THE INFLUENCE OF DISEASE AND CLIMATE ON PINNIPED SPECIES AT LOCAL AND REGIONAL SPATIAL SCALES

by

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Birthweight and length distributed asymmetrically between the two sexes, with males having increased length and weight compared to females.

Correlation of weight and length for all individual sea lions marked in this study. The estimated Pearson’s coefficient of correlation is 0.86 (P-val = 2.2e-16), which suggests a strong positive correlation.

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Generalized linear models fit to first year survival data for pups born from 1990-2006.

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The Influence of Disease and Climate on Pinniped Species at Local and Regional Spatial Scales

Abstract

by

KATHERINE DIXON

This thesis addresses the threats to two closely related species of sea lion, the Galápagos sea lion (*Zalophus wollebaeki*) and the California sea lion (*Zalophus californianus*) using mathematical modeling and statistical methods. We address the potential for a novel disease outbreak in the endangered Galápagos sea lion using a simulation model, which predicts the combined effect of El Niño and disease and how this influences the efficacy of options for management practices. We then characterize how El Niño influences life history traits, including birthweight and survival, in the California sea lion, and examine the characteristics that shape dispersal. We test these effects using statistical methods and identify how and at which life stages sea lions are susceptible to stressors. The broader implications for this work are to make recommendations for management and highlight the importance of understanding the threats facing these species.
Thesis Introduction

How can the effects of a climate event and an introduced disease interact in a susceptible population, and how does a climate event influence condition and survival? This thesis aims to address these questions using two closely related species of sea lion, the Galápagos sea lion, *Zalophus wollebaeki*, and the California sea lion, *Zalophus californianus*. The Galápagos sea lion is an endangered, endemic species in the Galápagos Islands and is the focal species of this work. The California sea lion is a closely related species inhabiting the Pacific Ocean along the coasts of Canada, the USA, and Mexico, with an consistently expanding population. We include the California sea lion in this thesis because there is an abundance of data available and it is closely related to the Galápagos sea lion, which has less data currently available and a pressing need for conservation. Experimental manipulations and invasive tracking is hard to justify for such fragile species like the Galápagos sea lion so the tools used in this study to circumvent that barrier include simulations using a mathematical disease model and statistical modeling on a long term dataset. Mathematical modeling using estimated parameters is an extremely useful predictive tool when experiments are impossible or data is limited and studying an ecologically similar species is useful for comparative analysis and to infer parameter values when information is missing on the less-studied focal species.

This thesis focuses on two major stresses threatening Galápagos sea lions: disease and El Niño events. Disease can dramatically impact a population’s growth abilities.
When a disease is introduced in a naïve population, the magnitude of the impact can be large because the population likely won’t have strong defenses against it. In this case the disease may a have long-lasting influence on the population structure as some of the population is lost due to disease mortality and future generations are lessened due to reduced fecundity. The spread of disease can be difficult to predict given multi-host dynamics (Dobson, 2004), external processes (Altizer et al., 2006), and spatial structure (Keeling et al., 2001). The Galápagos sea lion has a great potential to be exposed to novel diseases due to close encounters with introduced species and human activity. An increase in human activity and tourism in the Galápagos Islands brings a multitude of stressors into this unique environment. Humans bring with them their waste, pollution, food (including farm animals), and pets. Each of these factors has the possibility of spreading infectious and non-infectious diseases to the endemic species in the Galápagos Islands. To address the potential for a novel, infectious disease outbreak in the Galápagos sea lions, the first chapter of this thesis includes a second host, introduced dogs, and spatial heterogeneity in pack location, with sea lions occurring on the rim of the island and dogs inhabiting the interior. The study also examines the how presence of an external climate event, El Niño, influences the magnitude and dynamics of a disease outbreak. We selected the Galápagos sea lion for the focal species of this study because of conservation implications and to better our understanding of how a virulent disease operates in a naïve, two-host system.

El Niño is a very important event in both sea lion systems included in this study. It has been well recorded that there is increased mortality, increased number of stranding events, and reduced recruitment during El Niño events, but it has not previously been quantified in the same manner as this study. Reduced fecundity and high pup mortality rates in the sea lion populations are likely to have persistent impacts on the system as that cohort would have aged and reached sexual maturity. This issue is pervasive across trophic levels in systems like the Galápagos Islands, where many
populations have still not recovered from a massive El Niño event that occurred in 1997-98. There are also indications of changes in behavior during El Niño events, which in sea lions may include increased foraging rates, increased time spent in the tidal area in relation to time spent on the beach, and changes in local population densities (Ono et al., 1987). Recent research suggests that El Niño severity and frequency are likely to increase as climate change becomes more prominent, and that pattern has already presented itself over the past century (Cai et al., 2014). This could make El Niño an even more extreme event in the Pacific, so it is valuable to address questions like those included in this study.

Life history traits, like size at birth and survivorship, can be influenced by the life stage at which an individual encounters stressors, including the gestational, juvenile, and adult periods. These changes in life history traits can also have a ripple effect that will affect other life history traits, like dispersal and fecundity. The temporal and spatial scale at which an individual experiences these stressors in its local and regional environment may have different effects on the individual animal or population level response to the stressor. It is possible for an individual to have both positive and negative impacts by dispersing, through gene flow and disease dispersal respectively (Hess, 1996). How the spatial structure and connectivity of a population affects disease spread is important to understanding small scale disease transmission in a local population and large scale disease dispersal events. The likelihood of a dispersal or movement event is a stochastic process shaped by inherent and extrinsic traits of an individual, the population, and the environment. Here, we aim to understand how a stressor shapes life history traits and how that in turn affects dispersal and connectivity.
Thesis aims

This thesis addresses the threats to sea lions in two closely related species and similar context using mathematical modeling and statistical methods. Chapter One aims to address the potential for a novel disease outbreak in the endemic, endangered Galápagos sea lion using a mathematical simulation model. This chapter predicts the combined effect of El Niño and disease in the sea lion population and how this influences the efficacy of common options for management practices. The broader implications for this work are to make recommendations for management and highlight the importance in understanding the interaction of threats on an endangered species.

Chapter Two aims to address how El Niño influences life history traits, including birthweight and survival, in the California sea lion, and examines the characteristics that shape dispersal probabilities. Chapter Two tests these effects using statistical methods and identifies how and at which life stages sea lions are susceptible to stressors. Information on how the Galápagos sea lion reacts to El Niño is lacking, so information from the California sea lions is used to infer what may happen in the Galápagos sea lions.
Chapter 1

Interactive effects of a climate event and introduced disease on a threatened endemic

1.1 Abstract

Prior research shows that climatic factors and infectious disease can interact to have profound effects on host populations. The Galápagos sea lion, *Zalophus wollebaeki*, is vulnerable to disease and climate perturbations. Using a spatially explicit, two-host SEIR model, we predict the interactive effects of a climate event, El Niño (EN), and a novel disease, Canine distemper virus (CDV), on Galápagos sea lion populations. We found there were interactions between the two extrinsic sources of mortality, disease and climate. EN shortened the CDV epidemic and decreased the number of individuals that became infected, but also increased total population disease mortality. We found that location of disease introduction in the dog population and timing of implementation were important for management efficacy in sea lions. Predictions on how stressors interact is key to understanding the vulnerability of this endangered
CHAPTER 1. INTERACTIVE EFFECTS OF A CLIMATE EVENT AND INTRODUCED DISEASE ON A THREATENED ENDEMIC SPECIES AND MAKING MANAGEMENT PLANS.

1.2 Introduction

Endemic species are widely threatened by the spread of non-native disease from anthropogenically-introduced species (Daszak et al., 2000). When trying to understand and manage the spread of a disease to a naïve endemic population, the effects of climate and other external factors on the survival and reproduction of vector, host, and reservoir species must be considered (Stapp et al., 2004). Here, we present a mathematical disease model to improve our understanding of imminent threats and their persistent impact on the dynamics of an endangered species. The Galápagos sea lion, *Zalophus wollebaeki*, is endemic to the Galápagos Archipelago and faces numerous threats, including non-native disease, anthropogenic disturbances and climate perturbations. The threats that we address specifically in this paper are climatic El Niño events (EN) and canine distemper virus (CDV).

While empirical and theoretical research have come far in understanding how climate and seasonality are involved in vectored diseases, including malaria (Paaijmans et al., 2010) and lyme disease (Ogden et al., 2014), the effects of temperature on directly transmitted diseases are not as well understood. There is still uncertainty and controversy surrounding how global climate change will impact pathogen abundance and range (Lafferty, 2009; Rohr et al., 2011), but the impact of climate variability experienced during EN events on disease dynamics has been more clearly established (Weinberger et al., 2014; Stapp et al., 2004; Rohr and Raffel, 2010). The human disease cholera is a well-documented example of how an increase in ambient and water temperature due to EN promotes the growth and reproduction of the bacteria that causes cholera, *Vibrio cholerae* (Pascual et al., 2000; Speelmon et al., 2000). The human and rodent disease, plague, has also been shown to cycle with the EN oscillation...
CHAPTER 1. INTERACTIVE EFFECTS OF A CLIMATE EVENT AND INTRODUCED DISEASE ON A THREATENED ENDEMIC

tion (Stapp et al., 2004). Such patterns have been established empirically, but little modeling work has been done to understand the mechanisms underlying the changes in disease dynamics due to EN.

Climate and seasonality can shape host-pathogen interactions by directly impacting the host or by influencing pathogen life history. Examples of how the pathogen itself can be affected include changes in reproduction rates, survival in the environment, and relaxed overwintering restrictions (Harvell et al., 2002). Temperature can directly impact the host by affecting survival and fecundity, and by changing behaviors related to transmission probability, modifying host susceptibility, and influencing the immune response to the disease (Harvell et al., 2002). For this study, we will be focusing on the influence on the host, since we know of no evidence that the CDV virus itself is impacted by temperature or seasonality in any of its hosts. On the other hand, it is well documented that the Galápagos sea lion population is greatly reduced and individuals are weakened by EN (Trillmich and Limberger, 1985; Salazar and Bustamante, 2003a). We model the effects of EN-induced temperature changes on Galápagos sea lions through increased background mortality and reduced birth rates, in addition to changes in the parameters dictating transmission and immune response.

The goals of this study are to understand how EN and CDV might interact to affect Galápagos sea lion dynamics, propose management strategies, and identify important parameters that we need more information on. We use a two-host, deterministic model of CDV in Galápagos sea lions and domestic dogs to investigate a potential outbreak. We tested the sensitivity of model outcomes to temperature dependent parameters, characterized CDV outbreaks during EN and non-EN years, and tested the viability of three management strategies. While we begin by considering naïve populations, we also considered a partially recovered population, representing the situation if there had been an undocumented epidemic in the Galápagos sea lion population in the past.
or if there are repeated outbreaks in the future.

The simulation results show EN has a smaller epidemic, both in total proportion infected and outbreak duration, but much higher mortality than during a non-EN year. This is important when considering management response time, since there are no prophylactic measures in place, and highlights the potential interaction of EN and disease to have a large impact on the sea lion population. The model results are very sensitive to changes in many of the parameter values selected to be temperature dependent. The mortality rate and total dead from disease were strongly influenced by parameter manipulations, while the duration of infection was slightly impacted, and the proportion infected was hardly sensitive. We also found that vaccination and reduction in dog population management strategies are sensitive to both the location of the introduction of infection as well as timing of the implementation.

1.3 Methods

Study system

Galápagos sea lions are endemic to the Galápagos and cosmopolitan throughout the islands, located about 1,000 km from the coast of Ecuador. Despite intense regulations to protect the archipelago, a growing human population and lack of compliance has led to several non-native species introductions in recent years (Usseglio et al., 2014; González et al., 2008). For example, domesticated dogs, Canis lupis familiaris, are regularly imported to the islands and while they technically have owners, they are free to roam the town and beaches and are a risk to public health and wildlife populations (Gingrich et al., 2010). There is urgent concern over the possibility that with these dogs, novel generalist diseases are also being introduced to the Galápagos islands (Gingrich et al., 2010; Levy et al., 2008).

One disease of concern that has been documented in Galápagos’ dog populations
is canine distemper virus (CDV) (Alava and Salazar, 2006). CDV is a highly virulent single-stranded negative RNA morbillivirus has caused epidemics in many other carnivores, such as Serengeti lions (Guiserix et al., 2007), Catalina foxes (Timm et al., 2009), Yellowstone carnivores (Almberg et al., 2010), and polar bears (Fagre et al., 2015), as well as primates, such as the Japanese monkey (Yoshikawa et al., 1989) and Chinese rhesus monkeys (Yoshikawa et al., 1989), and ungulates, such as the collared peccary (Appel et al., 1991). CDV has been documented as having particularly negative effects on Pinnipedia where, for instance, it caused mass die-offs in Caspian Seals (Phoca caspica) in the early 2000s (Kuiken et al., 2006) and Baikal seals (P. siberica) in 1987-1988 (Butina et al., 2010). A closely related morbillivirus, Phocine Distemper Virus (PDV), has had multiple well studied epidemics in European harbour seals, (P. vitulina) (Swinton et al., 1998; Härkönen et al., 2006), and a large mortality event in North American harbor seals (P. vitulina), grey seals (Halichoerus grypus), and hooded seals (Cystophora cristata) in the Northeastern United States has been attributed to PDV (Earle et al., 2011). In many of these systems, the reservoir species or amplifier of the disease is known or suspected to be the domesticated dog (Guiserix et al., 2007; Timm et al., 2009). In 2001, there were outbreaks of CDV in introduced dogs on two inhabited islands in the Galápagos which killed approximately 600 dogs (Levy et al., 2008). A comprehensive study on the island of Santa Cruz in 2014 revealed a 36% prevalence of dogs with positive antibody titers to CDV in both urban and rural dogs (Diaz et al., 2016). Here, we assume that a high population turnover rate in dogs will remove those individuals with antibodies from the population, so our initial conditions include a completely susceptible dog population with no recovered dogs. The sea lions were tested for exposure to CDV after the outbreak in dogs in 2001 and after a high pup mortality event in 2011 and there was no evidence that it transmitted from dogs to any sea lions (Diaz et al., 2016). However, the potential for the zoonotic to spread to the sea lions is alarmingly high considering CDV is a
CHAPTER 1. INTERACTIVE EFFECTS OF A CLIMATE EVENT AND INTRODUCED DISEASE ON A THREATENED ENDEMIC

generalist pathogen capable of infecting other pinnipeds.

Another important threat to Galápagos is climatic stress associated with El Niño, which appear to be happening with increased frequency and severity (Vargas et al., 2006). The effect of EN on Galápagos sea lions stems from the loss in marine productivity in and around the Galápagos ecosystem. This reduction in food drastically reduces the production of new pups, increases pup abandonment by mothers, as increases pup mortality (Trillmich and Limberger, 1985). There is also increased mortality in juveniles (Trillmich and Limberger, 1985) and adult male sea lions (Salazar and Bustamante, 2003b) during EN. These impacts have the potential to influence disease dynamics by reducing population density from low birth rates and high population mortality. We propose that starvation stress will also reduce immune function, increasing the likelihood of transmission, shortening of the latent period, lengthening of the infectious period, and increasing the likelihood of an individual succumbing to the infection.

Since introduced dogs on the island subsist on food from humans, their trash, and rodents, rather than on oceanic resources, we do not predict that EN will impact their disease susceptibility or population density. In fact, rodent populations are shown to increase during an EN event in the pacific because of the increase in rain (Jaksic, 2001; Campos et al., 2007). We therefore model EN effects in sea lions only, and not in dogs. We keep the dog population constant in these models to be conservative with respect to the sea lion risk for CDV. If we were to increase the dog population, it might increase the likelihood of transmission. However, we uncertain of what happens to the Galápagos dog population during EN, so we keep the initial dog population constant in this study.
1.3.1 Spatial structure

We used a hexagonal lattice (Figure 1) to model an island with discrete habitat patches. We implement our models on a hexagonal lattice to reduce the effect of abnormal dynamics in the corners, which can be exaggerated for square lattices. Each hexagon on the grid is occupied by either one pack of feral dogs or one sea lion colony (hereafter also called a “pack,” for simplicity). Sea lions occupy the outer ring of hexagons, and dogs inhabit the island interior due to differences in habitat usage. The entire island has radius \( r \), which counts the number of rings around a central hexagonal point. A hexagonal lattice with radius \( r \) has \( 3(r + 1)^2 - 3(r + 1) + 1 \) total patches, of which \( 3(r)^2 - 3(r) + 1 \) are occupied by dogs and \( 6r \) are occupied by sea lions. Cross-pack (including cross-species) transmission can occur when individuals from different packs come into contact. We assume that this occurs when individuals make brief forays away from their home pack; given the territorial nature of dogs (Gingrich et al., 2010) and high site fidelity in sea lions (Meise et al., 2013), we do not model permanent movements of individuals among packs.

1.3.2 Two-species model structure

We model transmission of CDV within a pack with parameter values appropriate for either dogs or sea lions depending on the type of pack present. Using the subscript \( k_i \) to denote species \( k \) (\( k = s \) [sea lion] or \( d \) [dog]) in pack \( i \),

\[
\begin{align*}
S_{k_i,t+1} &= S_{k_i,t} + b_k - \lambda_{k_i,t}S_{k_i,t} - \mu_kS_{k_i,t} \\
E_{k_i,t+1} &= E_{k_i,t} + \lambda_{k_i,t}S_{k_i,t} - \sigma_kE_{k_i,t} - \mu_kE_{k_i,t} \\
I_{k_i,t+1} &= I_{k_i,t} + \sigma_kE_{k_i,t} - \gamma_kI_{k_i,t} - \delta_kI_{k_i,t} - \mu_kI_{k_i,t} \\
R_{k_i,t+1} &= \gamma_kI_{k_i,t} - \mu_kR_{k_i,t},
\end{align*}
\tag{1.1}
\]

where \( \lambda_{k_i,t} \) is a function of \( I_{\bullet,t} \) describing the total transmission of CDV to species \( k \) in
CHAPTER 1. INTERACTIVE EFFECTS OF A CLIMATE EVENT AND INTRODUCED DISEASE ON A THREATENED ENDEMIC

pack $i$, from both con- and heterospecifics, during $t$ (see Equation (1.4) below). $S_{ki,t}$, $E_{ki,t}$, $I_{ki,t}$, and $R_{ki,t}$ are, respectively, the number of individuals of species $k$ in pack $i$ that are susceptible to CDV, exposed to CDV but not yet infectious, infectious, and recovered (and therefore immune) on day $t$. $b_k$ is the number of births on day $t$, as described below. A fraction $\mu_k$ of the population dies of non-disease-related causes each day, and a fraction $\delta_k$ of infectious individuals die from disease. The parameter $\sigma_k$ is the rate at which individuals move from the exposed to infectious class (i.e. $1/\sigma_k$ is the latency period) and $\gamma_k$ is the recovery rate ($1/\gamma_k$ is the infectious period). Within a daily time step, we assumed the ordering of events to be mortality, birth, and then transmission.

In this model, we assume that dogs breed year-round and have relatively stable population sizes in the Galápagos so for dog packs, we model daily births as,

$$
b_d(N_{di,t}) = \mu_d N_{di,t}. \quad (1.2)
$$

where $N_{di,t}$ is shorthand for the total population size of dogs in pack $i$ ($N_{di,t} = S_{di,t} + E_{di,t} + I_{di,t} + R_{di,t}$). Sea lions, in contrast, have seasonal births that depend on carrying capacity, number of reproductive females in the population, and pup survival. We therefore model sea lion births as,

$$
b_s(N_{si,t}) = \begin{cases} 
p_r \frac{N_{si,t-T}}{122} \left(1 - \frac{N_{si,t-T}}{K}\right) \left(1 - \mu_{\text{pup}}\right) & 0 \leq T < 122 \\
0 & 122 \leq T < 365
\end{cases} \quad (1.3)
$$

where $T = t \mod (365)$ and $N_{si,t-T}$ is the total number of individuals alive at the end of the previous year (i.e. $t - t \mod (365) = \text{day 365 of the preceding year}$), $p_r$ is the proportion of individuals that are reproductive and female, $K$ is the carrying capacity, and $1 - \mu_{\text{pup}}$ is the proportion of pups that survive. $\mod ()$ is the modulo operator, which gives the remainder of a number after division by its argument. Therefore, $t$
mod (365) is the day of the year, with day 0 corresponding to the first day of the pupping season. Pups are born at a constant daily rate for 4 months (i.e. until day 122), when births cease until the following year.

We used the two-host, spatial transmission model from Almberg et al. (2010) to calculate $\lambda_{k,t}$, the force of infection on day $t$, as a function of the number of infectious individuals at each location and the spatial range of contact for both species. Accounting for both within and between pack transmission,

$$\lambda_{k,t} = 1 - \exp \left( - \left[ \beta_k \sum_{j=1}^{n_k} I_{k,j,t} \exp(-\varepsilon d_{ij}) \right] - \left[ \beta'_k \sum_{j=1}^{n_l} I_{l,j,t} \exp(-\varepsilon d_{ij}) \right] \right). \quad (1.4)$$

The first term in square brackets represents intraspecific transmission among individuals of species $k$, of which there are $n_k$ packs. $d_{ij}$ is the distance between pack $i$ and pack $j$. Transmission among individuals within the same pack ($i = j$ so $d_{ij} = 0$) occurs at per-capita rate $1 - \exp(-\beta_k I_{k,t})$, where $\beta_k$ is the intraspecific transmission rate of CDV and describes the contract rate and the probability of transmission during a given contact between an infected individual of species $k$ and a susceptible individual of species $k$. When $i \neq j$, transmission decreases exponentially with increasing distance. The parameter $\varepsilon$ governs the steepness of this decline, with larger values corresponding to a sharper drop in transmission with distance. We therefore refer to packs as “more isolated” when $\varepsilon$ is higher. The second term in square brackets is analogous to the first and models transmission to species $k$ from species $l$. We assume the same drop in transmission with distance, $\varepsilon$, within and among species, but we allow for a different overall level of transmission by using a different coefficient, $\beta'_k$, for the maximum among-species transmission. Accounting for both within- and between-species transmission, we assume that the number of successful transmission events during day $t$ to each susceptible individual of species $k$ in pack $i$ is Poisson distributed with mean $\left[ \beta_k \sum_{j=1}^{n_k} I_{k,j,t} \exp(-\varepsilon d_{ij}) \right] + \left[ \beta'_k \sum_{j=1}^{n_l} I_{l,j,t} \exp(-\varepsilon d_{ij}) \right]$. The right-hand
size of equation (1.4) is 1 minus the zero term (probability of no successful transmis-
sions) of this Poisson distribution, and therefore gives the expected proportion of the
population to become infected on day $t$.

1.3.3 Simulations

We used our model to compare baseline CDV dynamics in non-El Niño years with dy-
namics during El Niño. Baseline dynamics were simulated using parameter estimates
reported in the literature for these and closely related species (see below and Table 1). We then adjusted the parameters one at a time and in combination to evaluate
their effect on model outcomes. We used these results to make predictions about
the effect of EN on CDV dynamics, given knowledge of which sea lion parameters
are likely to be sensitive to EN-induced temperature changes and in which direction
we expect each to change. We assumed the Galápagos sea lions would be impacted
by the reduction in their food resources during EN events, which would reduce their
immune function and background mortality rate. The sea lion parameters we chose
to manipulate were within-species transmission rate ($\beta_s$), latent period ($1/\sigma_s$), infec-
tious period ($1/\gamma_s$), disease mortality rate ($\delta_s$), background mortality rate ($\mu_s$), and
the pup mortality rate ($\mu_{pup}$). The values can be found in Table 3.

Parameter values

The Galápagos sea lion parameters used in our baseline (non-EN) simulations are
based on the life history traits of European harbor seals, *Phoca vitulina*, and outbreaks
of a closely related disease, phocine distemper virus (PDV) in the harbor seals. The
parameter values for the dogs are based on other urban dogs (Fielding and Plumridge,
2005) and Yellowstone coyotes (Almberg et al., 2010) due to similar physiology and
behavior. Both birth and death rates are very high due to high juvenile mortalities
and turnover rate in both species (Aurioles and Trillmich, 2008; Daniels and Bekoff,
We included a sea lion carrying capacity, $K$, in the model to simulate realistic dynamics for the births of new susceptible individuals. The sea lions are seasonal breeders so their birthing period lasts four months, which begins on the first day of our simulations.

For the parameters that we expect to change during El Niño, we chose a separate set of values for EN and non-EN years. Values for all temperature-insensitive parameters can be found in Table 1, and both EN and non-EN values for temperature-sensitive parameters are shown in Table 2.

**Sensitivity analysis**

Because we lack temperature-specific parameter estimates, there is a fair amount of uncertainty around the values we selected as reasonable for EN and non-EN years (Table 2). We therefore manipulated each of the parameters one at a time and in pairs to assess the sensitivity of our model predictions to changes in parameter values. One dog pack was randomly selected to be the first case of CDV (hexagon with the bolded outline in Figure 1). All simulations were run for seven years after the introduction of a single infected dog into this same pack. We recorded the values for $S_{k_i,t}$, $E_{k_i,t}$, $I_{k_i,t}$, and $R_{k_i,t}$ at each time step, the mortality from disease, the cumulative number of infected individuals, and the number of sea lion pups introduced into the population.

**Infection History**

To estimate the effect of EN in conjunction with disease in the Galápagos sea lion population, we first ran simulations with a completely naïve population of both dogs and sea lions. One new infected dog (e.g. a new arrival from mainland Ecuador) was placed in the randomly selected pack of dogs on the first day of the first year of the simulation (hexagon with the bolded outline in Figure 1). All other individuals of both species were susceptible at the initiation of the simulation. We ran each simulation
for seven years and recorded the values for $S_{ki,t}$, $E_{ki,t}$, $I_{ki,t}$, and $R_{ki,t}$ at each time step, the mortality from disease, the cumulative number of infected individuals, and the number of sea lion pups introduced into the population.

Next, we estimated the effects of EN and disease in a sea lion population that had already experienced the disease. To model disease in a partially recovered sea lion population, 30% of the population was recovered at the beginning of the simulation; all other individuals were initially susceptible. We do not include a partially recovered dog population in the second type of simulation, because we assume a high population turnover rate in dogs. We introduced an infected dog in the same dog pack as in the sensitivity analysis and the naïve population model and recorded the same information.

**Management**

We investigated three potential management options for the sea lions, vaccination, fencing, and reducing the dog population. To look at vaccination, we moved a proportion of the susceptible sea lions at the beginning of the simulation to the recovered class and then introduced the disease to the dogs. To look at a reduction in contact between dogs and sea lions (accomplished, for example, by fencing the beach) we reduced the maximum interspecific transmission rate, $\beta'$. To look at controlling the dog population, we reduced the initial number of dogs in each pack. The values considered in each of these management strategies can be found in Table 4. To test for an effect of where the disease was introduced on the island on the efficacy of management for these three strategies, the initial infected dog was introduced into each ring on the island for each set of management parameters (Figure 1), where five is the dog pack furthest from the sea lions and one is the dog pack closest to the sea lions. The introduction of the disease to further dog packs (pack 3, 4 and 5 on Figure 1) were grouped, and the nearer dog packs (pack 1 and 2 on Figure 1) were grouped,
to simplify visualization because they were qualitatively similar. For the vaccination management strategy, we also tested the impact of the day that vaccination was implemented. The days tested were 1, 92, 183, and 274 which correspond to the first day, three months, six months, and nine months after the disease was introduced into the dog population.

### 1.3.4 Analysis of simulation results

To characterize the size, shape and outcome of the epidemic in the sea lions, we looked at the proportion of sea lions to become infected, the total number that died from disease, the mortality rate (proportion of infected individuals to die from disease), and the duration of the epidemic. The proportion infected was calculated as the total number of individuals to become infectious, divided by the number of susceptible individuals present initially or born during the simulation. To measured the duration of island-wide the epidemic, we first defined the $P_i$ as the day of peak infection within pack $i$:

$$P_i \text{ such that } \max_{t=[0,7\times365]} \{I_{s_i,t}\} = I_{s_i,P_i}.$$  \hspace{1cm} (1.5)

We then defined the duration of the epidemic as the amount of time between the peak in the earliest-infected pack to the peak in the latest-infected pack of the $n_s$ total packs,

$$\text{Duration} = \max_{i=[1,n_s]} \{P_i\} - \min_{i=[1,n_s]} \{P_i\}. \hspace{1cm} (1.6)$$

All simulations and analyses were conducted in R (R Core Team, 2016).
1.4 Results

1.4.1 El Niño simulation model

For a naïve sea lion population, the overall mortality due to CDV was higher during an EN year even though there were fewer individuals infected (Table 5). The epidemic during an EN event had a similar sized peak (Table 5), but occurred earlier in relation to the introduction of disease (day one of the simulation), was shorter in duration, and had a higher disease mortality rate than during a non-EN year (Figure 2).

For a partially recovered population, there were fewer total infected sea lions and less total mortality. The partially recovered population experienced a later peak of infection, a shorter epidemic, and a later epidemic relative to a naïve population. The disease mortality rate was the same.

1.4.2 Sensitivity Analysis

Reductions in the transmission rate, $\beta_S$, lowered the proportion infected (Figure 3) and the number of sea lions dead from disease (Figure 4), but increased the epidemic duration (Figure 5). Increasing the case disease mortality, $\delta_S$, increased the disease mortality rate (Figure 6) and the total dead from disease (Figure 4). Increasing the background mortality, $\mu_S$, slightly reduced the proportion infected (Figure 3) and the total dead from disease (Figure 4), but not by much. Decreasing pup mortality, $\mu_{pup}$, increased the total dead from disease (Figure 4) and had a slight dip in the proportion infected at intermediate values (Figure 3). Increasing the infectious period, $1/\gamma_S$, decreased the total dead from disease and increased the epidemic mortality rate. Increasing the latent period, $1/\sigma_S$, increased the epidemic duration.

Several parameter combinations showed that there were non-linear interactive effects on the results from the model. An example of two parameters that interacted are proportion of pup survival and transmission rate (Figure 7).
1.4.3 Management

Where the infection began on the island mattered to the outcome of the management strategies. When the first case of CDV was introduced closer to the center of the island and dog packs were small, low populations of dogs could allow the epidemic to burn out before spreading to the sea lions (Figure 8). Location of introduction mattered somewhat for the vaccination strategies (Figure 9). If the infection was introduced in a dog population further away from the sea lions, the total number of infected sea lion and total dead from disease increased. This was due to new susceptible pups being introduced into the population during the extended time it takes the disease to transmit to the sea lions if it is introduced in the dog population further away. The timing of when the vaccination management plan was implemented was incredibly important in determining the total number of infected individuals in year one and the total number of individuals that died from disease (Figure 10). As the delay in management implementation increased, the efficacy of vaccination was reduced. In the case of EN, waiting nine months to implement vaccination was not effective at all, while in the non-EN case, waiting nine months to vaccination showed a very small reduction in total infected and total dead from disease. The fencing strategy, which reduced the interspecific contact rate, showed no efficacy in reducing the size of the epidemic or the disease mortality rate in the sea lions (Figure 11).

1.5 Discussion

Extreme El Niño occurrences are projected to double in response to greenhouse warming (Cai et al., 2014), which will likely have severe impacts on the Galápagos Islands biota, by influencing population viability and community structure. El Niño had a big impact on the outcome of the model and the shape and duration of the epidemic. The EN model had an epidemic that occurred earlier with fewer infected sea lions,
but had with higher sea lion mortality. The higher mortality from CDV during EN years could have long lasting impacts on the sea lion population and its continued existence. While this model is specific to CDV, there are many diseases that the Galápagos sea lions have proven susceptible to (Coria-Galindo et al., 2009), as well as other diseases, like Leptospirosis (Acevedo-Whitehouse et al., 2003; Gulland and Hall, 2007), which have infected their sister taxa, California sea lions \((\textit{Zalophus californianus})\). The probable influence of EN on the sea lion immune system and disease mortality is an important factor when taking potential epidemics into account.

Besides the number dead from disease, the duration and timing of the epidemic is an important aspect in this system for two reasons. First, the epidemic during an EN year occurs much earlier in relation to the introduction of CDV into the dog population. This could mean that if an epidemic is seen in the dog population, there would be less time to take action to quarantine dogs and reduce contact between the two species before an epidemic begins in the sea lion population. Second, the duration of the epidemic is much shorter during EN years. This means that there is less time from the onset of the epidemic to launch a management program as it moves through the population at a much faster rate. This is highlighted in the importance in the timing of vaccination implementation. This stresses the importance of having a fleshed out plan for very virulent diseases like CDV when they are a threat to stressed populations.

This model was sensitive to many changes in parameters. The parameters that most strongly shape disease dynamics out of those tested are the interspecific transmission rate, the disease mortality rate, and the infectious period. The transmission rate is responsible for changing the duration of the infection and the proportion infected, which is incredibly sensitive to low levels of transmission. The disease mortality parameter and the infectious period are responsible for both the proportion and the number of individuals that died during the epidemic. Increasing the disease
mortality rate and infectious period, as we predict will happen during EN events, increases the overall mortality rate and the number of dead from disease.

The qualitative response to dog population management during EN and non-EN is very similar, but there is always a higher number of infected sea lions during a non-EN year and a higher number of dead individuals during EN years. Introductions in the center of the island could not spread the epidemic to sea lions at low population densities. There is a very slight change in the response to a vaccination program depending on where the epidemic begins in the dogs. However, most of the dogs inhabit where people live on the island, which is generally closest to the edges of the island, so an introduction near the sea lions is the most likely scenario. The timing of vaccination implementation shows drastic responses in both EN and non-EN years. The earlier a vaccination program is put in place, the greater the reduction in infected sea lions. A very late vaccination during an EN year will do nothing for reducing the epidemic because the infection has already completed. The response in EN years is very steep compared to non-EN years, especially for vaccination at the onset of the simulation, but gets reduced as the management is delayed.

We have shown that timing of management, location of the introduction of disease, and EN are very important in shaping disease dynamics in the Galápagos sea lion population. There is much more information about certain parameters that needs to be collected to elucidate uncertainties in how disease and EN could affect the Galápagos sea lion population.

In order to best understand what accurate predictions are for this system, it would be very helpful if we had more information on parameter values, like the background and pup mortality in EN and non-EN years, transmission rate in sea lions, and infectious period in sea lions. Important tests could be establishing contact rates between sea lions separately for EN and non-EN years and gaining a metric for sea lion immune response during those years. We have good estimates for PDV in the
seal system, but we don’t know how different it would be for a closely related disease in a related species. The limitations on collecting such data are that the sea lions are an endangered species and collecting experimental results of infection would be inhumane and unwarranted.

An important aspect in this system could be modification of behaviors during EN events. This could include changes in dispersal capabilities and likelihood, changes in habitat usage, and change in time spent at sea. In this model, these behavioral changes could influence the level of isolation as well as pack density. While there is an overall reduction in total population density during EN, it’s possible that there are changes in local densities as sea lions use their habitat differently, potentially aggregating at locations with higher food availability. Timing of the introduction of disease in relation to an EN event may also pose an important influence on the model outcome. While there is uncertainty in many of our parameter estimates in our EN model, the sensitivity analysis and simulations highlight the importance of studying the potential impact of EN and disease on the threatened Galápagos sea lion population.
Chapter 2

Mechanisms driving life history patterns in California sea lions

2.1 Abstract

Imperiled populations face interacting threats to their existence, including land use change, disease, and climate perturbations. We use statistical models to improve our understanding of the physiological stress that occurs during El Niño and its impact on the California sea lion, Zalophus californianus. We found that birthweight decreased with increasing sea surface temperatures (SST, which is an indicator of El Niño severity) and that first year survival increases with increasing birthweight and decreases with higher SST. Some animals display behavioral differences in range, which is partially explained by sex and age, and can influence the potential for disease spread. This information improves our understanding of threats and their impact on the dynamics of a charismatic species, which can aid our understanding of an ecologically similar endangered species, for which this kind of information is lacking.
CHAPTER 2. MECHANISMS DRIVING LIFE HISTORY PATTERNS IN CALIFORNIA SEA LIONS

2.2 Introduction

As individuals are born, disperse, and reproduce, they experience different threats at different magnitudes and at both local and regional scales. An individual’s ability to survive the newborn and juvenile stages can be influenced by how maternal investment, environmental factors, and genetics shape their condition. Physical characteristics, like birthweight and sex, can be used as metrics to attempt to disentangle those influences. Birthweight has been shown to have lasting effects on fitness and survival (Kruuk et al., 1999; Alados and Escos, 1991) and differential mortality rates between the sexes are observed in many systems both early (Clutton-Brock et al., 1985) and later in life (Jorgenson et al., 1997). Sex and condition can also mold behavioral traits, such as movement patterns and permanent dispersal events, as well as fecundity and lifespan. How individuals move on the landscape is important for factors like disease spread, gene flow, and population connectivity (Hess, 1996). How all of these factors influence population dynamics is poorly understood in many sensitive systems.

Populations globally face many interacting threats to their persistence, including land use change, disease, and climate perturbations. These threats shape life history traits, such as number of offspring, birthweight, survival, fecundity, and dispersal events (Forchhammer and Post, 2004). As individuals disperse across the landscape, they experience these threats at both local and regional scales. This is problematic, for example, when stressors threaten survival or when dispersal enhances disease spread. Here, we analyze a long-term dataset on California sea lions, Zalophus californianus, to elucidate and understand the imminent threats and their impact on the dynamics of a charismatic species.

The California sea lion is a species of pinniped native to the western shores of Canada, Mexico, and the United States. These animals were historically exploited and hunted for bounty, however their population has since rebounded and is continuously
increasing. This population is useful for exploring the relationship between physical characteristics, stressors, and life history traits because it is a healthy population with lots of available data. Studying the California sea lion can also aid our understanding of related species that experience similar stressors, but are not as thoroughly studied, like the endangered Galápagos sea lion, *Zalophus wollebaeki*.

The main threats that the California sea lion population faces are reduced prey availability during El Niño events (EN) (Shirasago-Germán et al., 2015), infectious diseases (Lloyd-Smith et al., 2007; Ávalos-Téllez et al., 2014), and pollution (Le Boeuf et al., 2002), which they experience across local and regional scales due to a dispersal capability that encompasses the entire species range. It is not fully elucidated how life history traits shape demographic rates and dispersal ability, and how large-scale climate modifies these rates directly and indirectly.

**Questions**

How do EN and sex influence birthweight? How do birthweight and presence of EN influence first year survival? How does EN influence mortality rates for different life stages? What factors dictate movement and permanent dispersal patterns?

**2.3 Methods**

**2.3.1 System**

California sea lions are sexually dimorphic, with adult males weighting three to four times more than adult females. Both sexes reach sexual maturity at four to five years of age. Males establish a harem and defend their territory during breeding and pupping season, which off the coast of California is from mid-May through July. Male pups accrue weight more rapidly than female pups by nursing. At two weeks of age males weigh on average 9.01 kg and females weigh 7.6 kg (Le Boeuf et al., 1983). The
gestational period is approximately 11 months and females generally produce one pup per year.

California sea lions are majorly impacted by EN events (Melin, 2002) during which there is a collapse in marine productivity due to reduced upwelling and rising sea surface temperatures (SST). This increases starvation stress, the amount of time sea lions spend hunting, and mortality. While studies have shown there is a reduced number of pups being born during EN, here we are focusing on the animals that are born into the population and how EN presence and sex affects their survival and propensity to disperse. There is evidence of reduced maternal investment during EN events which influences pup growth rates and mortality (Ono et al., 1987).

2.3.2 Data

The dataset analyzed in this study was of the California sea lions (Zalophus californianus) on San Miguel Island, Channel Islands, California, USA and was downloaded from the NOAA National Centers for Environmental Information (NCEI) (Melin et al., 2016). San Miguel Island is home to one of the largest breeding colonies in the United States (DeLong and Melin 2000, Melin et al. 2010). The NOAA study was conducted from 1987 to 2014 by the Alaska Fisheries Science Center. The dataset includes birthweight, sex, and length for 11322 individuals for all years, with 6840 females and 4482 males captured and marked on San Miguel Island. Marking of pups occurred between September and November and re-sight data was recorded May through August. There are 95985 unique re-sight observations for 5837 individual sea lions in 1988 and 1990-2009 at the natal site, San Miguel Island, and at two other sites in California, Ano Nuevo and the Farallon Islands. San Miguel Island to the Farallon Islands is ~ 470km, San Miguel Island to Ano Nuevo is ~ 385km, and the Farallon Islands to Ano Nuevo is ~ 92 km. Far more animals were re-sighted at Ano Nuevo than Farallon Islands, which is partially due to only seven years of re-sight
data at Farallon Islands compared to sixteen at Ano Nuevo. For this reason, most of
the re-sight data analyzed is for animals that went to Ano Nuevo or remained at San
Miguel Island.

The oldest age for females in this dataset is 22 years, which is limited by the
years of available data. The oldest age for male sea lions is 19 years. For most of the
analyses on age and survival, the number of cohorts were trimmed to 1990-2006 in
order to account for biases on either end of the dataset (i.e. inadequate accumulation
of marked individuals in the initial years of the study, missing years of re-sight data,
and inadequate time for re-sightings for individuals marked in later years). For each
analysis, males and females were separated due to differences in life history behaviors
and sexual dimorphism.

The index used to measure the intensity of EN was the Oceanic Niño Index (ONI),
downloaded from the NOAA website, which has historically been used as the threshold
for classifying EN events. This index is a three month running mean of sea surface
temperature (SST) anomalies measured in the equatorial pacific measured against 30
year base periods, which are updated every 5 years. These values are centered around
0, with positive values indicating abnormally warm SST (as expected during an El Niño event) and negative values indicating abnormally cold SST.

2.3.3 Analyses

We used R (R Core Team, 2015) for all analyses in this paper. For all individuals
branded in this study, weight was recorded at branding and sex was estimated and, if
necessary, later adjusted. For many, pup length was also recorded, but only for those
individuals born and branded in the later years. To test for differences in birthweight
between male and female pups, we performed an ANOVA using a linear model for the
birthweight of all individual pups marked in this study with sex as the explanatory
variable. The same test was used to measure if length was also explained by sex.
We estimated the correlation between birthweight and pup length with a Pearson’s test using the `cor()` function in R. We calculated the mean ONI value for January through April preceding the sea lions’ birth to test for an effect of EN on the initial birthweight for sea lions. This date range was used because it is during the last few months of the gestational period (Figure 13). We used an ANOVA on a linear model to test for these effects.

For each animal branded, we estimated year survival and the age the animal reached as the the last year they were seen in the study, at any of the three locations included in the observational data. We assumed that an animal was not likely to have left its natal colony in its first year, and was likely to be re-sighted if it survived that first year. To test whether birthweight was a predictor of the age a sea lion reached, we ran two linear models and tested them with ANOVAs, one testing the response of all individuals and one excluding individuals that didn’t survive their first year of life.

We tested whether birthweight had a significant impact on year one survival using a generalized linear model with a binomial distribution and a logit link function. We chose this test because the response variable was binary. Survival of pups beyond their first year was either zero, meaning they did not survive to the next summer, or one, meaning they survived at least until the next summer. An ANOVA using the chi-squared test was used to test the fit of the models since the dispersion is binomial. Only years 1990-2006 were included in order to account for biases in the beginning and ending years of re-sight data. To see whether the relationship between birthweight and year one survival was stronger or weaker in different environments, we then separated out years where the December following the pups’ birth was cool (ONI ≤ -0.5), warm (ONI ≥ +0.5), and normal (-0.5 < ONI < + 0.5). We used a chi-squared ANOVA to test the interaction between the main effects of weight and December category on survival using a generalized linear model with binomial
distribution and a logit link function. We analyzed this effect separately for both males and females.

For each year, we separated all of the alive animals into three different age classes: pups born that year, yearlings born the previous year, and adults born two or more years prior. For each group, we calculated the proportion that was never seen again following that year, which we interpreted as the mortality rate. For each class, we explored the relationship between the mortality rate in each year and the ONI values for each individual month in that year and the following year. For pups, we took the months that showed a relationship, which were the months July of that year through April of the following year, and also calculated the mean ONI value for those months, which are the first ten months of the pups’ life. We then tested for a relationship between that mean ONI and proportion of survival of each age class using an ANOVA on a general linear model.

For the 5820 animals that survived their first year, we characterized where they were seen among the three locations (San Miguel Island, Ano Nuevo, and Farallon Islands), what age their first movement to another location was, and whether or not they returned to San Miguel Island (the natal island for all individuals in the study). We classified seven different types of sea lions based on their re-sight data. The descriptions for each and the number of sea lions that fell into each class can be found in Table 6. For further examining connectivity and dispersal, we moved forward only with the animals that were re-sighted at Ano Nuevo. This was because far more years were included in the re-sight data and more animals dispersed or moved there. For animals that moved to Ano Nuevo, we recorded what years they dispersed there and what their ages were.

We estimated the differences in number of sites visited based on sex, age, and birthweight. We also estimated the differences in number of times re-sighted at Ano Nuevo based on sex and age. To see if present or recent losses in oceanic productivity
CHAPTER 2. MECHANISMS DRIVING LIFE HISTORY PATTERNS IN CALIFORNIA SEA LIONS

were important in dispersal patterns, we estimated the proportion of individuals that dispersed and the proportion of dispersers for each sex in response to multiple ONI means using generalized linear models with a binomial error distribution. The ONI predictor variables used in these models were the ONI mean for the current year, the ONI mean for the previous year, and the ONI mean during the re-sight period.

2.4 Results

There were large fluctuations from year to year in mean birthweight, but in general, female and male birthweight fluctuated similarly (Figure 14). Birthweight was explained by sex, with males being on average 20.76 kg and females being 17.99 kg (Figure 15a), as was length, with males being 96.85 cm and females being 92.35 cm (Figure 15b). Weight and length had a high, positive Pearson’s correlation coefficient of 0.86, which suggests a strong correlation (Figure 16).

We found a relationship between individual birthweight and the average ONI value for January-April during the gestational period before the pup was born (Figure 17). Pups born after a warmer deviation from normal temperatures had a reduction in birthweights. This suggests a loss in maternal investment after EN events.

For the linear model including all animals that tested the effect of birthweight on longevity, we saw that animals with higher birthweight had longer lives. We found that the relationship between initial birthweight and the age last seen was not significant for pups surviving at least one year for males (Figure 18), indicating that first year survival was driving the pattern that individuals with higher birthweight lived longer. We saw that females showed the opposite relationship, where increasing birthweight decreased lifespan, although we expect that this is not a mechanism in the system but an artifact of the large number of data points included in this analysis. We found that first year survival depends on birthweight (Figure 19a) and length (Figure...
19b) for both male and female sea lion pups. We tested the interaction between the main effects weight and December ONI categories, which were cool, normal, and warm, on pup survival. For females, we saw a significant effect of weight (df = 1, deviance = 101.154, P-val < 2.2 e -16), and a significant effect of December ONI category (df = 2, deviance = 42.764, P-val = 5.2 e -10), and no significant interaction between weight and December ONI category on survival. This shows that for females, weight and December ONI have an effect on pup survival (Figure 20). For male pups, we saw a significant effect of weight (df = 1, deviance = 92.572, P-val < 2.2 e -16), a significant effect of December ONI category (df = 2, deviance = 57.545, P-val = 3.19 e-13), as well as an interaction between weight and December ONI (df = 2, deviance = 9.831, P-val = 0.0073). The important driver in the interaction model for males was the difference in slopes between cool and warm Decembers. This could suggest that for males, birthweight is more important for survival under stressful conditions, but we do not see this effect in females (Figure 20).

Pup mortality was highly variable, with a mean and standard deviation of 0.371 ± 0.120 for years 1990-2006. For yearlings, the mean and standard deviation was 0.105 ± 0.077 and for adults 0.081 ± 0.037. For adults and yearlings, no clear relationship was seen between mortality and the ONI in individual months, nor the average ONI value for July of that year though April the following year. However, for pup survival, the effect of ONI in each individual month between July of that year through April of the following year was significant, as was the average over those months (Figure 21).

The sea lions were often seen at multiple locations in one year, sometimes even in the same month, which attests to the dispersal capabilities of this species. Of the animals that survived their first year, many had a high rate of re-sighting at their natal location, San Miguel Island, at a young age (Figure 22). However, there were many that weren’t re-sighted at their natal location until much later in their lives.
It is unclear whether these individuals mainly remained at their natal site and had been consistently missed or if they resided elsewhere for most of their adult lives.

Out of the 5820 animals that survived their first year, many were re-sighted at another location, either Farallon Islands or Ano Nuevo, and some were re-sighted at all three sites, with different patterns for males and females (Table 7). Sea lions that were sighted at more locations reached a higher age in both males and females (Figure 23), which is likely due to increased likelihood over their a longer lifetime to be sighted at those locations. The age of individuals who remained at their natal sight and were never seen elsewhere could be disproportionately lower because some young sea lions could have dispersed to a sea lion colony location other than Ano Nuevo and Farallon Islands, to live and reproduce and would have not been recorded. The lifetime number of sightings was not significantly correlated with birthweight in males or females (Figure 24). However, males did visit more sites, with an average of 1.70 sites while females visited an average of 1.36 sites (P-val = 2.2e-16). Of the animals that visited Ano Nuevo at least once (Table 8), females were sighted there in an average of 1.75 unique years, compared to an average of 2.36 unique years for males.

We looked at two classifications of sea lions that were seen at Ano Nuevo because they dominated the number of sea lions that dispersed (Table 6). The first was the animals that were only ever re-sighted at Ano Nuevo. These animals were likely to disperse there when they were younger, but not many of them stayed there past sexual maturity (Figure 25a). They were never seen again at their natal colony (San Miguel Island) so they were either consistently missed in sampling at Ano Nuevo, died, or dispersed to a location that was outside the census area to reproduce.

The next classification was sea lions that were re-sighted at both Ano Nuevo and San Miguel Island, which was further split into two categories. The first was sea lions that were first seen at San Miguel before dispersing to Ano Nuevo and never returning
CHAPTER 2. MECHANISMS DRIVING LIFE HISTORY PATTERNS IN CALIFORNIA SEA LIONS

to San Miguel Island, their natal colony. For the animals that never returned to San Miguel Island, many of them were never re-sighted after their first dispersal to Ano Nuevo (Figure 25b). These sea lions were either consistently missed in sampling at Ano Nuevo, died, or dispersed to a location that wasn’t sampled to reproduce. The second category was sea lions that were seen at Ano Nuevo at some point and then returned to San Miguel Island. For that category, many sea lions moved to Ano Nuevo and then returned to San Miguel Island at some point (Figure 25c), and these animals lived a long time.

For each individual that was re-sighted at Ano Nuevo, we recorded the number of unique visits and the age at each visit. We saw that younger sea lions were a large portion of the number of sea lions who visited Ano Nuevo in a given year (Figure 26). This could either be because younger sea lions move around more or because sea lions that were older died. Many sea lions were seen multiple times at Ano Nuevo (Table 8) and there was a lot of movement between Ano Nuevo and San Miguel Islands, where many animals were re-sighted often at both locations (Figure 27). This indicates a high level of connectivity between the two sights and often sea lions were re-sighted at both places in the same year.

It is still unclear how EN plays a role in dispersal and movement. We tested the proportion of individuals alive that were seen at Ano Nuevo with multiple values for ONI and saw no significant trends. We include the proportion seen at Ano Nuevo as a function of the ONI mean during the re-sight period (May-August) as an example of the lack of a relationship (Figure 28).

2.5 Discussion

Both sex and EN during the gestational period had an influence on birthweight. This is very important, because birthweight is predictive of whether or not an individual
pup survives its first year. We show that EN presence during the first year increases pup mortality. This highlights that there may be reduced maternal investment during times of low oceanic productivity, both during the gestational period and afterwards, and this could contribute to high pup mortality during EN years. The strongest EN during the period of this study was the 1997-98 EN event, which did show the highest pup mortality. Interestingly, yearling mortality and adult mortality didn’t seem to correlate with presence of EN. Previous work indicates that adult and juveniles are also affected by EN (Greig et al., 2005), which was not seen in this study. Birthweight is important for life history and fitness in many other animals, most notably the well-studied Red Deer (Kruuk et al., 1999). This study adds to research on the importance maternal investment on first year survival.

There is an important distinction between dispersal and movement, because they characterize connectivity in a population differently and where an individual reproduces is very important in a population. In this system, dispersal can be characterized as a type of movement that is a permanent move away from the natal location to one location, while other types of movement may be characterized by impermanent trips from one place to another. The data used in this analysis showed that both male and female sea lions left their natal location often enough to be sighted at other locations frequently. The study only included two other locations, the Farallon Islands and Ano Nuevo, and only made recordings during a short period during the year, so there could be many other movements not accounted for here. Of the animals that left their natal location, many of them returned to it. These movements from the natal location were dominated by young individuals, likely less than the reproductive age. Previously, we had assumed that high site fidelity recorded in other species (Meise et al., 2013; Robertson et al., 2006) and other subpopulations of California sea lion (Young et al., 2008) would indicate that movement would be strongly restricted for juveniles, but this was not seen. Still, a lot of adults were re-sighted away from the
natal location as well, but still returned to San Miguel Island. Very young individuals were seen at the distant locations, and some were even seen at another location during the first year of their life, which we found surprising. Males on average visited more locations and were sighted at other locations more frequently than females. This is consistent with an empirical study in New Zealand sea lions, which showed an unexpectedly high amount of movement in breeding males (Robertson et al., 2006), which suggests that males could be important for long-range disease dispersal and gene flow into other populations. Females often have to stay and take care of pups, but still do many trips to go find food during the nursing period. It is surprising that many of these older males are re-sighted at other locations during the breeding season, when it would be expected that they would stay in or near a breeding colony. Animals display behavioral differences in habitat use and range during breeding and non-breeding seasons that will impact density and dispersal and therefore disease and population dynamics.

There are a few years which have disproportionately high levels of movement, so there may be a driving mechanism other than EN acting in this system, for example domoic acid or a disease outbreak (Greig et al., 2005). Domoic acid is a marine phycotoxin produced by algae that accumulates in shellfish and small fish and poison animals in higher trophic levels. A recent study has shown that there is a strong relationship between domoic acid and two warm oceanic phases, El Niño and the Pacific Decadal Oscillation (McKibben et al., 2017). It is possible that something other than EN plays a role in dispersal dynamics.

While this study attempts to characterize the relationships between sex, birth-weight, EN, mortality, and dispersal, there is still much to be understood about the life history of California sea lions and other marine mammals and their relationship to EN. We expect that historic disturbances will have persistent effects in this system. For example, high pup mortality during an EN or disease event will reduce the
number of available mates and recruitment many years later when those sea lions become sexually mature. It is also possible that the selection pressure on birthweight could change as EN becomes more prevalent in this system due to climate change. In this study, we show that EN and sex have important roles in life history traits of the California sea lion and that movement between distant locations is very common in this population.

2.5.1 Management Implications and future directions

California sea lions are large marine predators that have a rapidly expanding population. They have increasing conflicts with fishermen, so this study will help to understand the basic demographics in this system so that the population can be monitored and controlled effectively. Until 2021 in Oregon and Washington, fishermen can euthanize sea lions if they are preying on certain species of salmon. This research suggests that the sea lion population might be threatened more in some years and this should be taken into account when a state decides to euthanize an animal. Managers can use this information as a tool to develop models to predict the spread of disease, predict pup mortality rates in the face of reduced productivity, and justify collecting informative data on this charismatic species.

On the other hand, we can also use this information to aid in understanding the Galápagos sea lion, which is an ecologically similar and phylogenetically related species. The Galápagos sea lion is endangered, and using this information on the California sea lions, we can begin to understand demographic information in which the role of climate is key. We plan to use the relationships studied in this system to build a dispersal model for the Galápagos sea lion which will account for large-scale movements and demographic information to test for the influence of stressors, such as disease and EN, in that sensitive system.
Table 1: Table of the non-EN sensitive parameters used in the simulation model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Sea lion value</th>
<th>Dog value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pack size (individuals)</td>
<td>20</td>
<td>10</td>
<td>(Alava and Salazar, 2006)</td>
</tr>
<tr>
<td>Number of packs</td>
<td>30</td>
<td>61</td>
<td></td>
</tr>
<tr>
<td>Total island population size (individuals)</td>
<td>600</td>
<td>610</td>
<td>(Alava and Salazar, 2006)</td>
</tr>
<tr>
<td>Isolation ($\varepsilon_k$)</td>
<td>1.5</td>
<td>1.5</td>
<td></td>
</tr>
<tr>
<td>Transmission rate ($\beta_k$)</td>
<td>0.4</td>
<td>0.16</td>
<td>(Swinton et al., 1998)</td>
</tr>
<tr>
<td>Interspecific transmission ($\beta'_k$)</td>
<td>$2.3 \times 10^{-5}$</td>
<td>$2.3 \times 10^{-5}$</td>
<td>(Brock, 2012)</td>
</tr>
<tr>
<td>Latent period ($1/\sigma_k$)</td>
<td>3 days</td>
<td>7 days</td>
<td>(Brock, 2012) (Almberg et al., 2010)</td>
</tr>
<tr>
<td>Infectious period ($1/\gamma_k$)</td>
<td>6 days</td>
<td>9 days</td>
<td>(Swinton et al., 1998)</td>
</tr>
<tr>
<td>Disease mortality rate ($\delta_k$)</td>
<td>0.094</td>
<td>0.111</td>
<td>(Swinton et al., 1998)</td>
</tr>
<tr>
<td>Background mortality rate ($\mu_k$)</td>
<td>$4.83 \times 10^{-4}$</td>
<td>$1.48 \times 10^{-3}$</td>
<td>(Almberg et al., 2010)</td>
</tr>
<tr>
<td>Proportion pup mortality ($\mu_{pup}$)</td>
<td>0.33</td>
<td></td>
<td>(Swinton et al., 1998)</td>
</tr>
<tr>
<td>Daily birth rate</td>
<td>Equation (1.3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Duration of birthing period</td>
<td>122 days</td>
<td>365 days</td>
<td></td>
</tr>
</tbody>
</table>
Table 2: Table of EN sensitive parameters used in the simulation model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Normal</th>
<th>El Niño</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transmission ($\beta_s$)</td>
<td>0.4</td>
<td>0.6</td>
</tr>
<tr>
<td>Latent period (1/$\sigma_s$)</td>
<td>7 days</td>
<td>5 days</td>
</tr>
<tr>
<td>Infectious period (1/$\gamma_s$)</td>
<td>6 days</td>
<td>8 days</td>
</tr>
<tr>
<td>Disease mortality rate ($\delta_s$)</td>
<td>0.1 (38%)</td>
<td>0.2 (60%)</td>
</tr>
<tr>
<td>Background Mortality ($\mu_s$)</td>
<td>$4.6 \times 10^{-4}$</td>
<td>$8 \times 10^{-4}$</td>
</tr>
<tr>
<td></td>
<td>(15% yearly)</td>
<td>(25% yearly)</td>
</tr>
<tr>
<td>Proportion up mortality ($\mu_{pup}$)</td>
<td>0.3</td>
<td>0.9</td>
</tr>
</tbody>
</table>
Table 3: Parameter values used in sensitivity analysis.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Values</th>
<th>Number of Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transmission ($\beta_s$)</td>
<td>0, 0.01, 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8</td>
<td>11</td>
</tr>
<tr>
<td>Latent period ($1/\sigma_s$)</td>
<td>2, 3, 4, 5, 6, 7 days</td>
<td>6</td>
</tr>
<tr>
<td>Infectious period ($1/\gamma_s$)</td>
<td>6, 7, 8, 9, 10, 11 days</td>
<td>6</td>
</tr>
<tr>
<td>Disease mortality rate ($\delta_s$)</td>
<td>0.1, 0.121, 0.145, 0.169, 0.2, 0.236</td>
<td>6</td>
</tr>
<tr>
<td>Background Mortality ($\mu_s$)</td>
<td>$4.6 \times 10^{-4}, 5.4 \times 10^{-4}, 6.3 \times 10^{-4}, 7.2 \times 10^{-4}, 8 \times 10^{-4}, 9 \times 10^{-4}$</td>
<td>6</td>
</tr>
<tr>
<td>Pup mortality ($\mu_{pup}$)</td>
<td>0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0</td>
<td>9</td>
</tr>
</tbody>
</table>
Table 4: Table of management strategies tested.

<table>
<thead>
<tr>
<th>Management Strategy (parameter)</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vaccination (initial proportion of sea lions recovered)</td>
<td>0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0</td>
</tr>
<tr>
<td>Fencing around beach (interspecific transmission $\beta'$)</td>
<td>$2.313e \times 10^{-5}$, $1.157e \times 10^{-5}$, $7.71e \times 10^{-6}$, $5.783e \times 10^{-6}$, $4.626e \times 10^{-6}$, $3.855e \times 10^{-6}$</td>
</tr>
<tr>
<td>Dog population control (initial number of dogs per pack)</td>
<td>0, 1, 2, 3, 5, 10, 20, 30</td>
</tr>
</tbody>
</table>
Table 5: The results of the comparison between EN years and non-EN years for naïve and partially recovered populations.

<table>
<thead>
<tr>
<th></th>
<th>Naïve population</th>
<th>Partially recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EN Year</td>
<td>non-EN Year</td>
</tr>
<tr>
<td>Day of infectious peak in first pack</td>
<td>37</td>
<td>47</td>
</tr>
<tr>
<td>Duration of epidemic on island (days)</td>
<td>215</td>
<td>312</td>
</tr>
<tr>
<td>Maximum number infected on island (individuals)</td>
<td>13.8</td>
<td>13.6</td>
</tr>
<tr>
<td>Day of island maximum</td>
<td>50</td>
<td>64</td>
</tr>
<tr>
<td>Maximum number infected in a pack (individuals)</td>
<td>6.16</td>
<td>6.22</td>
</tr>
<tr>
<td>Total infected (island-wide individuals)</td>
<td>548</td>
<td>647</td>
</tr>
<tr>
<td>Total dead from disease (island-wide individuals)</td>
<td>365</td>
<td>258</td>
</tr>
<tr>
<td>Disease mortality rate</td>
<td>0.66</td>
<td>0.40</td>
</tr>
</tbody>
</table>
Table 6: For the 5820 sea lions that survived their first year of life we classified them into seven different categories based on which sites they were re-sighted at during their lifespan.

<table>
<thead>
<tr>
<th>Classification</th>
<th>Number total</th>
<th>Number female</th>
<th>Number Male</th>
</tr>
</thead>
<tbody>
<tr>
<td>San Miguel Island Only (natal colony)</td>
<td>3103</td>
<td>2392</td>
<td>710</td>
</tr>
<tr>
<td>Ano Nuevo Only</td>
<td>543</td>
<td>222</td>
<td>321</td>
</tr>
<tr>
<td>Farallon Islands Only</td>
<td>21</td>
<td>8</td>
<td>13</td>
</tr>
<tr>
<td>Ano Nuevo and Farallon Islands</td>
<td>9</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Farallon islands and San Miguel Island (natal colony)</td>
<td>38</td>
<td>17</td>
<td>21</td>
</tr>
<tr>
<td>Ano Nuevo and San Miguel Island (natal colony)</td>
<td>1995</td>
<td>963</td>
<td>1032</td>
</tr>
<tr>
<td>All three locations</td>
<td>111</td>
<td>50</td>
<td>61</td>
</tr>
</tbody>
</table>
Table 7: Of the individuals that survived year one, some were only observed at their natal site of San Miguel Island, some were observed at their natal site and either Ano Nuevo or the Farallon Islands, and some were observed at all three locations.

<table>
<thead>
<tr>
<th></th>
<th>Natal site only</th>
<th>Two locations</th>
<th>Three locations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>3103 (53.3%)</td>
<td>2597 (44.6%)</td>
<td>120 (2.1%)</td>
</tr>
<tr>
<td>Females</td>
<td>2393 (65.4%)</td>
<td>1210 (33.1%)</td>
<td>54 (1.5%)</td>
</tr>
<tr>
<td>Males</td>
<td>710 (32.8%)</td>
<td>1387 (64.1%)</td>
<td>66 (3.1%)</td>
</tr>
</tbody>
</table>
Table 8: For each sea lion that visited Ano Nuevo at least once in their lifetime, we calculated the number of unique years that individual was re-sighted at Ano Nuevo for both males and females.

<table>
<thead>
<tr>
<th></th>
<th>Number of unique years re-sighted at Ano Nuevo</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Number of females</td>
<td>781</td>
</tr>
<tr>
<td>Number of males</td>
<td>571</td>
</tr>
</tbody>
</table>
List of Figures
Figure 1: The hexagonal structure of the island, with sea lions located on the outer ring and dogs located on the interior of the island. There are 91 individual packs, with 61 dog packs and 30 sea lion packs with 20 sea lions or 10 dogs in each pack at the beginning of each simulation. Each number is the distance away that that dog pack is from a pack of sea lions with pack five being the furthest dog pack from the sea lions and one being the closest dog pack to the sea lions. For the simulations testing the efficacy of management, we grouped packs 3-5 as the further packs and 1-2 as the nearer packs.
Figure 2: The spatial spread of the number of infected individuals as the epidemic moves from pack to pack for the EN and non-EN simulations. Each colored line is a separate pack, with red being the earliest pack to become infected and blue being the latest pack.
Figure 3: The proportion to become infected observed over the range of parameter values found in Table 3. The values selected for the EN simulation are red circles and the values selected for the non-EN simulation are blue circles.
Figure 4: The total number of individuals that died from disease observed over the range of parameter values found in Table 3. The values selected for the EN simulation are red circles and the values selected for the non-EN simulation are blue circles.
Figure 5: The duration of the epidemic in sea lions observed over the range of parameter values found in Table 3. The values selected for the EN simulation are red circles and the values selected for the non-EN simulation are blue circles.
Figure 6: The disease mortality rate observed over the range of parameter values found in Table 3. The values selected for the EN simulation are red circles and the values selected for the non-EN simulation are blue circles.
Figure 7: Example of how two parameters interact to influence total number of infected individuals, with six values of proportion of pup survival (which is $1 - \mu_{pup}$) and six values for intraspecific transmission.
Figure 8: The total number of infected individuals during the first year (left) and the total number of individuals that died from disease during the first year (right) for the management of the dog population simulations. Red lines are the EN model and black lines are the non-EN model. We simulated the introduction of the disease in the dog population at multiple distances away from the sea lion population (Figure 1). The further distances of introduction in the dog population are dashed lines, while the nearer distances of introduction are the solid lines.
Figure 9: The total number of infected individuals during the first year (left) and the total number of individuals that died from disease during the first year (right) for the vaccination management strategy when individuals were vaccinated on day one of the simulation. Red lines are the EN model and black lines are the non-EN model. We simulated the introduction of the disease in the dog population at multiple distances away from the sea lion population (Figure 1). The further distances of introduction in the dog population are dashed lines, while the nearer distances of introduction are the solid lines.
Figure 10: The total number of infected individuals during the first year (left) and the total number of individuals that died from disease during the first year (right) for the timing of vaccination management strategy. The infection was started in a dog pack next to a sea lion pack. Red lines are the EN model and black lines are the non-EN model. The thickness of the line indicates what day the vaccination strategy was implemented, with thicker lines occurring later in reference to the beginning of the simulation.
Figure 11: The total number of infected individuals during the first year (left) and the total number of individuals that died from disease during the first year (right) for the fencing management strategy. Red lines are the EN model and black lines are the non-EN model. We simulated the introduction of the disease in the dog population at multiple distances away from the sea lion population (Figure 1). The further distances of introduction in the dog population are dashed lines, while the nearer distances of introduction are the solid lines.
Figure 12: Map depicting the California, USA coastline and the three locations in this study. San Miguel Island is the natal location for all sea lions included in this study and the Farallon Islands and Ano Nuevo are the two other locations where re-sighting occurred.
Figure 13: Conceptual figure of when these events occur over a pup’s first year and a half of life. The pups are born during the blue period, they are marked during the black period, and the first re-sighting period is in green. As shown in Figure 17, EN during the red period can influence the pups birthweight. As shown in Figure 21 EN during the orange period can influence pups survival.
Figure 14: Mean initial birthweight (kgs) for male and female pups is located on the lefthand x-axis for the cohorts included in this study. Male pups are in blue and female pups are in red. The missing values are not shown. The mean year values for the Oceanic Niño Index is located on the righthand x-axis for each year included in this study, and the values are shown as a dotted-black line. Here, we highlight the dramatic fluctuations in birthweight seen across years.
Figure 15: Birthweight and length distributed asymmetrically between the two sexes, with males having increased length and weight compared to females.
Figure 16: Correlation of weight and length for all individual sea lions marked in this study. The estimated Pearson’s coefficient of correlation is 0.86 (P-val = 2.2e-16), which suggests a strong positive correlation.
Figure 17: For each individual, the mean ONI value for January through April preceding birth is shown with its corresponding birthweight. Each sea lion male born is in blue (slope = -0.449, P-val = 2.4 e - 0.7) and each female sea lion born is in red (slope = -0.409, P-val = 8.0 e - 13).
Figure 18: The influence of birthweight (kgs) on age reached with female pups in red and male pups in blue. We performed ANOVAs using two linear models, one that included all animals marked during this study (dashed line) and one that excluded those that died during their first year (age ≥ 1) (solid lines). For females, both models were significant but with different slopes. For females, the model including pups that died during their first year had a positive trend (Slope = 0.1024, P-val = 3.108e-07) and the model excluding pups that died during their first year had a negative trend (Slope = -0.1038, P-val = 1.56e-05). For males, the model including pups that died in their first year had a positive trend (Slope = 0.10269, P-val = 2.045e-09), and the model excluding pups that died during their first year had a negative trend and was not significant (Slope = -0.01746, P-val = 0.408). This shows that the survival during the first year is driving much of the trend in birthweight being important. It is likely that the model for females excluding pups that died during their first year is significant due to the number of points included in this analysis.
(a) Survival as a function of birthweight with standard errors for females on the left (red) and males on the right (blue).

(b) Survival as a function of length with standard errors for females on the left (red) and males on the right (blue).

Figure 19: Generalized linear models fit to first year survival data for pups born from 1990-2006.
Figure 20: Generalized linear models fit to first year survival data for pups born from 1990-2006 for females on the left (red) and males on the right (blue).
Figure 21: The proportion of pups never seen again in response to mean ONI value for July of the year they were born to April the following year with the linear model in black (Slope = 0.095, $P$ = val = 0.0075). The color of each circle is a relative index of the ONI mean value for July of that year to April the next year.
Figure 22: For all of the pups that survived, each point is the first time an individual is seen at the natal location in relationship to their cohort, with females in red and males in blue. The size of the circle indicates the total number of individuals in that category. This shows that most individuals are seen at their natal location at a young age and few are re-sighted during their first year of age.
Figure 23: The number of sites visited over time, with one being the natal site, San Miguel Island, two being the natal site and either Farallon Islands or Ano Nuevo, and three being the natal site, Ano Nuevo, and the Farallon Islands. Females are in red on the left and males are in blue on the right.
Figure 24: Birthweight shows no influence on whether individuals visit one site, two sites, or three for both females in red on the left and males in blue on the right.
Figure 25: This figure shows the ages first seen at Ano Nuevo and the maximum age recorded in this study for three types of sea lions that moved, where the size of the circle indicates the total number of individuals in that category. In this figure, the size of the point is the natural log of the number. On the top lefthand side are the sea lions that were only ever recorded on Ano Nuevo, and were never seen at their natal site (San Miguel Island). These animals may be considered early dispersers. In the top righthand side are the individuals that had initially been sighted at their natal site, and then moved to Ano Nuevo but never returned to their natal site (San Miguel Island), which we consider to be late dispersers. This shows that there is a strong relationship between the age that they were first seen at Ano Nuevo and the age when they were last seen at that location, with animals often not being seen after their first movement to Ano Nuevo. On the bottom lefthand side is the individuals that moved to Ano Nuevo and at some point later in their life returned to San Miguel Island, and the final age they were last seen. These animals are considered commuters. This shows us that there are many sea lions who traveled to Ano Nuevo and back to their natal location. They stayed in the study system and reached a high age.
Figure 26: For each re-sight data point across each year at Ano Nuevo, the current age of the animal was recorded.
Figure 27: For each animal that was seen at Ano Nuevo, we calculated the number of years they were seen at Ano Nuevo and San Miguel Island individually, where the size of each circle is the log value of the number of individuals in that category. This shows that there are animals that spend a lot of time at both locations.
Figure 28: Null result for the relationship between the ONI mean during the re-sight period and the proportion of animals that were re-sighted at Ano Nuevo (Slope = 0.0003, P-val = 0.99).
Bibliography


