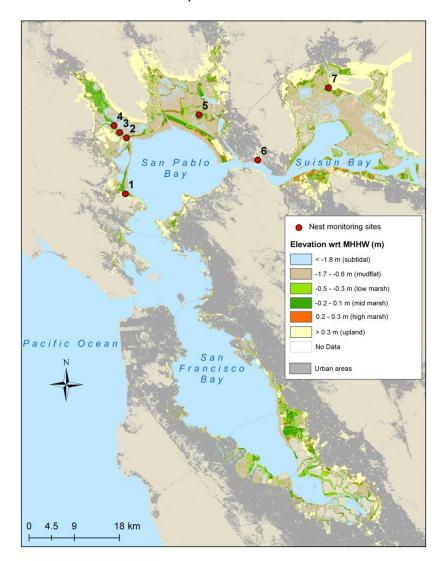


Figure 1. San Francisco Estuary, divided into three regions: Suisun Bay, San Pablo Bay, and San Francisco Bay (the latter includes "Central San Francisco Bay" and "South San Francisco Bay"). The seven nest monitoring study areas (for monitoring reproduction of tidal marsh species) are shown in clockwise order, with reference to numbers: 1) China Camp, 2) Petaluma River Mouth, 3) Carl's Marsh, 4) Black John Slough, 5) Pond 2A, 6) Benicia State Recreation Area, and 7) Rush Ranch. Also shown is habitat classification of marsh based on relative elevation with respect to mean higher high water (MHHW; Stralberg et al. 2011). In addition, the San Francisco Bay Bridge divides the combined San Francisco Bay and San Pablo Bay into two sections: "North Bay" (north of Bay Bridge) and "South Bay" (south of Bay Bridge).

Project Objective and Justification

To assess the vulnerability of tidal marsh-dependent bird species to anticipated climate change and to provide guidance in management to reduce such vulnerability, this project considers impacts of environmental change on two key demographic processes that are critical to the sustainability of populations: survival and reproductive success. Here we have developed population-dynamic models to help assess the long-term population viability of focal species of concern. The models can be used to project population trends over time, under a variety of environmental conditions, for each of four key tidal marsh-dependent species: Black Rail (Laterallus jamaicensis), Clapper Rail (Rallus longirostris), Common Yellowthroat (Geothlypis trichas), and Song Sparrow (Melospiza melodia). In the San Francisco Estuary, each species is represented by one or more subspecies that are entirely or mainly confined to the tidal marsh habitat in this one region: California Black Rail (L. j. coturniculus), which is a California Threatened species, California Clapper Rail (R. I. obsoletus), which is a Federally Endangered species, Saltmarsh Common Yellowthroat (G. t. sinuosa), a California Species of Special Concern, and three tidal marsh subspecies of Song Sparrow, all of which are California Species of Special Concern: Alameda (M. m. pusillula), Samuel's (also referred to as "San Pablo"; M. m. samuelis), and Suisun (M. m. maxillaris). These species of concern are described in Nur et al. (1997), Goals Project (2000), Shuford and Gardali (2008), USFWS (2009), Tsao et al. (2009), and Takekawa et al. (2011). Whereas our results are of special relevance to wildlife resource managers in the San Francisco Estuary, the methods we have developed and described are applicable to estuarine bird populations anywhere, and thus the value of our approach extends beyond the specific species we have modeled.

To maximize the long-term persistence of threatened populations in the face of climate-change impacts, information on demographic processes is required. This project focuses attention on two key stages of the life cycle of tidal marsh wildlife, breeding and over-winter survival. Populations are imperiled or expected to decline if either life stage is compromised. In a similar fashion, depleted or threatened populations may be unable to recover or attain target population levels if survival or reproductive success is impacted. A single, severe storm/flooding event during the breeding season can cripple that year's reproduction (van de Pol et al. 2010, Bayard and Elphick 2011). Similarly, during the winter, an especially high tide will lead to flooding of key roosting or foraging habitat of tidal marsh species, making them vulnerable to predators (e.g., herons and egrets) unless high-tide refugia are available (Evens and Page 1986). Two such extreme events, resulting in extensive flooding of marsh habitat in the San Francisco Estuary, occurred in January 2010 and March 2011 and were documented by Thorne et al. (in review). In addition, weather variables, including precipitation and temperature, can have direct effects on reproductive success and survival, as well as indirect effects acting through vegetational change (Zedler 2010). Indeed, climate scientists anticipate substantial changes in patterns of precipitation and temperature (Knowles et al. 2006, Hamlet and Lettenmaier 2007, Day et al. 2008, Ramirez and Jarvis 2010).

A recently completed California Landscape Conservation Cooperative (CALCC) project, conducted by PRBO and collaborators, Tidal Marsh Bird Population and Habitat Assessment for San Francisco Bay under Future Climate Change Conditions (see www.prbo.org/sfbayslr) developed scenarios of future marsh distribution and extent in relation to anticipated sea-level rise and marsh accretion (Stralberg et al. 2011), and then projected future marsh vegetation composition and bird populations in relation to a set of physical variables (Veloz et al. 2011). That project focused on the anticipated availability and suitability of habitat for marsh bird populations. Habitat is a necessary requisite for the continued persistence of tidal marsh-dependent wildlife, and information on the future distribution and extent of habitat and the suitability of habitat to support target populations is very valuable. However, habitat by itself does not ensure long-term viability of robust wildlife populations (Beissinger 2002, Keith et al. 2008). For this reason, we developed and applied a modeling approach that can aid managers, agencies, and other groups, in developing and implementing climate adaptation strategies and other responses that will maximize the long-term persistence of threatened populations. For three of the tidal marsh species (Black Rail, Clapper Rail, and Common Yellowthroat) we developed relatively simple models that provide insights that inform managing for the long-term persistence of these threatened populations and provide a foundation for subsequent, more detailed modeling efforts in the future. For the fourth tidal marsh species, the Song Sparrow, we provide an example of a more complex, mechanistic model that incorporates specific anticipated climate change impacts on the long-term viability of these populations. Our modeling provides insights into the vulnerability of these species of concern to climate change by explicitly considering their population viability at present and how viability will be affected in the future, whether due to climate change of through management action.

Overview of Analysis and Modeling Approach

In this project, we have taken a two-tiered approach to developing models to inform managers regarding the future viability of populations in the light of climate change. First, we present four deterministic population models, one for each of the focal species, compiling and synthesizing the best estimates of demographic parameters for each species and calibrating model results with respect to San Francisco Estuary data. We illustrate the uses and insights provided by these models. These models are interactive, so that users can make full use of their capabilities. We refer to these simple models as first-order models, or Model 1, for short. Then, for one of the four species, represented by the three tidal marsh-dependent subspecies of Song Sparrows, we present a more complex population model, one that incorporates specific ecological drivers and how they impact long-term viability.

The more complex model for tidal marsh Song Sparrows includes: (1) explicit effects of environmental change on specific demographic parameters identified through statistical analysis of a long-term data set, and (2) **stochasticity**—that is, unpredictable variability—in demographic parameters (Burgman et al 1993, Nur and Sydeman 1999). Such stochasticity is due in part to unpredictable variability in environmental parameters (i.e., uncertainty regarding future

environmental conditions) and in part is due to variability in rates of survival and reproductive success, even when environmental conditions are known. We refer to this more complex population-dynamic model as a "second-order model" or Model 2, for short. We use Model 2, as developed for tidal marsh Song Sparrows to project, over the next 50 years: (i) future behavior of the populations if current conditions were to continue into the future, and (ii) future behavior of the populations under several climate-change scenarios. The future climate-change scenarios include anticipated changes in precipitation and temperature, changes in sea-level, and changes in the frequency of extreme high tides. Finally, we use the model to (iii) demonstrate the long-term impact of management actions on viability, actions that can mitigate the deleterious effects of anticipated climate change.

Our objective in presenting the detailed statistical analysis and stochastic Model 2 for tidal-marsh Song Sparrows is three-fold:

- (1) provide guidance to managers in assessing vulnerabilities tidal marsh-dependent species that are expected to face environmental challenges in the next 50 years or more,
- (2) provide guidance to managers in assessing and comparing the efficacy of potential management actions that may increase population viability and thus decrease vulnerability of target species,
- (3) identify important gaps in knowledge through the use and refinement of models presented here, as well as applying our approach to other tidal marsh-dwelling species, plant and animal.

Demographic parameters for population modeling of the tidal marsh species

Information on six key demographic parameters is needed to model the dynamics of a single population (Nur and Sydeman 1999, Caswell 2001). The parameters are:

- 1. Adult survival,
- 2. Survival of individuals from fledging to adulthood, here referred to as "juvenile survival,"
- 3. Probability that an adult attempts to breed per year,
- 4. Number of nesting attempts per year for breeders,
- 5. Probability that an individual attempt is successful, and
- 6. Number of fledged young per successful nesting attempt.

Here we consider a population that either (a) has no immigration or emigration, or (b) immigration and emigration balance each other. If there is net movement of individuals into or out of the population, then this would add a seventh parameter.

Of the enumerated parameters, parameters 2 and 6 are modified for the two rail species considered, since there is no post-hatching period of parental care (i.e., no nestling stage). Thus, for

rails, juvenile survival (parameter 2) refers to survival from **hatching** to adulthood, and parameter 6 refers to number of hatched young per successful nesting attempt. However, for simplicity we will use the single term "fledged" young to apply to all four species, whether parental care includes the post-hatching period (the two songbird species) or not (the two rail species).

Parameters 4, 5, and 6 taken together constitute "reproductive success" as it is usually defined and measured (Nur & Sydeman 1999). Specifically, the product of parameters 4, 5, and 6 is **the number of fledged young produced per year per breeding individual**. For the purposes of demographic modeling, however, we must also include the probability an adult attempts to breed per year (equivalently, the proportion of adults that attempt to breed per year, parameter 3). The product of parameters 3, 4, 5, and 6 is annual **fecundity** of adults (Nur & Sydeman 1999, Caswell 2001).

In applying the population models, we also refer to **productivity**, which we define as annual fecundity multiplied by juvenile survival. Thus, productivity is **the number of offspring produced per year that survive to adulthood, calculated per adult**. A simplification of our models, justified by field studies, is that we assume "adulthood" is attained at age 1 year, i.e., one-year olds of all species are capable of breeding (see below for further discussion). For species with delayed maturation, one would need to consider survival of subadults as well (Nur & Sydeman 1999).

For the purposes of our population models, we further divide Parameter 1, annual adult survival, into "breeding season" survival and "non-breeding season," which, for convenience we also refer to as "over-winter" survival, though this period includes fall as well as winter. Among the four species, non-breeding season survival has only been estimated for Clapper Rail (C. Overton et al. submitted), but we think the division of annual survival into two components is potentially useful for management, especially in considering specific threats or specific actions, which may impact only one season or the other.

Overview of approach

For both Models 1 and 2, we evaluate **relative rates** of population performance under different climate change scenarios and/or management options, consistent with recommendations of Beissinger and Westphal (1997). As much as possible, we draw on published or unpublished parameter values for the species-specific models (including estimates obtained from PRBO, USGS, and other field studies). Where information is lacking, we use parameter values that, in combination with other, better known, parameter values, produce the population behavior observed in recent field studies in the San Francisco Bay region. Thus, we first develop population dynamic models that reproduce **current population trends**, "Current Model." As part of this process we also determine a combination of parameter values that will produce a **stable population** (i.e., the annual population growth rate, lambda, symbolized $\lambda = 1.0$), informed by studies of other populations of the same species. We refer to these as "Base Models" because such models provide a valuable baseline. We then consider the population consequences of changes in the individual demographic rates (i.e., relative change in the six parameters) and/or changes in the environment that will then result in changes in species-specific demographic parameters.

Population projections are shown assuming a starting population size of 10,000 individuals, of both sexes (i.e., 5000 females, 5000 males), in year 0 of the projection, which is 2010. Our main objective is not to make projections regarding specific population size in a specific year in the future, but rather to estimate size of the population relative to the starting year, that is, population growth or decline. Oftentimes absolute population size is very difficult to determine, but existing monitoring programs are well-suited to providing information on relative change (i.e., percent change; Nur 2008). In general, results are scalable so that for Black Rail, instead of assuming 10,000 in year 0, one could start with e.g., 12,400 individuals in year 0, corresponding to number of Black Rails estimated by Veloz et al. (2012) for the entire San Francisco Bay Estuary. For Common Yellowthroat, instead of 10,000, one could start with, e.g., 11,800 individuals in year 0, corresponding to the number of Common Yellowthroats estimated for Suisun Bay (Veloz et al. 2012). With regard to Song Sparrows (the subject of the stochastic Model 2), 10,000 individuals corresponds to the approximate number of this species in a single watershed in the San Francisco Estuary (e.g., Petaluma River). We consider a single watershed to be an especially relevant spatial scale for a manager or agency, and so the starting population size of 10,000 Song Sparrows provides a desirable metric.

We first present Methods and Results for Model 1 for each species before presenting Methods and Results for the more complex, stochastic Model 2, developed here for tidal marsh Song Sparrows. We conclude with a combined section on Discussion and Management Implications.

POPULATION DYNAMIC "MODEL 1" FOR THE FOUR TIDAL MARSH SPECIES Methods – Model 1

Demographic Assumptions Applying to All Four Species

Two Simplifications: We have adopted the commonly used convention of restricting the demographic modeling to one sex, in this case, females (Caswell 2001). Females are the usual sex chosen for modeling purposes on the assumption that, as egg-layers, they are the limiting sex. We assume the sex ratio in the population is 1:1. Where males may, instead, be limiting, e.g., in Snowy Plovers (Nur et al. 2007), a population dynamic model of the type developed here, would be restricted to males. However, for purposes of depicting model output we show the change in the number of individuals of both sexes, assuming a 1:1 sex ratio (e.g., starting population size is 10,000; 5,000 of each sex).

As noted above, for all four species, one-year old individuals are capable of successful breeding (Arcese et al. 1992, Eddleman et al. 1994, Foin et al. 1997, Guzy and Ritchison 1999). Furthermore, we know of no evidence, for any of these four species, that female adults do not attempt to breed. However, for Song Sparrow males, there is evidence that some one-year olds are not able to secure a mate and/or territory and are "floaters" (Arcese et al. 1992, Nur et al. 2000), which provides further justification for developing a female-only model for this species. Therefore, for the population models presented here we assume that Parameter 3 is equal to 1, i.e., all individuals aged 1year or more attempt to breed. This assumption is not likely to be strictly true for any of the four species, but we maintain that errors and/or uncertainty associated with estimating the proportion of adults that do not attempt to breed is small compared to the errors and/or uncertainty associated with estimation of other parameters.

<u>Density Dependence</u>: We assume no density dependence with regard to demographic parameters for Model 1. This is a simplifying assumption. While there is no evidence of density-dependent survival or reproductive rates for any of the four species, we cannot exclude the possibility. It may well be that one or more of the species may exhibit density dependence due to territorial behavior on a local scale (C. Overton, pers. comm.). Nevertheless, we have too little information at present to incorporate density dependence. Model results that project substantial population increases should be viewed with caution.

<u>Sex-ratio</u>: We assume a 1:1 sex ratio among offspring. Therefore, **reproductive success** is calculated as the total number of offspring produced per breeding pair per year multiplied by 0.5 and this is equivalent to the total number of offspring produced per breeding individual per year, assuming the number of male breeders equals that of female breeders.

Age of first breeding: We assume all individuals (i.e., females) attempt to breed at age one (see above for justification).

<u>Immigration and emigration:</u> We assume that any emigration is balanced by immigration.

<u>Maximum longevity:</u> We assume there is no maximum lifespan for these species. This assumption is surely violated, but we argue that results are little affected by such a violation. For example, Song Sparrows have been reported to live 12 years or more (data from Bird Banding Lab, USFWS). If annual adult survival is 50% per year and is constant with age, then we expect that only 0.1% of one-year olds will live to age 11. Hence future population dynamics are little influenced by the assumption of no maximum age.

Species-specific values of demographic parameters

Demographic parameters were estimated under two conditions: 1) A set of values corresponding to current conditions, i.e., values that will produce a population trend corresponding to recently observed trends, which we refer to as "Current" Population Model, and 2) a set of values that produce a population with a lambda of 1.0, which we refer to as "Base" Population Model. Table 1 lists, for each species, the parameter values used for Current Models. Tables 2, 3, 4, and 5 list parameter values used for Base Models. While there is uncertainty regarding individual parameter values for each of the species, one of the strengths of our approach is that robust population trend estimates are available for each of the four species, based on extensive field studies of PRBO, USGS, and collaborators, and these trend estimates inform the Current Models.

We present specifics for each species starting with the species with the most extensive field data, Song Sparrows, then Clapper Rails, and finally the two species with modest field data, Black Rail and Common Yellowthroat.

Song Sparrow

Here we describe parameter values for Model 1 for tidal marsh Song Sparrows; see "Methods – Model 2" for explication regarding Model 2. We rely as much as possible on intensive field studies conducted by PRBO at seven tidal marshes in the northern part of the San Francisco Estuary, San Pablo Bay and Suisun Bay (Figure 1).

Current Model: The three components of reproductive success were estimated based on extensive field studies (Liu et al. 2007): over 3100 nests were monitored over a 12 year period. **Nest survival** was estimated using methods described in Shaffer (2004); the mean value calculated among years was 0.233. The mean **number of fledged young** per successful nest was determined from these field data: 2.408. The estimate of the **number of nesting attempts** is the most elusive of the three reproductive success components. Based on intensive field studies of uniquely color-banded females, the mean number of nesting attempts was 2.966 (see "Methods – Model 2: Field Methods" for details). We are certain that this estimate underestimates the true number of nest attempts per female, since unsuccessful attempts are difficult to identify in the field, even under the best circumstances. Increasing this estimate by 16.7% to 3.461 attempts per female produced a population growth rate that matched the recent population trend observed in San Pablo and Suisun Bays, given all the other parameter values used.

Adult survival of tidal marsh Song Sparrows is not known. We used an estimate based on results from a long-term study of color-banded Song Sparrows at the Palomarin Field Station, located 30 to 90 km from the seven tidal marsh study sites. Adult survival value of 0.600 was used based on capture-recapture analyses of females (Nur et al. 2000). We further broke down annual adult survival into breeding season and non-breeding season on the assumption that breeding season survival is high, i.e., 0.90. This assumption is consistent with field observations of low (but non-zero) levels of mortality of breeding Song Sparrows (PRBO unpublished). Juvenile survival for tidal marsh subspecies is unknown, so we used an estimate that concurs with values in the literature for this species (i.e., Arcese et al. 1992, Chase et al. 2005). The juvenile survival value used (0.391), given all the other parameter values used, produced a population growth rate that matched observed recent trends, as determined for San Pablo and Suisun Bays (PRBO, unpublished). Trends differ slightly between San Pablo Bay and Suisun Bay; for Current Model we used a mean lambda value of 0.979.

Base model: To produce a lambda of 1.0, we increased nest survival from 0.233 to 0.246. We did this based on comparison of our estimates with estimates of nest survival from other Song Sparrow populations (Arcese et al. 1992, Chase et al. 2005). All other parameter values were the same as for Current Model. Thus, we attributed observed, recent population decline among these tidal marsh Song Sparrow populations to levels of nest survival below that needed to sustain the population, a conclusion consistent with our observations of high levels of nest failure of tidal marsh Song Sparrows due to high rates of nest predation and extensive flooding of nests (Greenberg et al. 2006b, Liu et al. 2007). Note that nest survival of tidal marsh Song Sparrows (whether 0.233 or 0.246) is much lower than that empirically observed for the other three tidal marsh species (see below). Historically, Johnston's study of San Pablo Song Sparrows (1956) reported a nest survival rate of 0.493, also suggesting that an increase from 0.233 to 0.246 under favorable conditions is not unreasonable, and could be much greater.

Clapper Rail

Population trends in the North Bay and the South Bay have been very different in the most recent period analyzed for this study (2005-2010). Therefore, separate "Current" models were developed for these two regions.

Current Models: Reproductive success (number of female offspring produced per female per year) in the South Bay was assumed to be 1.855 young (consistent with mean value used by Foin et al. 1997), broken down as follows: Nest survival (i.e., nest success) was set at 0.371 based on composite of South Bay Clapper Rail data (Harvey 1988, Foerster et al. 1990, and Schwarzbach et al. 2006). Note that these field studies all date from 1999 and earlier and so may not reflect nest survival during the period of recent decline in the South Bay. In the North Bay, nest survival was assumed to be 0.39, equal to overall mean value reported previously for North Bay marshes (Schwarzbach et al. 2006). Number of hatched young per successful attempt was five (similar to value of 5.3 reported by Schwarzbach et al. 2006). The mean number of nesting attempts was

assumed to be 2. Clapper Rails are known to "sometimes [have] a second brood" (Schwarzbach et al. 2006:46; Eddleman and Conway 1998). Renesting has been observed "up to five times" (Eddleman and Conway 1998). While there is some uncertainty regarding values used for individual components of reproductive success used for Clapper Rails, given estimates of adult survival (below) and our assumption regarding juvenile survival, a reproductive success value of 1.855 young per adult per year replicates recent population trends observed for the South Bay population and that of 1.95 young per adult per year replicates the corresponding trend seen for the North Bay population. Again, our objective in Model 1 was not to project future population growth rates but to evaluate and compare effects of change in the different components (e.g., change in survival vs. a change in reproductive success).

Annual survival was estimated at 0.280 in the South Bay by Overton et al. (submitted); we used this value. For Current Model in the North Bay, survival was assumed to be 0.377, consistent with the smaller rate of decline in this region, compared to the South Bay, and a value that is more similar to other studies of this species (Foin et al. 1997; Eddleman and Conway 1998). Annual survival was broken down further on the assumption that breeding season survival was approximately 85% proportionately higher than survival during the non-breeding season (fall and winter, also referred to as "over-winter survival"), also based on Overton et al. (submitted); this breakdown was also applied to North Bay population. Higher overall mortality, as estimated by Overton et al. (submitted), during the non-breeding season was due to two factors: a) the longer period of the non-breeding season compared to the breeding season (35 weeks vs. 17 weeks) and b) the higher weekly mortality rates during the winter period compared to breeding season. The latter finding is consistent with other studies that found little mortality during the breeding season (Conway et al. 1994). Juvenile survival was assumed to be 0.3 in both regions of the Estuary, similar to the value of 0.32 used by Foin et al. (1997) but reduced slightly in line with lower adult survival values used here. Note that juvenile survival rate (= 0.3) is for the period from the end of the breeding season to the end of the winter and thus should specifically be compared with the adult over-winter survival rate (= 0.473, 0.389 in the North Bay and South Bay, respectively).

The combination of demographic parameter values used for the two Current Models produced population growth rates of 0.837 in the South Bay, and 0.962 in the North Bay, matching observed trends for 2005-2010 (PRBO unpublished).

Base Model: To construct models with lambda = 1.0, annual adult survival was increased to 0.4, and juvenile survival to 0.308. The same Base Model applied to North Bay and South Bay populations. Higher adult survival for a stable population is consistent with findings for other Clapper Rail subspecies (Eddleman and Conway 1998). Nest survival was kept at 0.39, the same value as used in the Current Model for North Bay Clapper Rails. Number of young per successful nest and number of nesting attempts were unchanged at 5 and 2, respectively, compared to Current Model. Thus, for Clapper Rail, we assumed that negative population trends (strongly negative for South Bay or weakly negative for North Bay) were primarily due to low survival rather than low reproductive

success, based on the findings of Overton et al. (submitted) and Schwarzbach et al. (2006), when these were compared with other studies of Clapper Rail populations.

Black Rail

Current Model: Annual adult survival was assumed to be 0.50, based on estimate of 0.53 for the Virginia Rail (Conway et al. 1994). Lower adult survival for Black Rail compared to Virginia Rail is consistent with the former's smaller body size. Annual survival was further broken down into breeding season survival and non-breeding season survival on the assumption that the former is relatively high, i.e., 0.90. Juvenile survival was assumed to be 0.3. Such a value is consistent with reported value for hatching year Virginia Rails (0.32; Conway et al. 1994). Nest survival was set at 0.42 based on field studies at marsh study sites (PRBO, unpublished); number of young per successful nest was 5 (PRBO, unpublished; Eddleman et al. 1994). The number of nesting attempts per female was assumed to be between 1.5 and 2.0 based on Eddleman et al. (1994) and PRBO (unpublished). The specific value of 1.81 nesting attempts per female was used in the Current Model because doing so yielded a population growth rate, given the other parameter assumptions (above), of 1.070, that matched observations of mean population trends for San Pablo and Suisun Bays combined, for 2000-2009 (PRBO, unpublished).

Base Model: We kept all values the same as for Current Model, except decreased number of nesting attempts to 1.59. Thus, we assumed the difference between the current, positive trend and a stable trend is due to differences in reproductive success rather than differences in survival. Alternatively, one could assume that Black Rails are increasing in number due to high adult survival rather than high reproductive success. This possibility can be examined for this species and the other three tidal marsh species in the Population Model 1Tool available at http://data.prbo.org/apps/sfbslr/demography and as discussed below.

Common Yellowthroat

Current Model: Annual adult survival was set at 0.497, a value obtained from analyses by Institute of Bird Populations for this species and for this region of the United States (available from IBP website, www.birdpop.org). We further broke down adult survival into breeding season and non-breeding season survival by assuming survival during the breeding season is high, i.e., 0.90. Juvenile survival was then set at 60% that of adult survival, similar to the value used for Song Sparrows. For components of reproductive success, we used values of 54% nest survival and 2.73 fledged young per successful nest attempt, both values based on field studies of tidal marsh populations of this species (PRBO unpublished). The final component was nesting attempts, which we assumed was between 2 and 3 (based on Guzy & Ritchison 1999). The value of 2.45 nesting attempts per female, in conjunction with the other parameter values stated above, yielded a lambda of 1.033, corresponding to observed population trends in the San Francisco Estuary (PRBO, unpublished).

Base Model: The base model used all the same values as Current Model except that the number of nesting attempts was 2.3 instead of 2.45. We chose to modify number of nesting attempts because that is the parameter that is most uncertain for this species and/or subspecies. As with Black Rails,

we assumed that current population growth, compared to a stable population, can be attributed to relatively high reproductive success rather than high survival. Again, these two alternatives can be compared using the Population Model 1 Tool.

Results - Model 1

Model 1 represents a first step in providing guidance and insights that will assist agencies and organizations that are managing natural resources in tidal marsh habitat, especially with regard to climate change. One use of Model 1 is to highlight situations in which population behavior is sensitive to parameters that are poorly known (see Model 2 results, below, for a case where parameters are better known). Tables 2, 3, 4, and 5 summarize each of the Model 1's (Current and Base) for each of the four species. Recall that "Base" models, by definition, produce a lambda of 1.0. In the Excel spreadsheet contained in the **Population Model 1 Tool** (see http://data.prbo.org/apps/sfbslr/demography), there is a "modification to base model" section that is interactive: in section A for each Table/Spreadsheet (i.e., in the spreadsheet for each species), one can alter one or more demographic parameters, six in all, by specifying the percent change for the parameter(s). Press "Calculate" and the spreadsheet calculates a new set of parameter values and a new lambda value, given plus x% and minus x% change in the parameter(s). Press "Reset" to restore the original base values. If you want to carry out another calculation, you will need to click on an empty cell, and then press "Calculate". Section B allows one to estimate a target value for one or more parameters to bring about a desired change in lambda. Section C allows one to graphically display alternative trends: Current trend vs. trend if productivity is increased or decreased by 10% or trend if adult survival is increased or decreased by 10%.

Species-specific Results

Here, we illustrate species-specific results for each of the four focal species using specific examples. We encourage the reader to explore the 3 sections of the Tool (A, B, and C) developed for each species, available from http://data.prbo.org/apps/sfbslr/demography.

Song Sparrow

In part A of the Tool (illustrated in Table 2A), the spreadsheet allows one to compare the vulnerability and population resiliency due to change in one demographic parameter vs. another. For example for Song Sparrows (Table 2A), a 5% increase/decrease in nest survival for Song Sparrows results in new lambda values of 1.0209/0.9808, compared to a "base" lambda of 1.00 (illustrated in Table 2A), whereas a 5% increase/decrease in adult over-winter survival results in new lambda values of 1.0308/0.9708 (not shown). Furthermore, the same **absolute change in lambda** applies no matter what the baseline value of lambda is.

In particular, a modest 5% relative increase in nest survival is sufficient to turn a population declining by 2.1% per year (as has been recently observed for San Pablo and Suisun Bay Song

Sparrows) into one that is stable. In addition, the Tool can be used to evaluate counteracting effects (e.g., decrease in overwinter survival, increase in nest survival), that is, given a specified change in one parameter, what change in one or more other parameters is needed to counteract that effect. In section 2 of this study ("Stochastic Model of Climate Change Impacts for a Focal Tidal Marsh Species"), we explore the value of management-induced changes in nest survival for tidal marsh Song Sparrows that may counteract climate change impacts.

In part B of Tables 2, 3, 4, and 5 we consider: What are the new values of individual parameters needed to bring about a lambda value different from that of Base Model (defined as lambda = 1.00)? The user inputs the desired change in lambda (relative to lambda = 1.0). Part B of each Table depicts alternative parameter values required to bring about the desired lambda value, given that the rest of the parameter values are maintained as in Part A. Parameter values depicted are with respect to productivity or its individual components: number of nesting attempts, nest survival, number of fledged young per successful attempt, and juvenile survival. In addition, we display the target values for survival (either overwinter survival or breeding season survival) needed to bring about the new lambda value. We also demonstrate target values required if two parameters are to be changed simultaneously (among productivity, overwinter survival, and breeding season survival) assuming the percentage change is the same for both parameters. For Song Sparrows, we demonstrate part B of the Model 1 Tool assuming lambda will be increased 5% (to 1.05) in Table 2B, but any percentage change relative to lambda = 1.0 can be used. This may help a resource manager evaluate whether the target value is feasible or not. For example, nest survival of 0.277 (Table 2B) may be very feasible to attain, but breeding season survival of 0.975 may not be. The bottom 3 rows demonstrate target values needed to change two of the three parameters simultaneously.

In part C of Tables 2, 3, 4, and 5 we depict graphically three simple demographic scenarios: (1) Productivity is increased or decreased by a relative 10% (both increase and decrease are shown), (2) Adult survival is increased or decreased by a relative 10%, or (3) both productivity and survival are increased or decreased by 10%. Here, the 10% change is relative to **Current Model** values. To aid in comparison we also depict the **current trend extrapolated into the near-term future**. The intent here is to present future population trend and population size under three alternatives (increase in parameter(s), decrease in parameter(s), or no change from current). Note "current" trend is only shown once one chooses one of the three options by which to change survival and/or productivity.

For Song Sparrows, a given change in lambda will require a greater percent change in nest survival than in over-winter survival of juveniles and adults, but the former may be easier to achieve, especially given the current high rates of nest failure for tidal marsh Song Sparrows (approximately 77% failure rate).

Clapper Rail

For this species, "Current" models (Table 3A and 3C) are specific to North Bay and South Bay (Figure 1). For illustration, in Table 3A, we show the effect of a 7% change in nest survival (positive

and negative) in the North Bay section in contrast to a 10% change in adult overwinter survival in the South Bay section. However, in both cases such changes are calculated relative to the same "base" model. Interestingly, our results show that Clapper Rail population growth is relatively sensitive to nest survival (as compared with over-winter survival). For example, the effect of a 7% change in nest survival is to change lambda by 0.042, whereas the effect of a 10% change in over-winter survival only changes lambda by 0.040. This is the case whether the changes in the nest-survival and overwinter survival parameters are both positive or both negative. The Population Model 1 Tool on the project website allows one to consider a wide range of percentage changes in parameters.

All else being equal, a manager wishing to increase population growth rate, e.g., turn the negative population growth rate observed in the North Bay during 2005-2010 into a stable or growing population, might best focus on increasing nest survival rather than overwinter survival. However, the more important question is, **How malleable are the different demographic parameters?** For some species, e.g., tidal marsh Song Sparrows, nest survival may be more sensitive to environmental conditions, and in particular, more susceptible to management action than a parameter such as overwinter survival. For example, nest predation may be reduced by controlling predators or by reducing access of predators to nests. Nest flooding may be reduced by limiting tidal action. These specific possibilities are examined below, with respect to Song Sparrows in the Model 2 section.

However, for Clapper Rails, it may be overwinter survival that is most responsive to environmental conditions, including anticipated climate change. Analyses by Overton et al. (submitted) found that survival was a function of maximum tide (as measured on a weekly basis), with the effect of maximum tide being strongest during the winter. If weekly maximum tides during the winter were to increase by 20 cm, Overton et al.'s results indicate that overwinter survival would decrease by a relative ~16%. One can use the Population Model 1 Tool to evaluate such an impact (not shown in Table 3). If one does, the result is that lambda is decreased by 0.064. But by the same token, a 16% increase in overwinter survival, will increase lambda by 0.064, which could turn a declining population (such as in the North Bay) into a slightly increasing population. Table 3B depicts target values needed to change the base model for Clapper Rail from 1.000 to 1.064.

Just as one can use Model 1 to consider the effect of an extreme tide, one can also use the model to demonstrate the effect of an increase in survival due to management action, compared to not taking any action. In the case of overwinter survival of Clapper Rails, the management action may be provision of refugia from predators during extreme high tides (USFWS 2009). Table 3C depicts the effect of a 10% change in survival and productivity for the South Bay population compared to the "current" trend for 2005-2010. If adult survival is only 0.280 (see above) then a relative 10% increase (to 0.308), even if coupled with an increase in productivity by 10% (e.g., juvenile survival increases by a relative 10%) only dampens the decline, it will not reverse the decline. Other

scenarios can easily be examined using the Population Model 1 Tool at http://data.prbo.org/apps/sfbslr/demography.

Black Rail

For Black Rails, a 5% relative increase in Juvenile survival changes base lambda from 1.0009 to 1.0259 (as shown in Table 4A). A 5% relative decrease in juvenile survival causes a decrease in lambda of 0.025. In the latter case, juvenile survival declines from 0.300 (base value) to 0.285, an absolute difference of 0.015 in terms of juvenile survival.

Note that a decline in juvenile survival by this amount, 0.015 will cause lambda to decline by 0.025; that is the change will be from lambda = 1.001 ("base" model rounded to closest 0.001) to lambda = 0.976. The same change in juvenile survival, an absolute decrease of 0.015, will cause current lambda of 1.070 to drop to 1.045. For all four species, the absolute change in lambda depends on the absolute change in survival or productivity, irrespective of the original value of lambda. Thus, the Population Model 1 Tool can be used to explain or understand changes in population trends, past, present, and future trends.

To demonstrate the versatility of the Model 1 Tool, in Table 4B we consider what combination of parameters might cause lambda to decrease by 5%. For example, a decrease in number of young per nesting attempt, from 5.0 to 4.50 would cause lambda to decrease by 5%. Fewer young per nesting attempt reflects either a smaller clutch size or lower hatching success.

In Table 4C we display the expected population growth rates if productivity were to increase or decrease by 10%, compared to current trends. Thus, Black Rail populations in San Francisco Estuary appear to be robust, at least if current trends continue. Current trends (Table 4A, 4C) indicate an increase of 7.0% per year. Furthermore, even if productivity were to decrease by 10%, the population still shows an increasing trend, though only slightly so, suggesting low vulnerability of this species compared to Song Sparrow or Clapper Rail.

Common Yellowthroat

We illustrate the Model with a 10% change in number of nest attempts (Table 5A), which causes base lambda to increase or decrease by 0.05. The number of nest attempts per year may reflect the length of the breeding season, which in turn may depend on vegetation characteristics (see Model 2, below, for further discussion).

Like Black Rails, adult survival of Common Yellowthroats is close to 0.5, and therefore a given percent change in productivity is **as influential** as a comparable change in annual survival. Again the critical questions are: Will changes in environmental condition have as strong an effect on one parameter as another? To what extent can management actions influence these parameters? The modeling tool helps managers focus on these key questions.

We illustrate part B of the Tool, by considering the target values if lambda is to be increased by 5% from 1.00 to 1.05. The target of 3.0 fledged young per successful nest attempt may be feasible to

achieve (Table 5B), but altering only breeding season survival would require achieving 99% survival, which hardly seems feasible. Finally, for Common Yellowthroats, a 10% decrease in adult survival would be sufficient to turn the current, increasing trend into a declining trend (Table 5C). Thus, the tidal marsh Common Yellowthroats demonstrate vulnerability, as indicated by future population growth, to relatively small changes in over-winter survival or any of the three components of reproductive success.

Summary

One of the strengths of the Population Model 1 Tool is that it can facilitate comparisons among species, as well as consider environmental change that may influence more than one species. It is interesting that with respect to modifications of the Base Model, the impact of a change in adult survival is similar to that of a change in juvenile survival, or a change in any single component of reproductive success for two species: Black Rails and Common Yellowthroat. This is so because for these two species adult survival is about 50%. Hence, if lambda = 1.0, as in the Base Model, then survival + productivity (the second term being the product of reproductive success and juvenile survival) = 1 and therefore survival = productivity = 0.5.

For Song Sparrows, changes in adult survival have greater impact than the same percent change in juvenile survival or reproductive success because adult survival is 0.60. For Clapper Rails, in contrast, changes in adult survival have less impact than the same percent changes in juvenile survival or reproductive success because survival is presumed to be 0.40.

Keep in mind that adult survival has two components, breeding season survival and non-breeding season ("over-winter") survival. Thus, if annual survival were to be increased by 10%, this could be because one or the other is increased by 10%, or, for instance, both are increased by 4.88% (1.0488 x 1.0488 = 1.10). Similarly, reproductive success has three components. Increasing each component by 10% is equivalent to increasing overall reproductive success by 33.1% (1.331 = $(1.1)^3$).

MODEL 2: STOCHASTIC MODEL OF CLIMATE CHANGE IMPACTS FOR A FOCAL TIDAL MARSH SPECIES

Where there is more information regarding demographic parameters than was the case for the Model 1 results, it is valuable to consider more realistic and detailed models. Here we present a "next step" model, Model 2, for tidal marsh Song Sparrows. We have chosen this species to model because tidal marsh populations have been intensively studied by PRBO since 1996 (Nur et al. 1997, Spautz et al. 2006, Spautz and Nur 2008a, Spautz and Nur 2008b, Liu et al. 2007). Unlike several recent studies where climatic parameters are used to predict amount of suitable habitat in the future (e.g., Maschinski et al. 2006, Keith et al. 2008, Aiello-Lammens et al. 2011), here we incorporate climate change effects on population dynamics of the target species tidal marsh Song Sparrow by modeling demographic parameters as functions of climate variables and maximum tide height, while incorporating unpredictable (stochastic) variation in these parameter values.

Model 2 draws on the same adult survival and productivity parameters estimated for Model 1 of tidal marsh Song Sparrows. However, in Model 2, these demographic parameters are assumed to vary in time and in response to environmental conditions. Estimates of mean parameter values, their variance over time, and their dependence on environmental conditions, are all informed by PRBO's I2-year study of breeding tidal marsh Song Sparrows (Greenberg et al. 2006b, Liu et al. 2007). The two key features of Model 2, in contrast to Model 1, are that demographic parameter values can depend on specific environmental variables (reflecting climate variables and tide height), which are likely to change in the future, and that future demographic parameter values are stochastic (i.e., only partly predictable). The population dynamic model developed (Model 2) is then applied to multiple scenarios representing alternative future conditions (e.g., differences in sea-level rise or extreme events), as well as incorporating management actions that will influence environmental conditions or the demographic parameter values in the future.

We first determined the statistical relationships of individual demographic parameters (nest survival, etc.) in relation to the five environmental variables using the intensive field data collected (from 1996 to 2007), and then incorporated this information, modeling future environmental conditions, under multiple scenarios. In this manner we predicted the resulting future demographic parameter values and simulated population trajectories, based on projections of the future environmental conditions. We thus quantified future population viability and so characterize population vulnerability to change in future conditions.

Scenarios Evaluated

The stochastic population model was run under eleven scenarios summarized here and in Table 6. Methodological details are presented in the following section.

Scenario C, Current Conditions Continue. Environmental conditions continue in the future consistent with recent years. For this scenario we used PRISM data (for temperature,

precipitation) and NOAA data (for tides) from 1996 to 2007. Year to year variation in environmental conditions reflects a constant mean value (the recent historic value) plus stochastic variation around that value, as determined from the period 1996 to 2007 for each marsh location. Thus, the baseline value was constant (no trend in environmental variables).

The next six scenarios all incorporated climate change but no management action. Specifically, in Scenarios S-1, S-2, S-3, SX-1, SX-2, and SX-3, we used standard climate change projections of future temperature and precipitation, as described in detail below. Future temperature and precipitation were modeled in the same way for all these scenarios. However, tides experienced by breeding tidal marsh Song Sparrows were modeled under six different assumptions. Tide levels experienced by breeding birds reflected not only Sea-level rise, but also anticipated marsh accretion (Stralberg et al. 2011, Veloz et al. 2011). Future temperature and precipitation conditions for all future-climate-condition scenarios (all scenarios except Scenarios C, M-1, and M-2) were based on best available models as described below.

Scenario S-1, Low Sea-Level Rise. Future tides experienced by breeding tidal marsh Song Sparrows were incorporated in the model assuming global sea-level rise of 0.52 m over a 100 yr period, i.e., "low" sea-level rise (Stralberg et al. 2011).

Scenario S-2, Medium Sea-Level Rise. Future tides affecting breeding tidal marsh Song Sparrows were incorporated assuming global sea-level rise of 1.08 m over a 100 yr period, i.e., "medium" sea-level rise.

Scenario S-3, High Sea-Level Rise. Future tides affecting breeding tidal marsh Song Sparrows were incorporated assuming global sea-level rise of 1.65 m over a 100 yr period, i.e., "high" sea-level rise (Stralberg et al. 2011).

Note that "Low Sea-Level Rise" and "High Sea-Level Rise" Scenarios (S-1 and S-3; also SX-1, SX-3, M-3, and M-4) incorporate the same sea-level rise assumptions as was modeled in the PRBO SLR model (Stralberg et al. 2011, Veloz et al. 2011). The "Medium Sea-Level Rise" assumption used here (Scenarios S-2 and SX-2) was exactly intermediate between "High" and "Low" Sea-Level Rise assumptions. All future SLR scenarios in this study used the assumption of "low sediment concentration" and "low organic matter accumulation" as detailed by Stralberg et al. (2011).

The next three scenarios are the same as Scenarios S-1, S-2, and S-3, except that we also considered infrequent but very high tides. There is accumulating evidence that more extreme events, such as unusual storm surges will be more common in the future for coastal wetlands (Cubasch & Meehl 2001, Zedler 2010). Thus, we modeled the following scenarios in which a tide of 2.5 m occurred on average once per decade; note that such an event was independent of presumed sea-level rise. 2.5 m represents a tide height that is 0.18 m higher than the highest breeding season tides recently recorded at tide gauges used in our analysis. With medium to high sea-level rise, water levels equivalent to a tide of 2.5 m or more, though unusual now, will become more common (Cayan et al. 2009), and as demonstrated in this study (see below).

Scenario SX-1, Low Sea-Level Rise plus extreme tides. Same as Scenario S-1 but with extreme tides added.

Scenario SX-2, Medium Sea-Level Rise plus extreme tides. Same as Scenario S-2 but with extreme tides added.

Scenario SX-3, High Sea-Level Rise plus extreme tides. Same as Scenario S-3 but with extreme tides added.

Scenarios M-1 to M-4 considered impact of **Management Action**. Management action either increased nest survival (e.g., by lowering predation rates) or restricted the highest tides (presumably through physical barriers or impediments). For Scenarios M-1, M-2, and M-3 we assume that, through management action, nest survival was enhanced. This could be accomplished by reducing predator populations, reducing predator access to nests, reducing the vulnerability or conspicuousness of nests to predators, or through other means of reducing nest failure. In contrast, in Scenario M-4, maximum tides during the breeding season were capped (e.g., by building sea walls) at 2.3 m, near the current observed maximum.

Scenario M-1, Current Climate Conditions Continue; nest survival increased by 10.0% (relative increase) from 2015 up until, but not including, 2035. A moderate increase in nest survival is implemented, over a relatively short period (20 yr). We assume that it will take several years before nest survival can be enhanced though management action.

Scenario M-2, Current Climate Conditions Continue; nest survival increased by 5.5% (relative increase) from 2015-2060. A smaller increase in nest survival is implemented, but over a longer period than for M-1.

Scenario M-3, High Sea-level Rise; nest survival increased by 10.0% (relative increase) from 2015 up until 2035. We model the impact of high sea-level rise over the 50 year period as in Scenario S-3, but with an additional, moderate increase in nest survival over a 20 yr period as in Scenario M-1.

Scenario M-4, High Sea-level Rise; maximum tides are capped at 2.3 m from 2035 to 2060. This scenario is the same as Scenario S-3, but with addition of management action that limits the highest tides. We assume that it may take some time to reduce maximum tides, e.g., by construction of barriers to tidal action, alteration of marsh topography, or other actions; hence the implementation of management in 2035. Furthermore, it is only in later years that tides above 2.3 m are encountered relatively often. We did not model the effect of reducing maximum tides on juvenile or adult survival, only on nest survival.

Methods - Model 2

Model 2 is built on the demographic analyses of data from the 12-year study of tidal marsh Song Sparrows described in detail here.

Methods for Nest Monitoring

Field biologists searched for and monitored nests at 7 marsh sites in San Pablo Bay and Suisun Bay (Figure 1). The following summarizes nest monitoring methodology (additional information in Liu et al. 2007). Nesting attempts were located at all stages (nest-construction, egg-laying, incubation, and nestling periods). All known nests were monitored using a standard protocol (Martin and Geupel 1993). Nests were usually visited every 2-4 days (median = 3 days; range: 1 to 9 days) with careful attention given to minimize human disturbance. Frequent visits to nests allowed relatively accurate estimation of the dates of predation events as well as dates of egg laying, hatching of eggs, and fledging of young. Nest contents were recorded at each visit at which time the nest was judged to either be still active (i.e., the brood had neither fledged nor failed) or no longer active (i.e., brood fledged or nesting attempt failed). The ultimate outcome of each nest (success or failure) was determined based on resighting of fledged young or nest condition and behavior of the breeding pair (Martin and Geupel 1993). Song Sparrow nestlings were banded when they were about 7 days old with USGS numbered bands and a unique combination of colored leg bands to allow field identification after fledging. The location of each nest was recorded with a GPS. Thus we were able to attribute to each nest climatic covariates that were spatially and temporally specific (see below).

The above protocol was used at the 7 marsh sites over the period 1996 to 2007, for a total sample of 3,183 nesting attempts and 12,302 nest checks included in the dataset analyzed. From this data set, we estimated daily nest survival using the logistic exposure method (Shaffer 2004) as described below.

We estimated **number of young fledged per successful attempt** from the same dataset used for nest survival analysis (Liu et al. 2007). To estimate the **number of nesting attempts per breeding pair** we used a subset of the data, restricting attention to two marshes that were intensively studied: China Camp State Park (Marin County; Figure 1) and Benicia State Recreation Area (Solano County; Figure 1). We intensively searched for the nests of Song Sparrow, and other species within 2 to 4 small study plots per marsh ("intensive plots"); each plot generally was only 1 to 2 ha in area. Within these intensive plots a large proportion of breeders were uniquely color-banded, which facilitated the tracking of an individual pair's nesting attempts. We attempted to find and enumerate all nest attempts of each breeding pair in the intensive plots.

Statistical Analysis of Song Sparrow Demographic Parameters

The three demographic parameters associated with **survival** (juvenile survival, adult breeding season survival, and adult overwinter survival) were incorporated into Model 2 (see below), but

were not analyzed in relation to variation in environmental conditions (current or future) due to lack of specific data.

The three demographic parameters that constitute **reproductive success** were analyzed using the tidal marsh Song Sparrow field data: nest survival, number of nesting attempts, and number of young fledged per successful nesting attempt (see Model 1 section above). We carried out statistical analyses of each dependent variable in relation to four climate variables and maximum tide height per season. Because each nest record included spatial coordinates, and because the date for each nest observation was known, we were able to attribute individual nest records with climatic covariates that were spatially and temporally specific and appropriate for that nest record.

On the basis of prior analysis of the tidal marsh Song Sparrow nest data (Ackerman et al. 2011), we began by choosing four environmental variables to analyze in relation to the three components of reproductive success.

- Precipitation during the fall, winter, and spring preceding or including the breeding season (referred to as "bioyear" precipitation); this variable likely reflects effects of precipitation on vegetation, which in turn may influence plant herbivores and affect nest concealment.
- Precipitation during the breeding season only; this variable may reflect the more direct
 effect of precipitation on prey (e.g., insect abundance or activity) or effects on foraging
 success or, more generally, time and energy budgets of adults or nestlings. In addition,
 breeding season precipitation may directly affect vegetation.

Precipitation data were obtained from PRISM (2011) and were specific to the marsh study site in question and restricted to the appropriate time period (months, years).

- Minimum temperature during the breeding season, and
- Maximum temperature during the breeding season.

Minimum and maximum temperatures may indicate stress (cold or heat) on birds and/or temperature may affect prey availability and/or time/energy budgets. Data were compiled on two temperature variables: minimum temperature during the breeding season (March-July) and maximum temperature during the breeding season. Temperature data were obtained from PRISM (PRISM 2011) and were specific to the marsh study site in question.

In addition we chose a fifth variable, not previously analyzed with respect to components of reproductive success:

• Height of the maximum tide observed during the breeding season.

Tide data were obtained from NOAA website (NOAA 2011), using, for each marsh site, data from the closest of two tide stations that had appropriate and extended time series of tidal data: Richmond, CA, or Mare Island, CA.

Flooding of tidal marsh bird nests due to especially high tides has been noted in several studies (Johnston 1956, Takekawa et al. 2006, van de Pol et al. 2010, Bayard and Elphick 2011) and recorded in our own field studies (Nur et al. 1997, Greenberg et al. 2006b, Liu et al. 2007). In fact, at one primary monitoring site, China Camp, the percent of nests in a season failing due to flooding varied from 3% to as much as 55% (PRBO, unpublished). Recent evidence suggests that risk of future flooding of marsh bird nests, due to extreme tides and storm surges may be increasing in the future (van de Pol et al. 2010, Bayard and Elphick 2011, Thorne et al. in review).

For number of nesting attempts per season (analyzed per female breeder), we fit a generalized linear model, specifically Poisson regression, using the program glm in R (R Development Core Team 2011). Models included a "marsh site" variable, as a fixed effect, and zero, one, or more of the five environmental variables. Because of correlation between the two temperature variables we did not include both in the same model; the same was true for the two precipitation variables. Thus, at most four variables were considered in a model (marsh site, one of two temperature variables, one of two precipitation variables, and maximum tide height). Using this approach we identified marsh site (a categorical variable), the amount of precipitation during the breeding season, and the minimum breeding temperature as covariates significantly affecting the number of nest attempts and were included in the final predictive model. A quadratic of either continuous variable (precipitation, temperature) did not improve model fit, as determined by AIC. Because we had reason to suspect that number of nesting attempts per female were being undercounted (see Model 1 section above), for predictive purposes we made an adjustment of increasing the model-predicted number of nesting attempts by 16.7% (as described for Song Sparrow Model 1).

The statistical analysis revealed that the number of nesting attempts per season decreased as minimum temperature increased, but the number of attempts increased with breeding season precipitation (Figure 2). More nesting attempts reflect a more extended breeding season that in turn is favored by cooler, moister conditions during the spring, a result that was corroborated by findings of Chase et al. (2005).

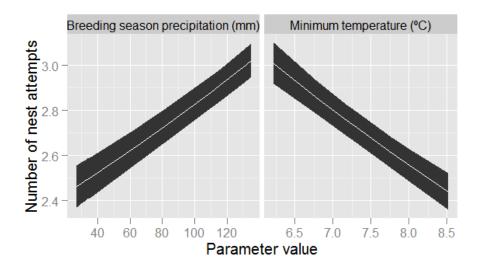


Figure 2. Results of statistical analysis of number of nesting attempts vs. breeding season precipitation (left) and minimum temperature during the breeding season (right) for tidal marsh Song Sparrows. Predicted values (light band) \pm 1 S.E. of the prediction (dark shading) are depicted.

The predicted values for number of nesting attempts were incorporated in Model 2.

For nest survival, we used logistic exposure analysis (Shaffer 2004), using the R package for the analysis (see http://www.npwrc.usgs.gov/resource/birds/nestsurv/index.htm). Models analyzed potentially included effects of marsh site, the two precipitation variables, the two temperature variables, and maximal tide height. Again, an individual model included either of the temperature variables or neither; the same was true for the precipitations variables. In addition, we incorporated age of nest in analyses (since we were analyzing daily nest survival which changes during the course of the 23-day nesting period; Grant et al. 2005). Age of nest was fit as a quartic function, the best supported polynomial fit, as determined by AIC. Finally, we included relative nesting date, which was measured as calendar date of the nest observation relative to the date the first egg was laid in a breeding season, for all nests that year. Relative date was fit as a cubic function, also the best supported polynomial fit to the data. The best supported model included bioyear precipitation (i.e., total precipitation in fall, winter, and spring), maximum temperature and maximum tide height during the breeding season, in addition to the age of nest and relative date variables. Furthermore, a quadratic of tide height provided a better fit than linear only and so we included the former.

The statistical analyses revealed that the probability an individual nesting attempt is successful increased with maximum temperature, decreased as bioyear precipitation increased, and decreased with increasing maximum tide (Figure 3). **The effect of tide** on nest success undoubtedly acts mainly through the flooding of nests leading to death of nestlings, loss of eggs, mortality of eggs and/or

abandonment (Johnston 1956). However, the majority of nest failure overall was due to predation (Greenberg et al. 2006b, Liu et al. 2007). Hence, **the weather effects** (temperature, precipitation) detected more likely involve variation in rates of predation on nests, such that nests are less likely to suffer predation during years that are warmer and with less total bio-year rainfall.

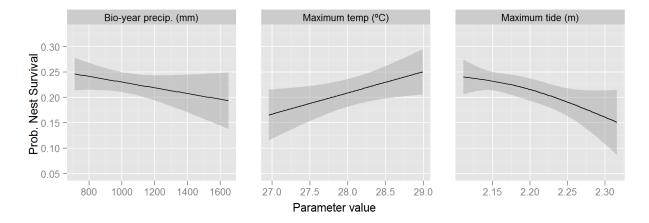


Figure 3. Results of statistical analysis of nest survival probability vs. "bio-year" precipitation (left panel), maximum temperature during the breeding season (middle panel), and maximum tide height (right panel) for tidal marsh Song Sparrows. Predicted values (dark band) \pm 1 S.E. of the prediction (grey shading) are depicted. Note quadratic effect of maximum tide on nest survival.

The number of fledged young per successful attempt was also examined with Poisson regression (using glm in program R). Of all variables examined, only "marsh site" was significant. This variability was due to differences in clutch size among marsh sites (Nur et al. 1997, PRBO unpublished). Thus, of the three components of reproductive success, Model 2 only incorporated effects of environmental variability (due to precipitation, temperature, and maximum tide) on **nest survival** and **number of nesting attempts**.

Adding stochasticity to Model 2

For three parameters, Model 2 used mean values, as explained for Model 1 (see above), but with the addition of stochastic variation around the mean values. These parameter values and associated variances are listed in Table 7. Mean adult survival was 0.600 (based on Nur et al. 2000), divided into **breeding season survival** = 0.90 and mean **non-breeding season survival** = 0.667. We treated breeding season survival as a constant (= 0.90) in all simulations, but for non-breeding season survival we incorporated annual variation, such that SD = 0.0667 (i.e., 10% of the mean value). This value is consistent with estimates of annual variation in female survival for Palomarin Song Sparrows (Nur et al. 2000). For variation in **juvenile survival**, we used SD = 10% of the mean

juvenile survival. For **number of fledged young per successful attempt**, we used the observed between year variation in mean number of fledged young per year, calculated as between-year SD, using the full dataset on tidal marsh Song Sparrows. Thus, each model simulation in each year drew a parameter value from a probability distribution for each of three parameters: overwinter survival, juvenile survival, and number of fledged young per successful attempt, with the specified mean and SD (Table 7).

For nest survival and number of nesting attempts we incorporated stochasticity in parameter values as well, but in a more complex manner. Unpredictable variation in these two parameters reflected two components: (1) environmental stochasticity and (2) residual stochasticity in parameter values not accounted for by environmental conditions, which we refer to as "demographic stochasticity". We began with estimates of "total stochasticity" for each parameter from the 12 year data set, which was determined from the estimate of variance among years in each of the two parameters. We then partitioned this total variance into two components. The first is the variation in demographic values due to year to year variability in environmental variables around the expected (baseline) environmental value. We know that precipitation, temperature and tides over the 12 year time span of the study all varied around their baseline values from one year to the next. That annual variability in turn induced variation in nest survival and number of nesting attempts per year. The second component is additional variation in demographic parameters not due to variation in the specified environmental variables. To estimate this second component, we subtracted variance due to environmental stochasticity alone (i.e., first component) from the total variance among years (the latter reflecting effects of both components, i.e., environmental and demographic stochasticity). The values for total stochasticity and demographic stochasticity are shown in Table 7.

To validate our assumptions of mean values and associated variances for the six parameters we ran simulations (n = 500) in which there was no change in baseline values: for each parameter, the simulation drew from a distribution with specified, fixed mean and a SD around that value (Table 7) that corresponded to the total between-year variation (due to both environmental stochasticity and demographic stochasticity). Population trajectory of the simulations obtained in this manner was consistent with observations of year to year variation in total population size and trends across time for San Pablo and Suisun Bay Song Sparrows (PRBO unpublished), the observed trend being a decline on average of ~2.1% per year.

In other words, for the validation exercise we assumed constant baseline values, but with stochasticity added to the constant baseline values. However, for scenario evaluation (see description of the 11 scenarios above and Table 6), we incorporated changes in baseline values for each parameter as dictated by the scenario, and added stochasticity to the new baseline values.

To summarize the incorporation of stochasticity: For three of the parameters, in each year of each simulation, we randomly chose a demographic parameter value from a probability distribution with specified mean and SD (see above; also Table 7). This was the case for **adult nonbreeding-season**

survival, juvenile survival, and number of fledged young per attempt. For nest survival for each year of each simulation, we first determined the values of environmental variables based on the expected values for that scenario (with respect to assumptions of precipitation, temperature, and maximum tide height) and then added additional variability in environmental values based on the between year variation observed for the environmental variable for 1996 to 2007, as described above. For each simulation, we then used the statistical model for nest survival to predict that year's nest survival given that year's environmental variables, and added additional (demographic-stochastic) variation around the predicted nest survival value. For number of nesting attempts we used the same approach, first determining that year's environmental variable values and from that predicting the expected number of nesting attempts given that year's environmental variables and then adding demographic stochasticity to the predicted value of number of nesting attempts.

Additional Details of Population Dynamic Modeling Procedure

The stochastic population dynamic model tracks the number of adult females as well as juvenile females in each year beginning in 2010 (year 0 of the simulation) and through 2060 (year 50). There are two time steps for each year with reference to (1) the beginning of the breeding season and (2) the end of the breeding season. Starting with the beginning of the breeding season in year t, the model enumerates the number of adult females, both those that were born the previous year (year t-1) and are now considered adult and those adults that survived from the end of the breeding season in year t-1 to the beginning of the breeding season, year t. For each breeding season in a given simulation, the model then determines the total number of fledged female young produced during the breeding season of year t. That number is a function of the number of adult females alive at the beginning of the breeding season and the three parameters pertaining to reproduction: number of nest attempts per adult female, nest survival probability per nest attempt, and number of fledged young per successful attempt. Two of these parameters (number of nesting attempts and nest survival) partly depend on environmental conditions and at the same time are partly stochastic. Number of fledged young per successful attempt also has a stochastic component, that is, in each year of each simulation it varies around a mean value (see above; Table 7).

90% of adult females alive at the beginning of the breeding season in year *t* survive to the end of the breeding season (a period of 5 months). In addition, the model keeps track of the total number of fledged female young produced by the end of the breeding season in year *t*, as described in the above paragraph.

During the next time step, the population model starts with the total number of fledged young produced by the end of the breeding season in year t and calculates the number that will survive the non-breeding season (i.e., survive from the end of the breeding season in their year of birth, year t, to the beginning of next year's breeding season, in year t + 1), which is a function of the juvenile survival probability, itself a random variable (Table 7). Individuals that survive from the end of their first breeding season (the year in which they were born and fledged, year t) to the beginning of the next breeding season, year t + 1, are now one year old at the beginning of the

breeding season in their second year of life. The model tracks this number: the number of young produced in year t that survive to the beginning of the breeding season of their second year of life, year t+1. In addition, the model tracks the number of adults alive at the end of the breeding season in year t that survive to the beginning of the next breeding season, in year t+1. These adults survive the seven-month non-breeding season with probability given by the adult non-breeding season survival probability, also a random variable (Table 7). The sum of the number of young produced in year t that survive to the beginning of the next breeding season in year t+1 plus the number of adults that survive from the end of the breeding season in year t to the beginning of the next breeding season in year t+1 gives us the number of adults at the beginning of the breeding season in year t+1. At all steps, the values of demographic and climatic parameters are retained.

All stochastic population models, for all scenarios, were started with abundances in each age class that approximated a stable age distribution as dictated by the fecundity and survival rates (Table 7). However, due to stochasticity of fecundity and survival rates, actual populations will deviate from a stable age distribution. To incorporate this realism, we simulated initial populations for a 5 year "break-in" period, from 2005 to 2010, under the scenario-specific assumptions of stochastic fecundity and survival rates. Results were discarded from this "pre-recording" period, whose purpose was only to produce a realistic age structure for the simulation. Simulation results were reported only from 2010, which was considered Year 0. Note that, for each scenario, population size in Year 0 of the simulation (2010) was adjusted to 10,000 adults (assuming 5,000 females and 5,000 males) at the beginning of the breeding season in that year. Rather than reporting change in number of females over time, we report change in number of adults.

Additional Density Dependence Consideration: Model 1, which is intended for short-term evaluation, assumes no density dependence. However, over the course of 50 years, as in Model 2, it is possible that future Song Sparrow population levels may become so high that density dependence in vital rates is applicable. In the simulations, we set a maximum population size of 60,000 adults (relative to 10,000 in Year 0); population numbers were not allowed to exceed this ceiling. Given current density of Song Sparrows, and reasonable assumptions regarding future habitat availability (as modeled by Veloz et al. 2012), a six-fold increase in total population seems to be a high-end estimate, a magnitude of increase that is unlikely but possible. Thus, the approach we took to density dependence was relatively simple (cf. Chu-Agor et al. 2011).

Future scenario models

The 11 scenarios evaluated differed with respect to their assumptions concerning two demographic parameters, nest survival and number of nest attempts. For Scenarios C, M-1, and M-2 current environmental conditions were assumed to continue into the future, either with (Scenarios M-1, M-2) or without (Scenario C) management action and simulation results reflect those assumptions. For Scenarios S-1 to S-3, SX-1 to SX-3, M-3, and M-4, we made assumptions about temperature,

precipitation, and maximum tide heights, based on future climate projections. Scenarios M-3 and M-4 included management action as well as future climate change.

Future climate projections for the seven nest monitoring sites were extracted from a statistically downscaled version of the CCSM3.0 GCM (http://gisweb.ciat.cgiar.org/GCMPage). The climate data were downscaled to a 2.5 minute grid (~4 x 4 km) using methods described in Ramirez and Jarvis (2010). We extracted data from the model using the A1b emission. The A1b emissions scenario is considered a moderate scenario but projects relatively high CO2 emissions during the first half of the 21st century and then stabilizes to a mid level of CO2 emissions during the second half of the century relative to other IPCC emission scenarios. The downscaled climate models included, for each month, predicted means for a 30 year period, centered on 2020, 2030, 2040, 2050, 2060, and 2070 with respect to precipitation, maximum temperature and minimum temperature.

We fit a smoothed quadratic regression on year, using these downscaled model-predicted decadal values to obtain a function for the expected **annual** value for temperature and precipitation parameters. The predicted function provided us with estimates of expected (i.e., mean) values of the climatic parameters for each year from 2010 to 2060. In addition, we added a correction factor so that the observed temperature and precipitation value in 2010 matched the model predicted value for 2010. That is, the correction factor ensures that the predicted value of the model matches the observed value of the climate parameter for the starting year; change **relative to 2010** was then dictated by the predictive model. In addition, each simulation added variability around the expected predicted value for each climatic parameter, based on the variability observed around the baseline values for 1996 to 2007 (obtained from PRISM; see above). Specifically, variability around the expected predicted value for each climate variable was equal to the S.D. of that variable as observed during the period 1996-2007. Thus, future variability around a future baseline value was held constant.

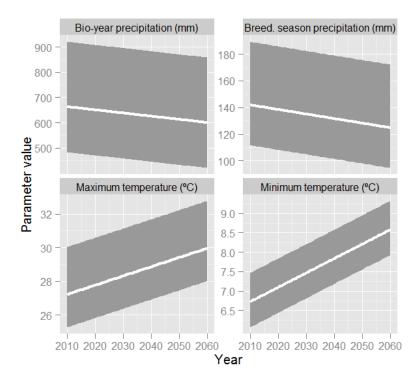


Figure 4. Bioyear precipitation (Oct-June), Breeding season precipitation (Mar-July), Maximum temperature during the breeding season, and Minimum temperature during the breeding season for years 2010 to 2060. Depicted are expected values over time from down-scaled GCM (see text), white band, and maximum and minimum values around expected value (grey band), based on 1996 to 2007 PRISM data (see text).

Figure 4 depicts expected values for precipitation and temperature used in all climate change scenario simulations (Scenarios S-1 to S-3, SX-1 to SX-3, M-3, and M-4).

Future maximum tide values were obtained by adjusting the mean value of the present-day maximum tide by the amount of "net sea-level rise" in the future for each marsh site, where net sea-level rise reflects both global sea-level rise and local marsh accretion (the latter as calculated in the model of Stralberg et al. 2011; see Veloz et al. 2011). To determine global sea-level rise we relied on the two SLR scenarios considered by Stralberg et al. 2011: low SLR (0.52 m over a 100 year period) and high SLR (1.65 m over a 100 year period). To this, we added a third scenario for global sea-level rise, "medium" SLR (1.08 m over a 100 year period), the simple mean value between the first two scenarios. The Stralberg et al. (2011) model estimates marsh accretion due to sedimentation (inorganic and organic) and then produces predictions of elevation relative to Mean Higher High Water (MHHW) that reflect global sea-level rise and marsh accretion. We used model output, for the years 2010, 2030, 2050, 2070, 2090, and 2110, calculated for each individual nest-site location from the 7 marsh sites studied in 1996-2007 (see above). We specifically used the output from the Stralberg et al. (2011) model to estimate the change in elevation relative to MHHW under the three SLR scenarios, under the assumption of low sediment concentration and low

organic matter accumulation. For this we considered years 2010 to 2110, fitting a model that included "year" and "year²" (thus allowing a quadratic trend in elevation over time), as well as a marsh level effect. The result was the estimated change in elevation relative to MHHW over time, as determined for the set of nest locations (1996-2007). Baseline values for maximum tide in the future were then modeled as "current" baseline value of maximum tide (from the period 1996 - 2007) plus the estimated change in net sea-level rise over time. To this, we added year to year variability in the maximum tide experienced based on the S.D. of maximum tide observed for 1996-2007 (obtained from NOAA tide gauges). Thus, for Scenarios S-1, S-2, S-3, M-3, and M-4 (see Table 6), we made the conservative assumption that maximum tides in the future would be no more variable than they have been recently. Note that we only project maximum tide for the period 2010 to 2060, though the quadratic trend over time was calculated for the period 2010 to 2110 (see Figure 5).

In addition, as with temperature and precipitation variables, we added a correction factor to the future predicted values so that model predictions for the 2010 baseline value matched the observed values for 2010. In this way, the average predicted value for maximum tide in 2010 was equal to the observed value that year. The model then predicted the **change in maximum tide** relative to 2010.

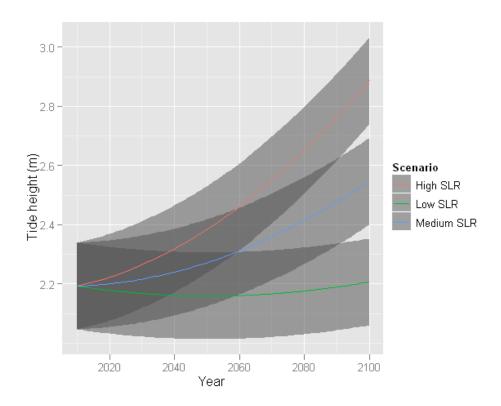


Figure 5. Maximum tide height during the breeding season for 2010 to 2100 on assumption of Low, Medium, and High SLR, together with change in elevation due to accretion (Stralberg et al. 2011). Expected value for simulations shown (colored bands) together with minimum and

maximum values around expected values (in grey). Scenarios S-1 and SX-1 assume low SLR; Scenarios S-2 and SX-2 assume medium SLR; Scenarios S-3, SX-3, M-3, and M-4 assume high SLR (Table 6). Infrequent extreme tides are not shown in this Figure.

Figure 5 depicts maximum breeding season tide heights under the three different SLR assumptions as calculated for 2010 to 2110. Model 2 used only the values for 2010 to 2060. Under assumption of low SLR, marsh elevation from 2010 to 2060 increases faster than sea-level rise, hence the tide height experienced by tidal marsh Song Sparrows declines somewhat until 2060, and then increases from 2060 to 2110. Under medium and high SLR, sea-level rise exceeds marsh accretion starting in 2010 and therefore tide heights increase on average in all years (note that all of these scenarios assumed low sediment concentration).

We also considered that extreme tide events, due to storm surges on other causes, may be more likely in the future (Cubasch & Meehl 2001, Mousavi et al. 2011). Scenarios SX-1, SX-2, and SX-3 were the same as Scenarios S-1, S-2, and S-3, except that for the former we added infrequent extreme tides. Thus Scenario SX-1 assumed low SLR (as in Scenario S-1), but with the addition of an extreme tide of 2.5 m that occurred randomly in each year with probability = 0.10. Likewise, Scenarios SX-2 and SX-3 were medium and high SLR, but with extreme tides added, just as with Scenario SX-1.

Scenarios M-1, M-2, M-3, and M-4 considered impacts of potential management action (Table 6). Scenarios M-1 and M-2 used current conditions projected into the future (as in Scenario C) but in which management actions either increased nest survival by 10% (relative increase) between 2015 and 2035 (M-1) or increased nest survival by 5.5% (relative increase) over a longer period, 2015 through 2060 (Scenario M-2). Scenario M-3 was the same as the High Sea-Level Rise Scenario S-3 except that nest survival was increased by 10%, between 2015 and 2035. The additional increase in nest survival modeled in Scenarios M-1 and M-2 was calculated after nest survival was calculated as for Scenario C; the additional increase in nest survival modeled in Scenario M-3 was calculated after nest survival was determined as in Scenario S-3. Scenario M-4 was the same as the High Sea-Level Rise Scenario S-3 except that highest tide per breeding season experienced by tidal marsh Song Sparrows was not allowed to exceed 2.3 m, for the period 2035 to 2060. Any tide height above 2.3 m was reduced to 2.3 m. Note that during the study period 1996 to 2007 the highest breeding season tide experienced by Song Sparrows was 2.32 m.

Model Output

To evaluate model outcomes for each of the 11 scenarios, we use several different ways to summarize results of the 500 simulations per scenario. However, for illustrative purposes, we also depict results from a single representative "run" (i.e., simulation) for a subset of scenarios.

Results of the 500 simulations were summarized using three different approaches. In the first, we plot mean \pm 1 S.D. for the 500 simulations per scenario for the period 2010 (Year 0) to 2060 (Year

50). In the second approach, we calculated the actual, realized population growth rate for each simulation, determined by 10 year intervals. For each scenario, we depict the median lambda by decade (2010-2020, 2020-2030, etc.) as well as quantiles of interest (5%, 25%, 75% and 95%) from the results of the 500 simulations.

For the third approach, we focused on the probability that the population will decline 80% or more compared to the starting population size over 50 years. For this, our goal was to provide a metric that was both **retrospective** and **prospective**. Retrospectively, the metric assesses population size in 2060 compared to population size in 2010; we report the proportion of simulations that exceeded an 80% drop over 50 years. Declines that exceed this criterion should sound an alarm ("red flag" warning). Note that a population that declines 80% over 50 years is declining at 3.17% per year, on average (lambda = 0.9683).

In addition, we used this criterion (average decline of at least 3.17% per year), to analyze population change, decade by decade, in a cumulative fashion. A population that declines at 3.17% per year, on average, will have declined by 27.52% after 10 years, by 47.47% after 20 years, and so on. After 50 years, it will have declined by 80.0%. These threshold values for 0-10 years, 0-20 years, 0-30, 0-40, and 0-50 years were used to indicate the probability that a population will exceed the "red flag" criterion after the specified number of years of the simulation (10, 20, 30, 40, or 50, respectively).

Our intent in applying this criterion on a decade by decade basis was two-fold. First, we wished to demonstrate how the probability of decline may change in the future, on a decadal scale. It is much more realistic to consider that climate and other environmental influences will change on a decadal scale and we wished to develop a means to demonstrate that. Second, our intent was to provide a tool for managers to evaluate the likelihood that a population, given a set of scenarios, will be "on track," after 10, 20, 30, or 40 years, to decline by a total of 80% after 50 years. Such a tool can help a manager plan for the future.

Results - Model 2

Scenario Results

Scenario C: Current Conditions Continue. If current conditions continue, Song Sparrows can be expected to continue to exhibit population declines. A sample simulation is shown in Figure 6.

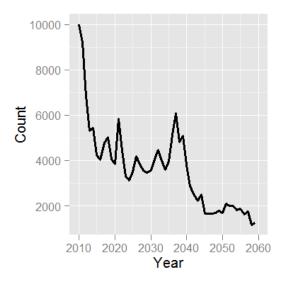


Figure 6. A single, sample simulation for Scenario C ("Current Conditions Continue"), 2010 to 2060. The simulation begins with 10,000 individuals in 2010 (Year 0). 500 simulations were carried out for each scenario.

On average, the population is expected to shrink from 10,000 to fewer than 2,000 by 2060 (Figure 7). However, a sizable proportion of simulations result in extinction as early as 2030. Note that we did not allow for re-colonization; thus, for a given simulation, once a population hit zero individuals it remained at zero throughout the simulation.

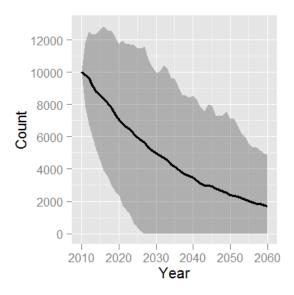


Figure 7. Results of 500 simulations depicting population trajectory of tidal marsh Song Sparrows from 2010 to 2060. Shown are mean number of individuals in each year (beginning

with 10,000 in 2010 for every simulation) and \pm 1 S.D. around the mean trajectory (grey shading), for Scenario C ("Current Conditions Continue").

Decade by decade, lambda can be expected to be below 1 during the 50-year period (Figure 8). Since current conditions are assumed to remain in place for the entire 50 years, there is no overall change in lambda by decade. Note that 25% of simulations exhibited a lambda that was very close to 1.0 or was greater than 1.0 in each decade; furthermore, 5% of simulations had a lambda (by decade) of about 1.03 or greater. Thus, population decline on a decadal scale is not assured, just likely. Note, too, that 25% of simulations exhibited a lambda of less than 0.91, calculated by decade (Figure 8).

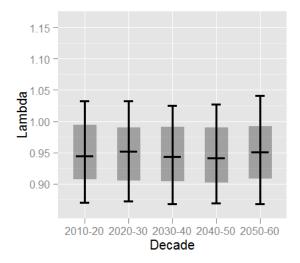


Figure 8. Results of 500 simulations depicting lambda as calculated decade by decade. Depicted are, from top to bottom, 95th percentile (top bar), 75th percentile (top of grey shaded box), median (middle bar), 25th percentile (bottom of grey shaded box) and 5th percentile (bottom bar) for the five decades from 2010 to 2060, for Scenario C ("Current").

The probability of an 80% decline is high under this scenario (Figure 9). After 50 years, 75% of simulations exceed this criterion. Even after 10 years, the simulations indicate a 60% probability that the population will decline by 27.5% or more, that is, equivalent to 3.17% decline per year. After 20 years, simulations indicate a 68% chance the population will have declined by 47.5%, exceeding the "red flag" warning criterion for a 20 year time period.

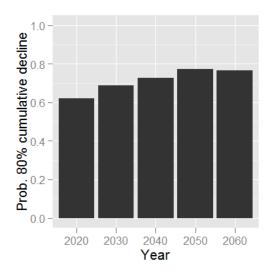


Figure 9. Results of 500 simulations depicting cumulative probability of population decline decade by decade, with respect to "red flag" warning criterion. For each panel, the bar on the left depicts the probability that the population will have declined by 27.5% or more by 2020; the other bars depict the probability that the population will have declined by 47.5% by 2030, by 61.9% by 2040, by 72.4% by 2050, and by 80.0% by 2060, respectively. Results are shown for Scenario C ("Current").

Scenarios S-1, S-2, and S-3: Effects of Low, Medium, and High Sea-level Rise

We discuss these three scenarios together, since they differ only with respect to the magnitude of future sea-level rise, with all other assumptions the same among these three scenarios. Recall that these scenarios all assume precipitation and temperature change according to the downscaled GCM (see Methods) as shown in Figure 4.

Under assumptions of climate change, Song Sparrow populations are expected to do well under the Low Sea-level Rise assumption (Scenario S-1; see Figure 10A for a sample run and Figure 11A for a summary of all 500 simulations). That is, expected numbers in 2060 are high (mean number of individuals in 2060 is about 40,000). Under the assumption of Medium Sea-Level Rise, the overall outcome is more or less stable, but as shown in Figure 11B, under Scenario S-2, the population is expected to decline somewhat before increasing in the last two decades (2040 to 2060). Under the assumption of High Sea-Level Rise, we see strong declines, comparable to that seen for Current Conditions, with the mean population only about 2500 individuals.

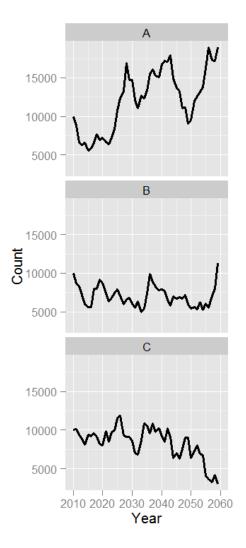


Figure 10. Single, sample simulations of change in population number (total number of individuals) for each of three scenarios. Panels A, B, and C refer to Scenarios S-1, S-2, and S-3 (Low, Medium and High Sea-level Rise).

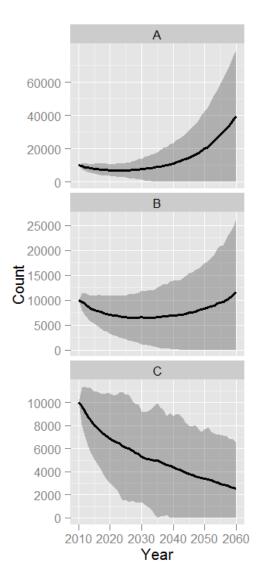


Figure 11. Results of 500 simulations depicting population trajectories of tidal marsh Song Sparrows from 2010 to 2060, under three scenarios of Sea-level Rise: S-1 (Panel A), S-2 (Panel B), and S-3 (Panel C), i.e., Low, Medium and High Sea-level Rise, respectively. Shown are mean number of individuals in each year (beginning with 10,000 in 2010 for every simulation) and \pm 1 S.D. around the mean trajectory (grey shading).

Under Low Sea-level Rise, lambda is below 1.0 in the first decade, hits 1.0, on average, in the second decade (2020-2030), and then exceeds 1.0 in the last 3 decades, reaching 1.06 (on average) by the fifth decade (Figure 12A). Thus, under Scenario S-1 we see **accelerating** population growth. For Medium Sea-level Rise (Scenario S-2), lambda is below 1.0 in the first half of the simulation and then exceeds 1.0, on average, in the second half of the 50 year simulation (Figure 12B). For High

Sea-level Rise, lambda on average stays considerably below 1.0. In about 75% of the simulations throughout the five decades, lambda is 1.0 or lower (Figure 12C).

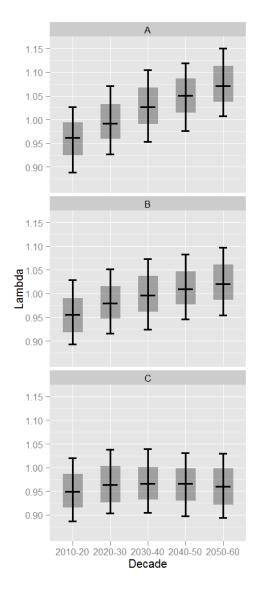


Figure 12. Results of 500 simulations depicting lambda as calculated decade by decade for three scenarios. Depicted are, from top to bottom, 95th percentile (top bar), 75th percentile (top of grey shaded box), median (middle bar), 25th percentile (bottom of grey shaded box) and 5th percentile (bottom bar) for the five decades from 2010 to 2060. Panels A, B, and C, refer to Scenarios S-1, S-2, and S-3 (Low, Medium and High Sea-level Rise).

The probability of 80% decline is very small for Low Sea-level Rise (Scenario S-1), at least by 2060 (Figure 13A). For Medium Sea-level Rise (Scenario S-2), there is, by 2060, a 10% probability of 80% decline, and for High Sea-Level Rise, the probability of 80% decline is about 60% (Figures 13 B, C).

For this last scenario, the probability that population declines exceed the "red-flag" criterion is consistently at about 60% across the whole five-decade span.

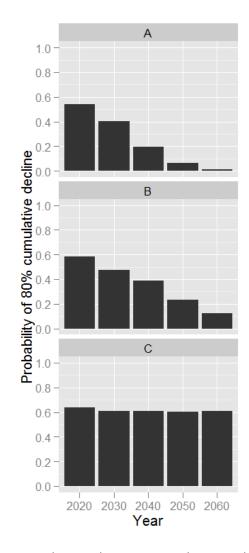


Figure 13. Results of 500 simulations depicting cumulative probability of population decline decade by decade, with respect to "red flag" warning criterion. For each panel, the bar on the left depicts the probability that the population will have declined by 27.5% or more by 2020; the other bars depict the probability that the population will have declined by 47.5% by 2030, by 61.9% by 2040, by 72.4% by 2050, and by 80.0% by 2060, respectively. Panels A, B, and C refer to Scenarios S-1, S-2, and S-3 (Low, Medium and High Sea-level Rise).

The positive trend for population size under Low Sea-level Rise is due to a strong increase in nest survival over the 50 year simulation (Figure 14). In contrast, predicted changes in number of nesting attempts under the three Scenarios (S-1, S-2, and S-3) show a decreasing trend (not shown). However, decreased tide height in the future (because marsh accretion outpaces Sea-level rise under Scenario S-1) and increased maximum temperature (which is the case for Scenarios S-1, S-2,

and S-3, as well as the other "climate-change scenarios") both act to increase nest survival. The predicted change in nest survival is illustrated in Figure 14. By 2060, nest survival under Scenario S-1 exceeds 36% which is a major improvement compared to "current" values, but still below the values observed by Johnston (1956) for tidal marsh Song Sparrows in San Pablo Bay. Note that it is the **increase in nest survival probability over time** that results in accelerating population growth rate. A 1% relative increase in nest survival per year, for example, will increase lambda by 0.4%, which, after 50 years, means a 22% increase in lambda over that time span. Such an increase in nest survival can well mean the difference between substantial population decline and substantial population growth.

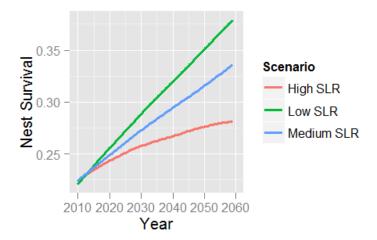


Figure 14. Change in tidal marsh Song Sparrow nest survival from 2010 to 2060 for Low, Medium, and High SLR (Scenarios S-1, S-2, and S-3). Nest survival increases due to increased temperature and decreased precipitation for all three scenarios. However, changes in maximum tide height act to counteract this increase to varying degrees. Note that even under High SLR, nest survival is predicted to increase because of positive influence of increasing temperature and decreased precipitation.

In contrast, for High Sea-Level rise, there is a more complex picture. As with Low and Medium Sea-Level rise, the number of nesting attempts decreases with time (due to temperature increasing and precipitation decreasing) from a mean of 3.46 nest attempts in 2010 to fewer than 2.8 in 2060. Nest survival increases slightly under this scenario (Figure 14). Essentially, the increase in nest survival is counter-acted by the decrease in nesting attempts; the result is an expected population decline, similar to that observed under Current Conditions (Scenario C). Thus, the overall lambda is similar under Scenarios C (Current Condition) and S-3 (High Sea-Level Rise), but the similarity of outcome is achieved with a different mix of values for nest survival and number of nesting attempts.

Scenarios SX-1, SX-2, and SX-3: Sea-Level Rise with Extreme Tides

Scenarios S-1, S-2, and S-3 only allowed for effects of changes in temperature, precipitation, and sea-level rise, but did not include the possibility of unusually high tides due to storm surges, as has been predicted by several studies (Cubasch & Meehl 2001; Mousavi et al. 2011, Thorne et al. in review). Scenarios SX-1, SX-2, and SX-3 correspond to Scenarios S-1, S-2, and S-3 except that we also included infrequent (once per decade on average) unusually high tides. Results are shown in Figures 15, 16, and 17.

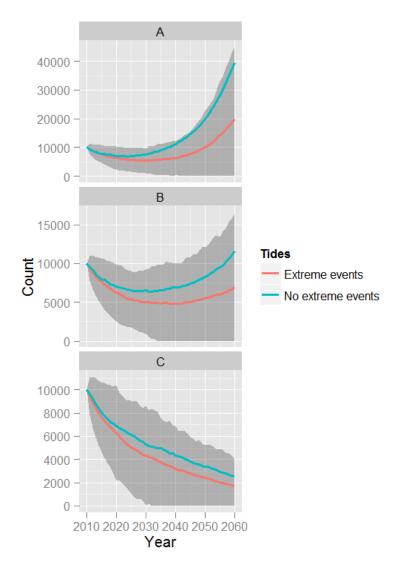


Figure 15. Results of 500 simulations depicting population trajectory of Song Sparrows from 2010 to 2060 under Scenarios SX-1, SX-2, and SX-3, corresponding to Low, Medium and High Sea-level Rise but with extreme tides. Trajectories shown as mean number of individuals (in red) and \pm 1 S.D around the mean trajectory depicted in grey shading. For comparison, aqua line depicts median results without extreme tides (as shown in Figure 7A, 7B, and 7C).

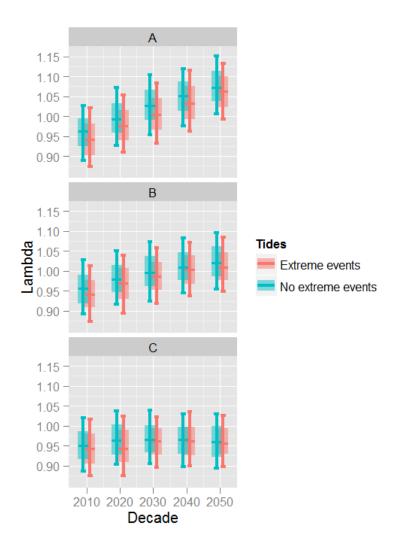


Figure 16. Results of 500 simulations depicting lambda as calculated decade by decade for three scenarios with extreme tides (in red) and three scenarios without additional, extreme tides (in aqua). Depicted in each panel, from top to bottom, are 95th percentile (top bar), 75th percentile (top of grey shaded box), median (middle bar), 25th percentile (bottom of grey shaded box) and 5th percentile (bottom bar) for the five decades from 2010 to 2060. Panels A, B, and C refer to Low, Medium, and High Sea-Level Rise Scenarios, respectively. Panel A depicts Scenarios S-1 in aqua and SX-1 in red; Panel B depicts Scenarios S-2 in aqua and SX-2 in red; Panel C depicts Scenarios S-3 in aqua and SX-3 in red.

A large impact of extreme tides is seen assuming low Sea-level Rise (cf. Scenarios S-1 and SX-1). For example (Figure 15A), populations are expected to grow only to about 20,000 (with extreme tides) compared to 40,000 (without extreme tides). With the addition of extreme tides, lambdas calculated by decade are shifted down by about 2% (Figure 16A).

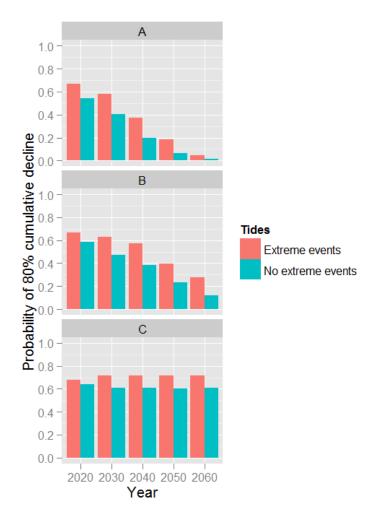


Figure 17. Results of 500 simulations depicting cumulative probability of population decline decade by decade, with respect to "red flag" warning criterion under three assumptions of sealevel rise, with (red) and without (aqua) extreme tides. For each panel, the first pair of bars on the left depict the probability that the population will have declined by 27.5% or more by 2020 (red with extreme tide; aqua without). The other four pairs of bars depict the probability that the population will have declined by 47.5% by 2030, by 61.9% by 2040, by 72.4% by 2050, and by 80.0% by 2060, respectively. Panels A, B, and C refer to Low (Scenarios S-1, SX-1), Medium (Scenarios S-2, SX-2) and High (Scenarios S-3, SX-3) Sea-level Rise assumptions, respectively.

For Medium Sea-level Rise, there is also a substantial effect of adding Extreme Tides. Rather than, on average, growing slightly after 50 years, the population is expected to show, if subjected to infrequent extreme tides, net population decrease (Figure 15B). Notably, the probability of 80% decline after 50 years more than doubles, from about 12% without extreme tides to about 28% with extreme tides (Figure 17B).

For High Sea-level Rise there is also an effect of adding extreme tides, but it is more subtle than the other two Sea-level Rise assumptions (Figure 15C). The small effect is for two reasons: 1) Under High Sea-level Rise, populations are already expected to show strong declines and 2) Under the assumption of High Sea-level Rise, a tide of 2.5 m is not so unusual (note, we used an absolute value of an extreme tide of 2.5 m in Scenarios SX-1, SX-2, and SX-3). A notable difference between Scenarios S-3 and SX-3 is seen with respect to the probability of 80% decline: without additional extreme tides, the probability of such decline after 50 years is about 0.60, but with additional extreme tides, the probability exceeds 0.70 (Figure 17C).

Management Scenarios

We evaluated four management scenarios. In the first two, M-1 and M-2, current conditions continue, but nest survival is enhanced, either a 10.0% relative increase from 2015 to 2035 only (Scenario M-1) or a 5.5% relative increase from 2015 to 2060 (Scenario M-2). Summaries of population trajectories under Scenarios C, M-1, and M-2 are shown in Figure 18. Increasing nest survival by 10% (from an average of 0.233 to 0.256) is effective at counteracting the population decline observed in Scenario C (see Scenario M-2, Figure 18B). But once the enhancement is discontinued (in 2035), the population resumes its downward decline (Figure 18B); the expected population size in 2060 under Scenario M-2 is about 4,000 compared to 2,000 if Current Conditions Continue (Scenario C). In contrast, increasing nest survival by 5.5% (from an average 0.233 to 0.246) for the period 2015 to 2060 does not prevent population decline, but it does slow the decline substantially (Figure 18C). Expected population size in 2060 is approximately 5,000 individuals under Scenario M-2.

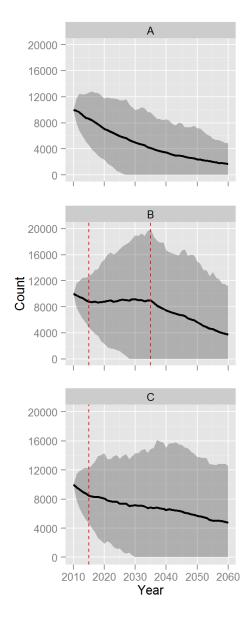


Figure 18. Results of 500 simulations depicting population trajectory of Song Sparrows from 2010 to 2060 under Scenarios C, M-1, and M-2 (Panels A, B, and C, respectively). Each simulation for each scenario began with 10,000 individuals in 2010. Trajectories shown as mean number of individuals (black band) and ± 1 S.D around the mean trajectory depicted in grey shading. For all three scenarios, future environmental conditions are the same as current conditions. Scenario C (Panel A) has no management action. Scenario M-1 (Panel B) increased nest survival by 10% from 2015 to 2035 only, shown with vertical dotted lines; and in Scenario M-2 (panel C) nest survival is increased 5.5% from 2015 to 2060, shown with vertical dotted line at 2015.

The probability of 80% decline over 50 years, and by cumulative decade, is shown for Management Scenarios M-1 and M-2, in comparison with Scenario C (Figure 19). These three scenarios assume Current Conditions Continue, except for the specific management intervention. There is a noticeable difference between the non-managed scenario (Scenario C, Figure 19A) and the two management scenarios with respect to the probability of exceeding the "red-flag" warning criterion (Figure 19B, 19C). The probability of observing a decline of 80% over 50 years decreases from about 0.75 in the absence of management to about 0.55 with management. This result (shown in Figure 19B, 19C) quantifies the benefit to management action, given our specific assumptions, but also demonstrates substantial risk of severe decline even with management.

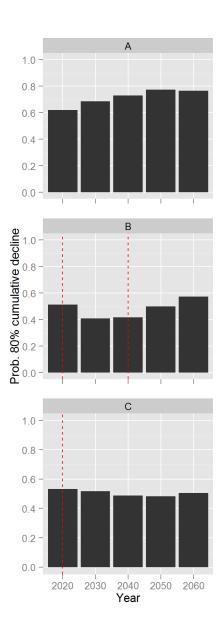


Figure 19. Cumulative probability of population decline, decade by decade, comparing scenarios with management (Scenarios M-1 and M-2) and without management (Scenario C); all three scenarios assume Current Conditions Continue. For each panel, the bar on the left depicts the probability that the population will have declined by 27.5% or more by 2020; the other bars depict the probability that the population will have declined by at least 47.5% by 2030, by at least 61.9% by 2040, by at least 72.4% by 2050, and by at least 80.0% by 2060, respectively. Shown are results for Scenario C (panel A), Scenario M-1 (panel B) and Scenario M-2 (panel C). Red vertical dotted lines indicate initiation and/or cessation of management action.

In the third and fourth management scenarios that we modeled (Scenarios M-3 and M-4), we assumed High Sea-level Rise, no additional extreme tides, and either that nest survival was enhanced by a relative 10.0% for a 20-year period, 2015 to 2035 (just as in Scenario M-1), or that extreme high tides were prevented (i.e., no tides could exceed 2.3 m) for the period 2035 to 2060. These results, depicted in Figure 20, were instructive. Enhancing nest survival by 10.0% was sufficient to reverse expected population declines under the High Sea-level Rise assumption (compare panels A and B, Figure 20). Under Scenario M-3, the population is expected to grow somewhat from 2015 to 2035, making up for the decline from 2010 to 2015 (Figure 20B). However, once nest survival is no longer enhanced, the population declines again. Thus, the trajectories under Scenarios M-1 and M-3 are similar (cf. Figures 18 and 20) even though one scenario assumes current conditions continue and the other incorporates anticipated climate change (including high sea-level rise).

In the fourth management scenario, M-4, high tides are capped starting in 2035. The result is that, starting from that year, the trajectory begins to change, first leveling off during the period 2040 to 2049, and then showing an accelerating increase from 2049 to 2060 (Figure 20). Thus by 2060, the population has regained some of its earlier decline. Under Scenario M-4, the population in 2060 is still below its starting value, but, nevertheless, on average exceeds 5,000 individuals, compared to 2500 or fewer individuals under Scenario S-3 (i.e., without management). Furthermore, in some simulations the population exceeds its starting size, as indicated for Scenarios M-3 or M-4 (Figure 20).

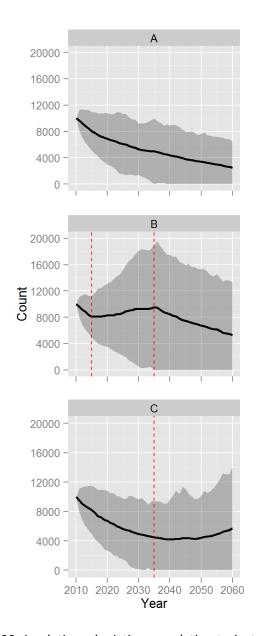


Figure 20. Results of 500 simulations depicting population trajectory of Song Sparrows from 2010 to 2060, under the assumption of High Sea-level Rise, either without management, Scenario S-3 (Panel A), or with management, Scenarios M-3 (Panel B), and M-4 (Panel C). Shown are mean number of individuals in each year (beginning with 10,000 in 2010 for every simulation) and \pm 1 S.D. around the mean trajectory (grey shading). In Scenario M-3 (panel B) nest survival is increased 10% from 2015 to 2035 only (see vertical dotted red lines) and in Scenario M-4 (panel C) no tides above 2.3 m are allowed from 2035 to 2060 (see vertical dotted red line).

The probability of 80% decline over 50 years, and by cumulative decade, is shown for Scenarios M-3 and M-4, in comparison with Scenario S-3 (Figure 21). These three scenarios assume High Sea-level

Rise and no increase in extreme tides, except for the specific management intervention. There is a substantial difference between the non-managed scenario (Scenario S-3, Figure 21A) and the two management scenarios with respect to the probability of exceeding the "red-flag" warning criterion (Figure 21B, 21C). The probability of observing a decline of 80% over 50 years decreases from about 0.60 in the absence of management (i.e., Scenario S-3) to between 0.30 and 0.40 with management, depending on the management scenario (Figure 21). In particular, suppressing the highest tides (Scenario M-4) would reduce the risk of 80% decline after 50 years to only half of what it is under Scenario S-3.

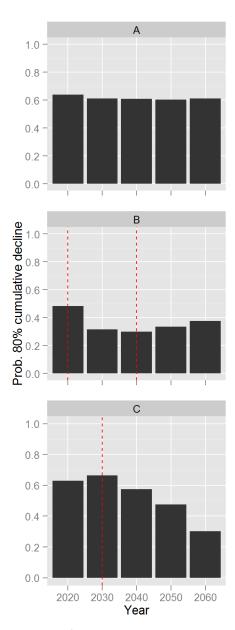


Figure 21. Cumulative probability of population decline, decade by decade, comparing scenarios with management (Scenarios M-3 and M-4) and without management (Scenario S-3); all three scenarios assume High Sea-Level Rise. In Scenario M-3 (panel B) nest survival is

increased 10% from 2015 to 2035 only (see vertical dotted red lines) and in Scenario M-4 (panel C) no tides above 2.3 m are allowed from 2035 to 2060 (see vertical dotted red line). For each panel, the bar on the left depicts the probability that the population will have declined by 27.5% or more by 2020; the other bars depict the probability that the population will have declined by at least 47.5% by 2030, by at least 61.9% by 2040, by at least 72.4% by 2050, and by at least 80.0% by 2060, respectively. Shown are results for Scenario S-3 (panel A), Scenario M-3 (panel B) and Scenario M-4 (panel C). Red vertical dotted lines indicate initiation and/or cessation of management action.

Comparing results for scenarios M-3 and M-4 reveals that, in Scenario M-3, the risk of 80% decline increases from 2040 to 2060 because nest survival is no longer enhanced after 2035, while in Scenario M-4, the risk of 80% decline decreases from 2040 to 2060 because highest tides are capped for the period 2035 to 2060 (Figure 21).

DISCUSSION AND MANAGEMENT IMPLICATIONS OF THE POPULATION DYNAMIC MODELS

Here we summarize and discuss our findings, for both the simple Population Dynamic Model 1 and the more detailed Stochastic Population Viability Model 2, placing our findings in a larger context, with focus on relevance for managers.

The principal objective of this study was to gain insight into the future viability of tidal marsh species that may be impacted by climate change as well as inform management action that may counteract such environmental change. We have done so focusing on tidal marsh-dependent bird species in the San Francisco Estuary. However, our results are applicable to many other habitats and many other taxa, not just birds, but other vertebrates and plants as well (see, e.g., Maschinski et al. 2006, Keith et al. 2008).

There have been, to date, relatively few studies that have utilized a demographic approach to evaluating impacts of climate change on animal populations. Several studies have considered impacts of sea-level rise and/or climate change on available habitat or habitat suitability. If carrying capacity is reduced, as a result of climate change, then this reduction will have implications for demographic rates, and, ultimately long-term viability (Keith et al. 2008, Aiello-Lammens et al. 2011; Chu-Agor et al. 2011). In this study, we have begun the process of considering the demographic impacts of climate change, but the integration of this study, which is not spatially explicit, with consideration of habitat extent and habitat quality (exemplified by Veloz et al. 2011), is the explicit goal of our next phase of work.

Even in its early stages, our study on demographic impacts of climate change on tidal marsh birds is of value because, in general, studies examining the direct impacts of climate change on survival and reproduction have been rare. One relevant example is provided by van de Pol et al. (2010). The authors determine the effects of nest flooding on reproductive success on shorebirds; they conclude that the increasing risk of nest failure due to flooding, which is increasing due to climate change, has now reduced reproductive output of Eurasian Oystercatchers below levels needed to sustain populations (i.e., below lambda = 1.0). The stage is set, therefore, in the case of the oystercatcher, to develop a population-dynamic model that will incorporate these environmental influences on long-term viability, similar to what we present here.

The population dynamic modeling developed here, whether the simple Model 1 or the stochastic Model 2, is of value in many different ways. It allows one to:

- partition population growth rate into six demographic components, and then explore the manner in which future environmental changes, natural or not, will impact future population growth or decline,
- (2) quantify the change in population growth rate as a function of changes in the individual components,
- (3) consider multiple concurrent influences on population growth, which may be acting in synergistic or antagonistic fashion,

- (4) make explicit assumptions regarding population response or parameter values, which can then be evaluated,
- (5) assess the sensitivity of results and predictions to assumptions or degree of uncertainty regarding model inputs,
- (6) identify important data gaps with regard to population response to environmental conditions or management actions, gaps that have important implications for future viability,
- (7) evaluate the effectiveness of proposed management actions in affecting the long-term viability of target populations, and thus facilitate prioritization of potential management response, and
- (8) provide a basis for setting target values (either parameter values or a change in a parameter) in order to achieve a desired trajectory or change in population growth rate.

In our approach we emphasize evaluating the impact of a **change** in a **parameter value** and/or comparison of the anticipated effects of a change in the environment or management action. In this way, managers can evaluate the feasibility and efficacy of bringing about change in a given parameter in relation to the change in population trajectory. As we demonstrate here, a **modest change** in **nest survival** for two of the species may be feasible and effective in stabilizing or reversing population declines. On the other hand, a parameter such as the number of young produced per successful nesting attempt may not be responsive to environmental and/or management influence, at least not among the four marsh bird species we have considered. The important point is that the models presented allow one to compare the population response over time in relation to changes in any one or several of the parameters.

Results presented here are, to an extent, sensitive to assumptions made regarding parameter values. A strength of our approach is that one can directly evaluate just how sensitive are the results to specific assumptions made. In this way, one can identify the parameters for which additional information is critical for successful management in contrast to other parameters, where results are more robust to initial assumptions.

In addition, the stochastic "Model 2" allows one to **manage for uncertainty**. Environmental conditions in the future will always be, to an extent, unpredictable as, too, will be the demographic response to a specified set of conditions. Stochastic models predict a range of outcomes, not a single, most likely outcome. In this way, one can manage for adversity; for example, what if future conditions are not as favorable as we currently project? Thus, a manager can be guided by minimizing the probability that a population will decline by 80% over a given time period. An 80% decline may not be a likely outcome, but reducing its likelihood may be an important management goal, which our modeling tool can address.

An important objective of this study was to obtain specific findings that could inform management. Our results point to the importance of **nest survival**, a parameter that is of high relevance to managers. Low nest survival appears be implicated in the observed population declines for Song

Sparrows, and may well for Clapper Rails as well. For tidal marsh Song Sparrows, recent (1996 to 2007) nest survival rates are less than half that observed by Johnston (1956) in the early-mid 1950's for the San Pablo Song Sparrows. Our interactive Model 1 for Song Sparrows, allows a manager to quantify the impact on population trends if one were to alter current nest survival rates.

Climate Change Impacts

The statistical analyses presented here demonstrate that climate change will likely have multiple impacts on demographic rates of tidal marsh birds. For Song Sparrows, the warmer, drier conditions expected in the future can be expected to increase nest survival but at the same time shorten the breeding season, and thus, lead to fewer nesting attempts. The population model demonstrated that the population benefit of increased nest survival is expected to outweigh the cost to the population of decreased number of nesting attempts. At the same time, we also provide statistical evidence for an effect of extreme tides on nest survival, due to increased flooding of nests leading to nest failure. If the incidence of high water events were to increase, either because of sealevel rise or infrequent extreme tides, there may be strong, long-lasting impacts and the result may be strong population decline, in some cases by 80% or more.

Thus, there are several important management implications that follow from our modeling. The first is to emphasize the importance of nest survival, both in terms of anticipated climate-change impacts and in terms of management actions that may alter or compensate for changes in nest survival rates. Nest survival may be especially responsive to management actions. Not paying sufficient attention to nest survival may mean that population recovery is prevented. The population models we have developed assist in identifying the most important population bottlenecks, which in turn will affect future viability or recovery.

Second, is to identify the importance of considering several simultaneous influences on population dynamics. The very conditions that may be favorable for one demographic parameter may be unfavorable for another parameter. The population models we present allow one to quantify the net impact of antagonistic or synergistic impacts.

Third, the modeling has identified important areas for further research or monitoring. One example is the impact of extreme events, such as very high tides or storms. Not only will these infrequent but important events affect demographic rates of tidal marsh birds (as demonstrated in our models), but such events will also likely impact habitat and vegetation (Zedler 2010, Thorne et al. in review), which we have not explicitly modeled.

Impacts of Management

For two of the species, Song Sparrows and Clapper Rails, nest survival may be key to maximizing long-term viability of populations and/or recovering depleted populations. Our results demonstrate that a relatively modest and feasible change in nest survival can turn a declining population (e.g., as has been observed in San Pablo and Suisun Bays) into an increasing population. The necessary

change in nest survival may be accomplished through reduction in predation rates, e.g., by reducing predator populations, including abundance of non-native predators (such as cats) or human-associated predators (e.g., raccoons), or by reducing access of predators to tidal marsh bird nests. The latter may be implemented through, for example, provision of "floating islands" for Clapper Rails and other birds to nest on.

A second means to dampen or reverse population declines may be to extend the breeding season, allowing for a greater number of nesting attempting per year. This may require management of habitat, especially vegetation in the breeding areas. It is not clear that such manipulations are feasible, but they are worth considering.

We have emphasized the importance of increasing nest survival rates, but that is not to say that over-winter survival may not be important. In the San Francisco Estuary considerable attention is currently focused on addressing the threat posed by low over-winter survival and considering means to reduce mortality associated with high water events. However, the population consequences of low nest survival also present a grave threat especially for populations that are declining, or have declined. One strength of our modeling is that it allows for quantification of the benefits of changing nest survival rates vs changing overwinter survival rates and provides target values, with respect to changes in these parameters.

Nevertheless, the most important question for a manager may not be, how much do we need to change a demographic parameter, but, rather, how responsive is the demographic parameter to management action? Indeed, nest survival may be more responsive to management action than is over-winter survival. In any case, even if over-winter survival is improved, a population, such as Clapper Rails in San Francisco Bay, may not be able to recover if the adequacy of current and future nest survival rates is not addressed as well.

Limitations of This Study

- 1. Values for some parameter are not as well established as other parameters. If our assumed values are not correct, results will be altered. We address this limitation in two ways. The first is that our parameter values are made explicit; models can easily be rerun with alternative values and results assessed, thus providing information on the sensitivity of results to specific assumptions. Second, our principal objective was to provide a tool to evaluate population sensitivity to changes in parameters, in other words to compare future population growth rate under different conditions. In this way, we can compare how a change in a demographic parameter, whether environmental or management-based, will alter population trajectory and so compare changes in different parameters (e.g., change in over-winter survival vs. change in nest survival).
- 2. Whereas Model 2 considers explicitly how climate change may affect nest survival and other components of reproductive success, we have not incorporated effects of climate change on survival of juveniles and adults. This is an important limitation. Modeling of hypothesized

effects of climate change on juvenile and adult survival is clearly called for, building on the work presented here. If either juvenile survival or adult survival, or both, are affected by climate change (due to temperature, precipitation, flooding of habitat, etc.) this could negate positive impacts of management on nest survival. Moreover, empirical field studies of marsh birds need to target the sensitivity of survival to climate variables. The study by Overton et al. (submitted) identified the dependence of over-winter survival of Clapper Rails on high tides. If the height of high tides increases due to climate change (as has been hypothesized; Cayan et al. 2008, van de Pol 2010), over-winter survival will be depressed. But the effect of other climate variables needs to be examined as well. To give an example in the marine realm, Lee et al. (2007) demonstrated that annual survival of adult Cassin's Auklets (*Ptychoramphus aleuticus*) was related to winter Southern Oscillation Index. If ENSO events become more common or more severe in the future (Lee and McPhaden 2010), such environmental change will depress population trajectories and perhaps lead to population crashes.

- 3. Models 1 and 2 are currently developed at a more generic, regional or watershed, spatial scale. There is a need for population dynamic modeling at the level of individual, specific marshes. We emphasize that this study represents just a first step on the road to construction and application of spatially-explicit, landscape-level population dynamic models for mangers (see Next Steps, below).
- 4. We have modeled future environmental conditions but there is considerable uncertainty about the future. This uncertainty affects all climate change modeling (Wiens et al. 2009), especially so with regard to consideration of future global SLR (Stralberg et al. 2011) and future storm events (Mousavi et al 2011). To model marsh accretion, we assumed low sediment concentration and low organic matter accumulation. We feel it is prudent to make such an assumption, especially given current, widespread concern about availability of sediment (Cloern et al. 2011). In addition, we made simple assumptions regarding future tides. Specific information was not available in time for our modeling exercise, however current efforts are now underway, as part of the "Our Coast Our Future" project, with specific application to the San Francisco Estuary (http://data.prbo.org/apps/ocof).
- 5. Neither Model 1 nor Model 2 incorporated net movement of tidal marsh birds. Ignoring dispersal, and thus movement, represents an over-simplification. Under Medium and High Sea-level Rise scenarios, current breeding habitat will be subjected to higher water levels, and we may expect that, if marshes can migrate, birds will move, too. However, it is difficult to project where marshes may move to in the future; it will depend on presence of levees, restoration efforts, suitability of habitat for tidal marsh birds, and other considerations. However, tackling the question of movement of habitat (and with that, movement of tidal marsh bird populations) is a high priority for the authors (see "Next Steps").

Next Steps

Our primary intent in the current study has been to provide information that can assist agencies and organizations in conserving, managing, and restoring the habitats and wildlife of the San Francisco Estuary, in the context of climate change. Next steps will build on this study in several ways. Our "next generation" model will specifically build on the CALCC project *Tidal Marsh Bird Population and Habitat Assessment for San Francisco Bay under Future Climate Change Conditions* developed by PRBO, by adding demographic considerations to the spatially explicit habitat suitability models already developed for tidal marsh bird species (Veloz et al. 2011; see www.prbo.org/sfbayslr).

For example, Figure 22 displays model-predicted probability of occurrence for tidal marsh Song Sparrows in the San Pablo Bay region for the current period (i.e., 2010) and for 2070 under the assumption of high sea-level rise and low sedimentation (corresponding to Scenario S-3 in this study). Heterogeneity of habitat suitability for tidal marsh Song Sparrow is readily apparent; furthermore, the distribution of future suitable habitat will change somewhat between 2010 and 2070.

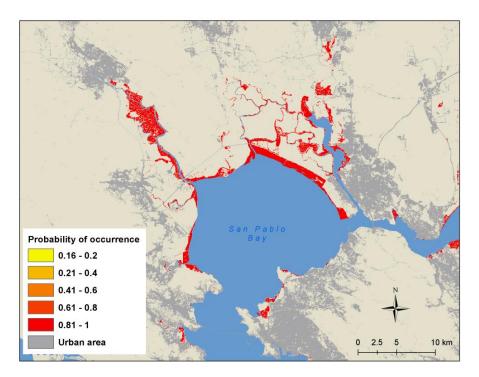


Figure 22a. Model-predicted probability of occurrence of tidal marsh Song Sparrows for San Pablo Bay and vicinity, 2010 (from Veloz et al. 2011).

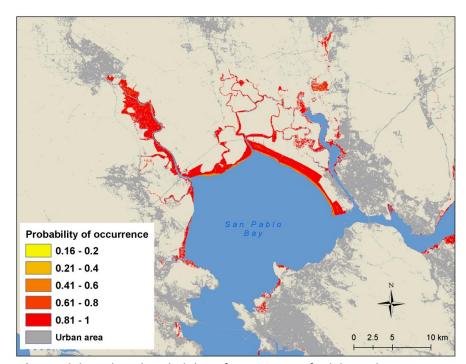


Figure 22b. Model-predicted probability of occurrence of tidal marsh Song Sparrows for San Pablo Bay and vicinity, for 2070, assuming high SLR and low sedimentation (see Veloz et al. 2011). These assumptions correspond to Scenario S-3, applied to the entire San Pablo Bay region.

This study has demonstrated that future population trajectory of tidal marsh Song Sparrows will depend on future environmental conditions, as well as possible management actions. At the same time, the expected spatial distribution of the same species, as modeled by Veloz et al. (2011), will also depend on future environmental conditions (i.e., sea-level rise, sedimentation, organic matter, and salinity). Our primary "next step" is to integrate these two complementary modeling approaches.

More specifically, we will develop a spatially explicit demographic model that adds demographic processes to the spatially explicit habitat suitability models developed by Veloz et al. (2011). Demographic rates, such as reproductive success, reflect habitat heterogeneity, both within a marsh, and in the surrounding landscape and the next generation model will incorporate that influence.

The proposed model will incorporate change in habitat over time, due to physical influences as well as restoration activities. Thus, habitat change within a marsh and adjacent to marshes will be modeled, whether due to changes in geomorphology, vegetation, and/or land-use.

An important feature of the "next-generation" model is that it will focus on individual marshes, or parcels that are connected to each other through dispersal, and are set in a larger landscape context of non-marsh habitat. Thus, the resulting model can be used by a manager for a specific marsh or marsh complex. Our objective will include evaluating the population-level benefits of specific restoration projects. At the same time, we will scale up from the individual marsh to the

entire estuary. Thus, the model to be developed will also be of direct value as a decision support tool for regional resource managers. It will allow users to consider changes in habitat due to climate change as well as land-use changes (i.e., conversion from one habitat type to another). Connectivity of habitat and what that means for the long-term viability of marsh bird populations will be explicitly modeled.

SUMMARY AND CONCLUSIONS

In this study, we have addressed the question of vulnerability of tidal marsh-bird species to consequences of climate change by modeling the long-term viability of populations, in the face of a range of possible climate-change impacts and management actions that may ameliorate those impacts. As part of this work we have developed population dynamic models, both simple and complex, for the four target species, Black Rail, Clapper Rail, Common Yellowthroat, and Song Sparrow.

Development and application of these models has provided important insights into threats that species of conservation concern in the San Francisco Estuary are facing as well as guidance to managers regarding potential, effective responses. The approach we have developed provides the means to evaluate the long-term contribution to population viability with respect to specific demographic processes (including survival and reproductive rates) as well as the environmental influences on those demographic rates. In some cases, the models may be currently missing key information; however, the models can still be effective in identifying which are the key uncertainties and which areas of ignorance are relatively unimportant. Thus, the models can prioritize future research and monitoring efforts.

An important strength of the population-dynamic models is that they are integrative: they provide a means to integrate opposing influences on the same parameter (e.g., nest survival may increase due to reduction of predation while at the same time decrease due to increased flooding of nests) as well as antagonistic or synergistic influences on different demographic processes. Thus, the models can be used to determine the increase in vital rate (e.g., as a result of management action) that is needed to compensate or overcome the deleterious impact of a climate change impact. The models can easily be used to determine target values of a parameter (e.g., nest survival) in order to achieve a desired population growth rate. We demonstrate that small changes in nest survival can turn population decline into population increase and vice versa. Easy-to-use interactive models are available at http://data.prbo.org/apps/sfbslr/demography.

Our work has identified the importance of nest survival and influences on this parameter with regard to long-term viability of marsh bird species. Tidal marsh Song Sparrow populations in the Estuary are vulnerable to climate change because their baseline nest survival rates are low, too low at present to sustain these populations, as a result of high levels of nest-predation, mainly from human-associated predators. For Song Sparrows and Clapper Rails, the climate-change impact of greatest concern is an increase in the severity and frequency of extreme tides experienced by marsh birds resulting from sea-level rise and/or severe storms. For Song Sparrows, such high-water events will reduce nest survival as a result of flooding of nests. However, for this species, an increase in temperature and decrease in precipitation (as predicted by downscaled Global Climate Models) are expected to increase nest survival in the future, as we demonstrate. As a result of these two contrasting climate-change impacts, one increasing nest survival and the other decreasing it, future sea-level rise can be sufficient to change future population growth into population decline.

Specifically, if sea-level rise exceeds c. 1.6 m per 100 years, Song Sparrow populations are expected to show strong declines. An unusually high tide, associated with storm events, even if it occurred only once every 10 years, on average, is sufficient to substantially depress population growth rates, increasing the likelihood of population decline, and thus preventing population recovery and/or increasing the likelihood of local extinction. However, relatively short-term management actions (e.g., of a 20 year duration) can be effective in arresting and even reversing these anticipated declines. For example, a relatively small reduction in predation on nests (by reducing predator populations or access to tidal marsh nesting habitat) can be sufficient to counteract expected population declines due to climate change.

An important conclusion, demonstrated by our modeling of all four tidal marsh species is that improvement in nest survival represents a realistic management action that can modify current population trends, leading to, or enhancing population recovery. Overwinter survival is still an important bottleneck and management actions may be able to improve this parameter; more study is needed in this regard. The population modeling tools we have developed can effectively address the efficacy of proposed management actions as well as allow quantitative evaluation of multiple influences on population viability. We conclude that our study demonstrates the feasibility of evaluating potential management actions that can effectively counteract threats posed by climate change.

We believe that our results are applicable to marsh bird species more generally in the San Francisco Estuary and elsewhere. The models developed here can be tailored to other species and other habitats, including estuarine and riparian. As part of this project, we will make our code freely available to others who wish to adapt our analytic and modeling approach (see http://data.prbo.org/apps/sfbslr/demography for code, tools, and this report).

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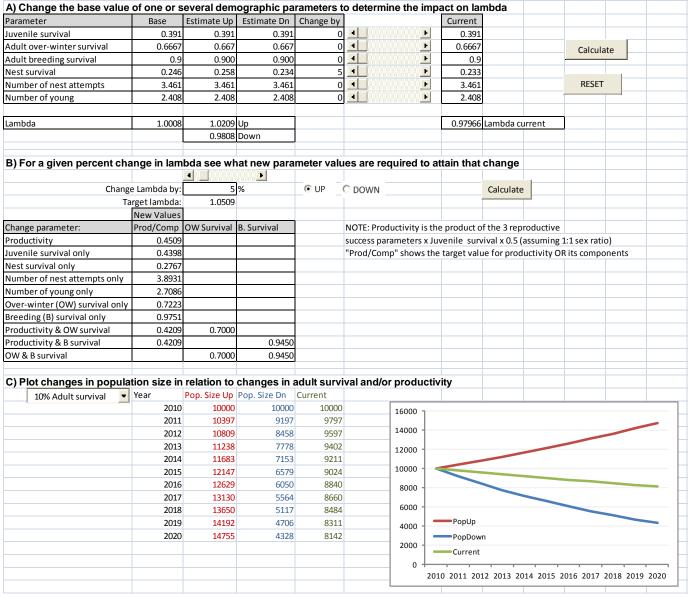
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TABLES

Table 1. Demographic Parameter Values for "Current Model." Observed lambda also shown. For explanation and justification see text.

Species	Parameter	Value
Song Sparrow	Adult breeding survival	0.9
Song Sparrow	Adult over-winter survival	0.6667
Song Sparrow	Juvenile survival	0.391
Song Sparrow	Nest survival	0.233
Song Sparrow	Number of nest attempts	3.461
Song Sparrow	Number of young per successful nest	2.408
Song Sparrow	Observed population growth rate (lambda)	0.9797
Clapper Rail - North Bay	Adult breeding survival	0.78
Clapper Rail - North Bay	Adult over-winter survival	0.483
Clapper Rail - North Bay	Juvenile survival	0.3
Clapper Rail - North Bay	Nest survival	0.39
Clapper Rail - North Bay	Number of nest attempts	2
Clapper Rail - North Bay	Number of young per successful nest	5
Clapper Rail - North Bay	Observed population growth rate (lambda)	0.9617
Clapper Rail - South Bay	Adult breeding survival	0.72
Clapper Rail - South Bay	Adult over-winter survival	0.389
Clapper Rail - South Bay	Juvenile survival	0.3
Clapper Rail - South Bay	Nest survival	0.371
Clapper Rail - South Bay	Number of nest attempts	2
Clapper Rail - South Bay	Number of young per successful nest	5
Clapper Rail - South Bay	Observed population growth rate (lambda)	0.8366
Black Rail	Adult breeding survival	0.9
Black Rail	Adult over-winter survival	0.556
Black Rail	Juvenile survival	0.3
Black Rail	Nest survival	0.42
Black Rail	Number of nest attempts	1.81
Black Rail	Number of young per successful nest	5
Black Rail	Observed population growth rate (lambda)	1.0701
Common Yellowthroat	Adult breeding survival	0.9
Common Yellowthroat	Adult over-winter survival	0.552
Common Yellowthroat	Juvenile survival	0.297
Common Yellowthroat	Nest survival	0.54
Common Yellowthroat	Number of nest attempts	2.45
Common Yellowthroat	Number of young per successful nest	2.73
Common Yellowthroat	Observed population growth rate (lambda)	1.0332

Table 2. Interactive Population Dynamic Models for Song Sparrow. See text for explanation. Example only; see http://data.prbo.org/apps/sfbslr/demography to manipulate the models.



PRBO Climate Change and Tidal Marsh Bird Demography

Table 3. Illustration of Interactive Population Dynamic Models for Clapper Rail. In Parts A and C, "Current" differs for North Bay and South Bay, but "Base" is the same. See text for explanation. Example only; see http://data.prbo.org/apps/sfbslr/demography to manipulate the models.

Parameter	Base	Estimate Up	Estimate Dn	Change by		Current		NORTH BAY
Juvenile survival	0.308	0.308	0.308	0	<u> </u>	0.3		
Adult over-winter survival	0.5	0.500	0.500	0	<u>+</u>	0.483		Calculate
Adult breeding survival	0.8	0.800	0.800	0	<u> </u>	0.78		
Nest survival	0.39	0.417	0.363	7	A D	0.39		
Number of nest attempts	2	2.000	2.000	0	T P	2		RESET ALL
Number of young	5	5.000	5.000	0	T	5		
Lambda	1.0006	1.0426	Up			0.96174	Lambda current	
		0.9586	Down					
Parameter	Base	Estimate Up	Estimate Dn	Change by		Current		SOUTH BAY
Juvenile survival	0.308	0.308	0.308	0	T D	0.3		
Adult over-winter survival	0.5	0.550	0.450	10	T D	0.389		Calculat
Adult breeding survival	0.8	0.800	0.800	0	<u> </u>	0.72		Carcarate
Nest survival	0.39	0.390	0.390	0	<u> </u>	0.371		
Number of nest attempts	2	2.000	2.000	0	<u> </u>	2		
Number of young	5	5.000	5.000	0	<u> </u>	5		
Lambda	1.0006	1.0406	Up			0.83658	Lambda current	
		0.9606						

Table 3, cont.

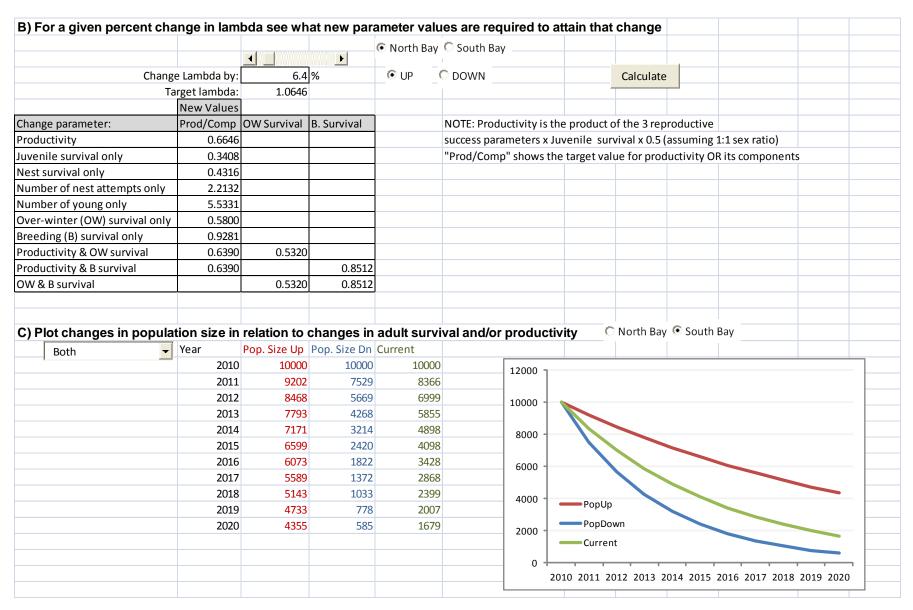


Table 4. Interactive Population Dynamic Models for Black Rail. See text for explanation. Example only; see http://data.prbo.org/apps/sfbslr/demography to manipulate the models.

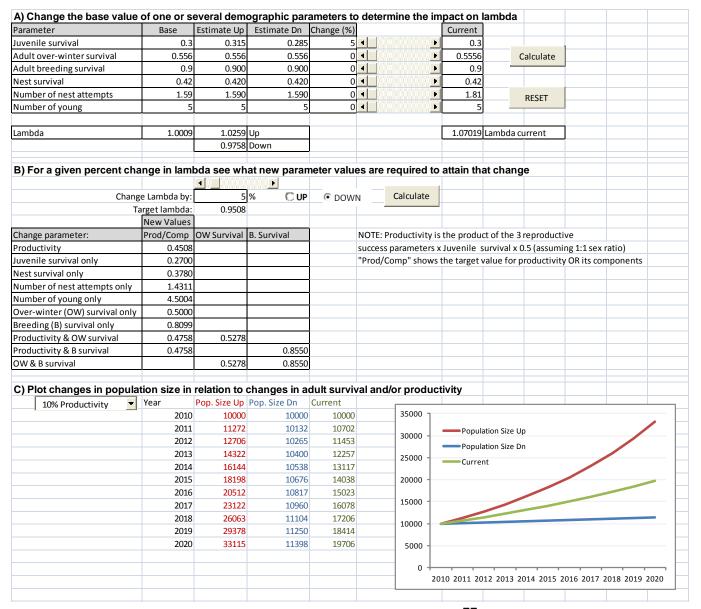
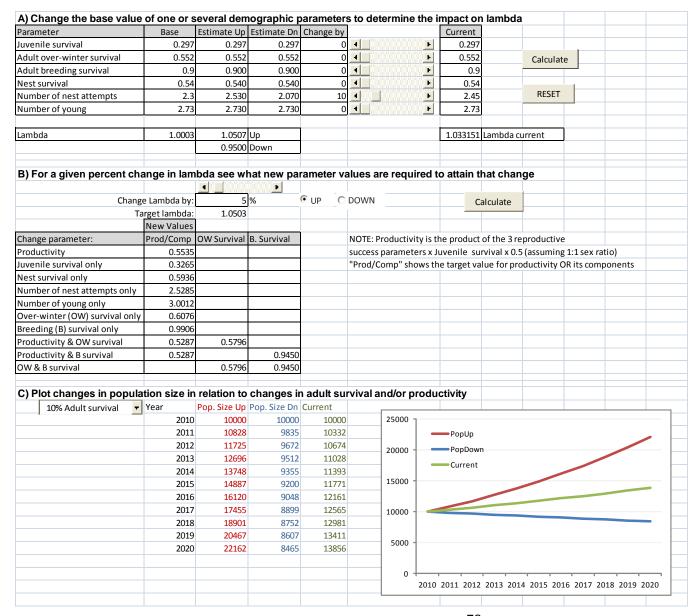


Table 5. Interactive Population Dynamic Models for Common Yellowthroat. See text for explanation. Example only; see http://data.prbo.org/apps/sfbslr/demography to manipulate the models.



PRBO Climate Change and Tidal Marsh Bird Demography

Table 6. Summary of Scenarios Evaluated.

Scenario Number	Description	Temperature- Precipitation	Tides Affected By	Management
С	Current Conditions Continue	Current	Current	None
S-1	Low Sea-Level Rise	Future, Low SLR Downscaled GCM		None
S-2	Medium Sea-Level Rise	Future, Medium SLR Downscaled GCM		None
S-3	High Sea-Level Rise	Future, High SLR None Downscaled GCM		None
SX-1	Low Sea-Level Rise, Extreme Tides	Future, Downscaled GCM	Low SLR, Extreme tides	None
SX-2	Medium Sea-Level Rise, Extreme Tides	Future, Downscaled GCM	Medium SLR, Extreme tides	None
SX-3	High Sea-Level Rise, Extreme Tides	Future, Downscaled GCM	High SLR, Extreme tides	None
M-1	Management, Current + Nest Survival, 5.5%	Current	Current	Nest survival increased 5.5% from 2015 to 2060
M-2	Management, Current + Nest Survival, 10%	Current	Current	Nest survival increased 10% from 2015 to 2035
M-3	Management, High SLR + Nest Survival	Future, Downscaled GCM	High SLR	Nest survival increased 10% from 2015 to 2035
M-4	Management, High SLR + Reduced Tides	Future, Downscaled GCM	High SLR	Highest tides capped at 2.3 m

PRBO Climate Change and Tidal Marsh Bird Demography

Table 7. Values used in stochastic simulations of Tidal Marsh Song Sparrows. See text.

Parameter	Mean	SD	Source of Standard Deviation
Adult breeding survival	0.9	0	N/A (treated as constant)
Adult over-winter survival	0.6667	0.0667	10% of mean
Juvenile survival	0.391	0.0391	10% of mean
Nest survival	0.233	0.0245	Annual Variation among means, observed.
Number of nest attempts	3.461	0.2966	10% of field-observed mean (see text).
Number fledged	2.408	0.2037	Annual Variation among means, observed.