THESIS

ABUNDANCE, SURVIVAL, AND BREEDING PROBABILITIES OF THE

CRITICALLY ENDANGERED WAVED ALBATROSS

Submitted by

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ABSTRACT

ABUNDANCE, SURVIVAL, AND BREEDING PROBABILITIES OF THE CRITICALLY

ENDANGERED WAVED ALBATROSS

The Galápagos Archipelago is recognized internationally as a unique eco-region, and

many of the species that inhabit these islands can be found nowhere else on Earth. The

Ecuadorian government recognized the value of this ecosystem, and, beginning in 1959, they

designated 97% of the Archipelago as Ecuador's first National Park. The Charles Darwin

Foundation also was founded in 1959 and, since then, the Park Service and the Foundation have

worked towards preserving the Galápagos' unique flora and fauna for future generations. The

waved albatross (*Phoebastria irrorata*) is the largest bird species found in the Galápagos

Archipelago and was recognized as an iconic species early in the Park's history; it is the only

tropical albatross in the world. This species spends the majority of its life foraging at sea and is

an important predator in the Humboldt Current off of the coast of South America. With the

exception of a few pairs, this albatross breeds entirely on the southeastern most island of the

archipelago, Española. Tourists visit Española every year to watch the elaborate courtship

dances of this species, and albatrosses in general have been the foci of legends among sailors for

centuries.

M.P. Harris (1969) began banding waved albatross as early as 1961, marking the

beginning of a long-term monitoring program with a focus on estimating age-specific first-time

breeding, abundance, and survival. This initial effort resulted in the first estimates of abundance

and survival for the waved albatross (Harris 1973). Following these initial estimates, the

population size of the waved albatross has been estimated in 1994 (Douglas 1998), 2001 (Anderson et al. 2002), and 2007 (Anderson et al. 2008). These estimates suggest that the population has been declining since 1994. Motivated by this apparent decline, Awkerman et al. (2006) investigated survival and concluded that survival estimates from 1999-2005 were lower than average survival from 1961-1970 (Harris 1973). Today, the waved albatross is considered critically endangered, with bycatch in artisanal longline fisheries and the increased occurrence of El Niño-Southern Oscillation events thought to be contributing to these observed declines in survival and abundance. Given these observed declines in the waved albatross, the importance of the species in the ecosystem, and its intrinsic value in terms of biodiversity, continued monitoring and analysis efforts to evaluate trends over time, to gauge the effectiveness of management actions, and to assess the status of the species are needed and are the foci of my thesis.

In Chapter 1:, I describe a framework to estimate abundance of wildlife populations, apply this framework to estimate population size of the waved albatross at a major breeding colony on Española Island, and I conclude by providing recommendations for future island-wide surveys of this species. Unbiased abundance estimates play a critical role in the management of species, yet abundance can be difficult to estimate. Through a combination of sampling design and model-based estimation, researchers may be able to achieve an unbiased estimate of population size by formally considering sampling error, a bird's availability for detection, and detection error in data collection protocols and analysis. When these issues are not explicitly addressed, biased estimates and poor inference can result which can lead to inappropriate management actions, especially for sensitive threatened or endangered species. I conducted a study to estimate the abundance of birds at a major waved albatross breeding colony using a

framework that accounts for these issues and provides an estimate of uncertainty. A double

sampling approach with ratio estimation was used on a stratum that included dense coastal

breeding colonies and I used a simple random sample to estimate abundance in a less dense,

inland vegetation stratum. This stratified sampling scheme was designed to minimize variation

caused by the sampling process. I addressed the variability in the availability of breeding birds

using counts of abandoned eggs and by timing these counts to occur late within the egg-laying

phase of the breeding season. Imperfect detection was addressed using a dependent double

observer data collection protocol to provide estimates of detection on each plot. I estimated 4324

breeding pairs (SE 361) for this breeding colony, and this estimate suggests a continued decline

in population size since 1994. These results advocate the need for an island-wide survey to

evaluate whether this trend is consistent across the entire breeding range of this species. Using

estimates from this study in a simulation exercise, I provide an optimal allocation sampling

scheme that could be used island-wide to estimate the entire population size of the waved

albatross.

In Chapter 2:, I revisit the dataset collected by M.P. Harris and the Galápagos National

Park from 1961-1981 as well as a more recent dataset collected by K.P. Huyvaert and colleagues.

I analyzed these datasets in a multistate mark-recapture framework to estimate and compare

estimates of adult survival as well as other important demographic parameters that have not yet

been evaluated for this species.

Bycatch from fisheries and extreme weather events have influenced survival and

breeding probabilities of many pelagic seabird species worldwide. Lower adult survival of the

waved albatross is thought to be associated with bycatch in the small-scale fishery located off of

the coasts of Peru and Ecuador as well as with El Niño-Southern Oscillation events. Previous

efforts to document these threats have not formally considered that a variable proportion of the population does not breed every year or that different life history stages may have different survival rates. Using a multistate mark-recapture framework to analyze Harris' historical and the contemporary datasets, I found that the majority of birds bred for the first time between the ages of 5 and 8, although this result needs to be tempered by the fact that the time series of data were only 10 and 13 years long, respectively. The probability of transitioning from a breeder to a skipped breeder was similar for birds in both datasets and ranged from 0 to 0.574, but the historic dataset showed some evidence that more birds skip breeding during years with higher sea surface temperatures while sea surface temperature had little effect on estimates from the contemporary dataset. Similarly, the probability of transitioning from a skipped breeder to a breeder was best modeled as a constant probability for the historic dataset, but, in the contemporary dataset, this transition probability was positively associated with annual sea surface temperature. These contrasts promote the need for research addressing foraging strategies, prey availability, and other factors that could be driving a bird's decision to transition to a breeding state from a skipped breeding state. I found no discernible difference in average adult survival probabilities between the historic and contemporary datasets. I did find evidence for a negative trend in apparent adult survival for the contemporary dataset. This trend suggests that the relatively recent increase of longline fishing in the foraging zone of waved albatrosses could be an important source of mortality. Mitigation actions to reduce bycatch in this fishery may be critical for the persistence of the critically endangered waved albatross.

The results from Chapter 1 suggest a continued decline in the principal breeding population of the waved albatross since 1994, and Chapter 2 shows indirect evidence that this decline may be linked to higher mortality associated with recent documented increases in small-

scale longline fishing effort off of the coast of South America. Outside of the Galapagos Marine

Reserve where fishing is heavily regulated by the Galapagos National Park Service, little is done

to directly manage artisanal fishing operations off of the coasts of Peru and Ecuador.

Conservation initiatives recognizing the environmental impact of fishing in this zone have been

promoting reduction of seabird bycatch by educating local fishermen. Despite these

conservation efforts, the results from my thesis suggest a continued population decline for this

critically endangered species and additional mitigation may be needed for the persistence of the

waved albatross.

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endangered waved albatross (*Phoebastria irrorata*)

Summary:

Unbiased abundance estimates play a critical role in the management of species, yet

abundance can be difficult to estimate. Through a combination of sampling design and model-

based estimation, researchers may be able to achieve an unbiased estimate of population size by

formally considering sampling error, animal availability, and detection error in data collection

protocols and analysis. When these issues are not explicitly addressed, biased estimates and poor

inference can result which can lead to inappropriate management actions, especially for sensitive

threatened or endangered species. The waved albatross (*Phoebastria irrorata*) is a critically

endangered seabird species for which earlier estimates of abundance suggest a decline in

population size from 1994 to 2007. Yet comparisons among estimates are limited due to

differences in data collection and survey effort. In addition, no measure of uncertainty is

available for these earlier estimates. I conducted a study to estimate abundance of a major

waved albatross breeding colony using a framework that accounts for sampling error, animal

availability, detection error, and provides an estimate of uncertainty. A double sampling

approach with ratio estimation was used on a stratum that contained dense coastal breeding

colonies and simple random sampling was used in a less dense inland vegetation stratum.

Variability in the availability of breeding birds was addressed using counts of abandoned eggs

and the timing of these counts within the breeding season. Detection was addressed using a

dependent double observer data collection protocol to provide estimates of abundance on each

plot. I estimated 4324 breeding pairs (SE 361) for this breeding colony, and this estimate

suggests a continued decline in population size. This one breeding colony comprises a large

portion of the world's waved albatross. With the exception of a few pairs, the entire population

breeds on Española Island. My results advocate the need for an island-wide survey to evaluate

whether this trend is consistent across the entire breeding range of this species. Using estimates

from this study in a simulation exercise, I provide an optimal allocation sampling scheme to

estimate island-wide population size of the waved albatross.

Introduction

Managers often focus on estimating population size when monitoring and managing

wildlife species. In most cases, conducting a census (i.e., a complete count) of a wildlife

population is unrealistic because not all individuals are easily detected and many species often

occupy a spatial extent too large to cover thoroughly. Through a combination of sampling

design and model-based estimation, researchers may be able to achieve an unbiased estimate of

population size by formally considering sampling error, animal availability, and detection error

through appropriate data collection and analysis (Seber 1973, Eberhardt and Thomas 1991,

Borchers 2002, Kendall et al. 2009).

Following Skalski (1994), Pollock et al. (2006) presented a general abundance estimator

addressing these issues:

$$\widehat{N} = \frac{C}{\hat{p}_a \hat{p}_{da} p_{area}}$$
Equation 1-1

where $\widehat{N}$ is an estimate of population size, C is the count of individuals, $\hat{p}_a$ is the probability of

being available, $\hat{p}_{da}$ is the conditional probability of detection given availability, and p_{area} is the

proportion of the total area sampled. Pollock et al. (2006) were motivated to include the $\hat{p}_a$ term

in their approach to estimate dugong (*Dugong dugon*) abundance because dugongs could be

under the water and unavailable for detection by observers on a survey craft.

The $\hat{P}_a$ term is also useful when the population of interest is not closed due to asynchronous behavior, as occurs when the start of the breeding season (e.g., egg-laying) is spread out over a period of weeks or months. In this case, the primary metric of interest may be the number of individuals that bred in, or used, an area during a season rather than an estimate of general abundance (i.e., superpopulation; Williams et al. 2011). Examples of a superpopulation include the number of salmon migrating up a particular river (Schwarz and Arnason 1996), migrating birds passing through a stopover area (Farmer and Durbian 2006), and the number of colonial birds nesting during a relatively protracted breeding season (Williams et al. 2011), all of which include animals that may be differentially available for detection. In my case, the $\hat{P}_a$ term should account for individuals that left the colony prior to the survey and individuals that have yet to arrive at the study area during the time of the survey.

Lack of geographic closure during the survey (i.e., movement of individuals on and off of the survey plot) is a common issue in abundance estimation for species that have large home ranges or for studies that occur over long periods of time. In this case, $\hat{N}$ will be biased high when extrapolating the counts from the portion of the area surveyed to the entire area of interest, because some birds could move to different portions of the sampling frame during the survey. One approach to deal with this problem is to adjust p_{area} to include a buffer zone (e.g., Wilson and Anderson 1985). Several methods exist to determine the size of the buffer zone, but these are usually data intensive and have been criticized as being ad hoc approaches (Ivan et al. 2013b). Another approach is to adjust the count statistic, C, by the proportion of time individuals are on the plot ($\hat{p}_{onplot}$), using auxiliary data such as radio-telemetry (Ivan et al. 2013a) or other information. I extend Skalski's (1994) and Pollock et al.'s (2004) framework (Equation 1-1) to a more general abundance estimator that includes this probability:

$$\hat{N} = \frac{C \hat{p}_{onplot}}{\hat{p}_a \hat{p}_{da} p_{area}} \qquad\qquad \text{Equation 1-2}$$

This general outline should be useful for thinking about many animal abundance estimation problems given the influence each parameter in Equation 1-2 can have on the design, data collection, and/or analysis of count data. When these parameters are not explicitly addressed, biased results and poor inference can lead to inappropriate management recommendations.

Case Study

The waved albatross (*Phoebastria irrorata*) is a critically endangered seabird species for which abundance estimates are important. With the exception of a few breeding pairs, the waved albatross breeds exclusively on Española Island in the Galápagos Archipelago (Harris 1973). In 2000 the waved albatross was considered vulnerable by the International Union for Conservation of Nature (IUCN), and, in 2007, its status was increased to critically endangered, in part due to an apparent population decline since 1994 (IUCN 2013).

Five major breeding colonies (Figure 1-1) are thought to exist on Española Island and include the majority of the waved albatross breeding population; however, a small portion of the population can be found breeding outside of these colonies on any south facing aspect of the island. Individuals have not been located on the north side of the island, probably due to the lack of a sea breeze associated with the Humboldt Current that the birds rely on for takeoff and/or managing heat loads. Whole-island estimates of population size have been attempted three times since the early 1970s. The population size was estimated to be 12000 breeding pairs in 1971 (Harris 1973), between 15581 and 20750 breeding pairs in 1994 (Douglas 1998), and 10475 breeding pairs in 2001 (Anderson et al. 2002). None of these studies explicitly addressed all of

the above sampling considerations. Further, these estimates are not directly comparable with each other as different survey and estimation methods were used. Fortunately, for two of the main breeding colonies (Punta Suárez and Punta Cevallos), where more intensive work and data collection have taken place, these three survey efforts can be parsed and limited comparisons made among them as well as with a fourth study (Anderson et al. 2008). Taken together, these estimates suggest that, in the recent past, the population has declined since 1994, although I again note that many of the sampling issues (e.g., P_{area} and P_{da}) discussed above were not considered explicitly in these studies.

In addition to differences in the survey and estimation methods, several aspects of waved albatross life history may contribute to variability in the abundance estimates. Evidence suggests that egg-laying (Rechten 1986) and hatching success (Anderson and Fortner 1988) in waved albatross are negatively influenced by environmental factors leading to variability in the size of each cohort of fledglings. After fledging, waved albatross are thought to remain at sea for several years (~5-8) until they are ready to breed (Harris 1969, 1973). Nevoux et al. (2010) propose that survival and first-time age-specific breeding probabilities of black-browed albatross (*Thalassarche melanophrys*) can differ among cohorts, adding to the variation in the proportion of the breeding population who are breeding for the first time in a particular breeding season. After successfully breeding, some of the larger albatross species such as the wandering albatross (*Diomedea exulans*) often skip breeding in the following year or years (Weimerskirch 1992). Smaller albatrosses, such as the waved albatross, are generally not as likely to skip breeding, but some individuals still may not breed every year (Rechten 1986). In the Laysan albatross (*Pheobastria immutabilis*), a similar-sized species, transition to a skipped breeder state varied

among years (VanderWerf and Young 2011) suggesting that the number of birds available to be detected could also vary among years.

Major changes in Española's vegetation since Harris' (1973) count have made the logistics of a standardized, island-wide, count challenging. To aid in restoring habitat for the Galápagos giant tortoise (*Geochelone nigra*), feral goats were eradicated from Española in 1978 (Douglas 1998, Anderson et al. 2002, Anderson et al. 2008, Gibbs et al. 2008). The result was a dramatic increase in thick, thorny, and woody vegetation that appeared to be associated with declines in the amount of inland nesting habitat for the waved albatross (Gibbs et al. 2008). Douglas (1998) observed the apparent disappearance of two inland waved albatross colonies within 20 years of the goat eradication. The increase in woody vegetation also makes access to inland colonies by researchers difficult. In May of 2008, 274 albatross were found at or near the Central Colony with an apparent encounter rate of at least one bird every 20 m (Gibbs and Woltz 2010). Gibbs and Woltz (2010) also noted that birds were seen in areas not reported by Harris (1973) or Douglas (1998). These observations suggest that birds could be dispersed widely throughout the interior of the island. This suggestion, coupled with inconsistencies and biases in previous efforts to estimate population size, advocate for a different approach to estimating population size of the waved albatross.

Below, using my general outline for estimating abundance while explicitly addressing the associated sampling issues discussed above (i.e., $\hat{p}_a$, $\hat{p}_{onplot}$, $\hat{p}_{da}$, and p_{area}), I focus on estimation of waved albatross abundance as a case study. I will estimate abundance of the Punta Cevallos colony, test methods to deal with the logistics of an island-wide survey, and, using the estimates from this study, I provide recommendations for obtaining an island-wide estimate of abundance.

Methods

Survey

The main purpose of the study is to obtain a robust estimate of abundance that can be compared to previous counts. A secondary purpose is to assess the amount of effort needed to survey the vegetated part of the island where current estimates of abundance are lacking. For my study, the area to which I wanted to make inference was the 91 ha Punta Cevallos colony located on Española Island, Galápagos Archipelago, Ecuador (1º22'37 S, 89º40'39 W, Figure 1-1). Punta Cevallos is a large and well-studied waved albatross breeding colony (e.g., Harris 1969, Huyvaert and Parker 2010). The count surveys were conducted May 21-25, 2011, and were timed to maximize the number of breeding birds available for detection. Waved albatross have no known predators on the island, and, as a result, respond very little to observers moving through the breeding colony. In addition, individuals nest on the ground, are easily observable, and any movements within the colony during counts are typically small, making the waved albatross an ideal species for abundance estimation. Specifically, I will estimate the number of breeding pairs as well as the number of walkers (i.e., birds with uncertain breeding status – see C- *count* below) using the terms in Equation 1-2. To address each parameter, I used a combination of design-based and model-based strategies.

C – count

The C term is the number of animals that are counted and is strongly influenced by field methods. Previous efforts to estimate waved albatross abundance have either been focused on egg counts (Harris 1973, Douglas 1998) or direct counts of birds (Anderson et al. 2002, Anderson et al. 2008). I primarily focused on direct counts of birds, but counts of abandoned eggs were also important to estimate availability (see $\hat{p}_a$ below). Some birds are known to be

breeders because they are observed incubating an egg. I refer to these birds as incubators. Only 1 parent incubates an egg at a time, while the other parent is most likely foraging at sea. To be consistent with the way previous investigators reported abundance of waved albatross, I report the number of breeding pairs instead of doubling the number of incubators.

Other birds were observed in the colony during counts, but their breeding status was not obvious. I refer to these birds as walkers. Biologically, walkers could be 1 of 3 possibilities. First, a walker could be a pre-breeder who is visiting the colony but not attempting to breed. Second, a walker could be a bird that is skipping breeding and not attempting to breed. Third, a walker could be attempting to breed, but not currently incubating an egg. I counted the number of incubators (C^I) and abandoned eggs (C^A) as well as the number of walkers (C^W).

$\hat{p}_{onplot}$ – probability of movement on and off of plots

I addressed the probability of movement on and off of plots with a design-based strategy centered on the biology of the species. I assumed that no movement occurred on or off of plots (I set $\hat{p}_{onplot} = 1$) because incubation bouts usually last about 1 week, but can last more than 20 days (Harris 1973), and counts on each plot took place quickly (< 0.5 hour; typically < 10 min). I timed surveys to maximize the number of walkers available for detection; surveys were not conducted between 11am and 3pm because walkers often retreat to the sea during this period to escape extreme mid-day heat (K.P. Huyvaert, unpub. data.) In addition, small movements of walkers are easily observed and I was able to keep track of any birds that moved on or off of the plots while conducting surveys.

$\hat{p}_a$ – probability of being available

The life history of the waved albatross affects the availability of incubators to be detected. The egg-laying period can last for several months (late March to late June; Anderson

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et al. 2008) and, because my surveys were conducted in less than a week, some individuals may not be available due to two reasons. First, they attempted to breed but abandoned the nest and left the colony prior to the survey. Second, they did not arrive at the breeding colony until after the survey. I was interested in estimating the total number of breeding pairs using the area throughout the breeding season. I conducted my surveys late within the laying schedule (May 21, 2011 through the May 25, 2011) because egg counts from previous years suggest that a large proportion of the eggs should have been laid prior to this point (Figure 1-2, Anderson et al. 2008). I made the assumption that any bird that was going to breed within that season would have laid an egg by this point. Due to the lack of nest predators on Española, a failed nesting attempt is characterized by an unattended (abandoned) egg. To obtain an estimate of the number of birds who had made an attempt to breed but left the study area, I estimated the number of abandoned eggs. Thus, an estimate of the number of breeding pairs ($\widehat{N}^B$) over the entire breeding season is equal to an estimate of incubators plus an estimate of abandoned eggs.

Availability of walkers is much harder to judge and interpret. Because walkers could represent a mix of biological states (i.e., pre-breeders, breeders, or skipped breeders), and are not sedentary, knowing what proportion is available is difficult to determine. Much more work would be needed to better define the make-up of the walker class as well as their availability. I assumed availability = 1 for walkers, for lack of a better estimate.

$\widehat{p}_{da}$- *probability of detection*

I recognized that, even if a bird or egg was available to be counted, I may not have detected it. Using 2 observers, I applied a dependent double observer methodology (Nichols et al. 2000) that allowed for the estimation of, and correction for, detection probability. The "primary observer" indicated to a "secondary observer" each bird and abandoned egg that the

primary observer detected. The secondary observer also recorded each bird and abandoned egg

that was only detected by the secondary observer. Following the encounter history designation

in Program MARK (White and Burnham 1999), this resulted in detection histories of "1." (if the

primary observer detected an individual) or "01" (if only the secondary observer detected the

individual). I used a closed-capture model developed by Huggins (1989, 1991) as implemented

in Program MARK to estimate $\hat{p}_{da}$ using the data collected following the double observer

protocol. I estimated a common $\hat{p}_{da}$ for all plots in each of the two strata (14 coastal plots and

28 vegetated plots; see p_{area} for additional details) separately for incubators, walkers, and

abandoned eggs.

p_{area} – proportion of the area surveyed

The proportion of the area surveyed generally involves a probabilistic sampling design

(Thompson 2002) of a well-defined area of interest. The entire area surveyed was a 7 km stretch

of coastline extending south and west from Punta Cevallos, on Española. The start point

(1º23'7.22 S, 89º37'24.84) was chosen because not many waved albatross utilized the area north

of this point likely because the sea breeze required for the birds to take off and/or to manage heat

loads is not present here. The westernmost endpoint (1º24'30.57. S, 89º38'46.14) was

determined as the point where observers could no longer walk uninhibited by the vegetation.

Beyond this point, dense vegetation encroached close to the coastline preventing many albatross

from using this area. This area is also essentially the same study area used by Anderson (2008)

allowing for comparisons with this earlier study.

I chose to use a stratified sampling design to sample a portion of this area. Most waved

albatross breed near the coast. However, some albatross breed in the vegetation and I extended

the study area 100 m into the vegetation to better estimate the number of these birds, and to test

methods for surveying other vegetated areas of the island. To do this, I delimited two strata –

coastal and vegetated (Figure 1-3). Due to difficulties in navigating through the vegetation, I

used separate survey designs in each stratum. I used a ratio estimator (see Coastal stratum,

below) to adjust the counts by p_{area} on the coastal (r) stratum (C_r^i) and a simple random

sampling scheme to adjust the counts by p_{area} on the vegetated (v) stratum (C_v^i). Because

abundance on each stratum ($\widehat{N}_r^i$ and $\widehat{N}_v^i$) was estimated independently, an unbiased estimator of

abundance within the entire study area is:

$$\widehat{N}^i = \widehat{N}_r^i + \widehat{N}_v^i$$
Equation 1-3

and an unbiased estimate of the variance around $\widehat{N}^i$ is

$$\widehat{var}(\widehat{N}^i) = \widehat{Var}(\widehat{N}_r^i) + \widehat{Var}(\widehat{N}_v^i).$$
Equation 1-4

I estimated abundance and variance for breeders ($\widehat{N}^B$) and walkers ($\widehat{N}^W$) on each stratum

separately.

Estimating abundance on the coastal stratum

I could walk unobstructed within the coastal stratum counting birds and eggs. I

subdivided the stratum into 100 m plots (68 total plots). I used a ratio estimator (Thompson

(2002) to estimate abundance in the coastal stratum ($\widehat{N}_r^i$). For this estimator, rapid counts (x_r^i)

are conducted on each plot and this count represents an auxiliary variable. Rapid counts were

conducted by a single observer on every plot. The observer counted the number of incubators,

the number of walkers, and the number of abandoned eggs in a single pass. The same observer was used on each plot.

Two observers conducted an intensive count (y_{rq}^i) where q is an individual plot out of a systematically chosen subset (14) of the 68 plots. The intensive counts took place immediately following the rapid count to minimize movement of birds between counts. Observers counted incubators, walkers, and eggs separately during the intensive counts to account for variability among these types when adjusting the intensive counts for detection (see $\hat{p}_{da}$ above).

The ratio estimator assumes a relationship between the auxiliary variable (single observer rapid count) and a known variable of interest (the adjusted intensive count, $\widehat{N}_{rq}^i = \frac{y_{rq}^i}{P_{da}}$). The ratio estimator is:

$$\widehat{N}_r^i = \sum_{r=1}^{U_r} x_r^i \left(\frac{\sum_{q=1}^{u_r} \widehat{N}_{rq}^i}{\sum_{q=1}^{u_r} x_{rq}^i} \right) \qquad \text{Equation 1-5}$$

where U_r is the total number of plots (i.e., 68), u_r is the number of intensive plots (i.e., 14), x_r^i is the rapid count on all plots, x_{rq}^i is the rapid count on plots for which an intensive count was also conducted, and $\widehat{N}_{rq}^i$ represents the estimate of abundance on the intensive plots.

When estimating the variance of $\widehat{N}_r^i$, accounting for the sampling variance around the ratio estimator and the variability of $\widehat{N}_{rq}^i$ are needed to achieve an unbiased estimate of variance of $\widehat{N}_r^i$ (Bowden et al. 2003). Because I estimated $\hat{p}_{da}$ as a common value across all intensive plots, my estimates of $\widehat{N}_{rq}^i$ are not independent. To minimize this bias, I incorporated the estimated covariance between the $\widehat{N}_{rq}^i$ into the variance estimator as outlined by Bowden (2003):

$$\widehat{Var}(\widehat{N}_r^i) = X_r^2 \left[\frac{U_r - u_r}{U_r u_r \bar{x}_{rq}^2} \left(\frac{\sum_{q=1}^{u_r}(\widehat{N}_{rq}^i - Rx_{rq})^2}{u_r - 1} - \frac{\sum_{q=1}^{u_r}\widehat{Var}(\widehat{N}_{rq}^i)}{U_r u_r} \right) \right.$$

$$+ \sum_{q \neq q'}^{u_r} \sum_{q'=1}^{u_r} \frac{\widehat{cov}(\widehat{N}_{rq}^i, \widehat{N}_{rq'}^i)}{u_r(u_r - 1)} \right)$$

<div align="right">Equation 1-6</div>

$$+ \frac{1}{u_r^2 \bar{x}_{rq}^2} \left(\sum_{q=1}^{u_r} \widehat{Var}(\widehat{N}_{rq}^i) + \sum_{q \neq q'}^{u_r} \sum_{q'=1}^{u_r} \frac{\widehat{cov}(\widehat{N}_{rq}^i, \widehat{N}_{rq'}^i)}{u_r^2} \right) \right]$$

where $X_r = \sum_{r=1}^{U_r} x_r^i$ and $R = \frac{\sum_{q=1}^{u_r}\widehat{N}_{rq}^i}{\sum_{q=1}^{ur} x_{rq}^i}$. The distribution of estimates obtained from ratio

estimators are often skewed to the right. Following Bowden (2003) I used a logarithmic

transformation that accurately reflects the true confidence interval around these estimates. I

calculated the confidence intervals around these estimates using:

$$\widehat{N}_r^i \left[\exp \left(\pm z_{1-\alpha/_2} \widehat{CV}(\widehat{N}_r^i) \right) \right]$$

<div align="right">Equation 1-7</div>

Estimating abundance within the vegetation stratum

　　To choose the location of 50 m x 50 m survey plots in the vegetation stratum, I first used

a systematic sampling design (Thompson 2002). I chose a random start point within the first

kilometer of this stratum and then placed 7 plots situated ~1 km apart as I followed the

vegetation line that bordered the coastal stratum. I repeated this systematic sampling 4 separate

times for a total sample size of 28 plots (u_v). From the point on the vegetation line selected by

the systematic sampling scheme above, I chose a random location within the 100 m vegetation

buffer to serve as the northwest corner of the actual plot. I visited each plot once to perform

counts of walkers, incubators, and abandoned eggs. I used a dependent double observer

approach as described above to estimate detection on 15 of these 28 plots. On these 15 plots the primary observer detected all birds resulting in a detection probability of 1. My detection probability estimates were assumed to be the same for the other 13 plots which were surveyed by a single observer.

To calculate the proportion of the area I surveyed and to extrapolate the counts, I used Arcmap 10 (ESRI 2011) to calculate the total area of the vegetation stratum and determined that a total of 276 possible plots (U_v) exist. An unbiased estimator for abundance in the vegetation stratum is:

$$\hat{N}_v^i = U_v \bar{C}_v^i$$

Equation 1-8

where

$$\bar{C}_v^i = \frac{1}{u_v} \sum_{v=1}^{u_v} C_{vj}^i$$

Equation 1-9

and C_{vj}^i is the count from each plot. The variance of $\bar{C}_v^i$ is estimated using:

$$\widehat{Var}(\bar{C}_v^i) = \left(\frac{U_v - u_v}{U_v}\right)\frac{s^2}{u_v}$$

Equation 1-10

where

$$s^2 = \frac{1}{u_v - 1} \sum_{v=1}^{u_v} (C_{vj}^i - \bar{C}_v^i)^2.$$

Equation 1-11

The variance of $\hat{N}_v^i$ is:

$$\widehat{Var}(\hat{N}_v^i) = U_v^2 \widehat{Var}(\bar{C}_v^i).$$

Equation 1-12

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Extension to an Island-wide survey plan

Due to the critically endangered status of the waved albatross and existing uncertainty

about the species' total population size, a formal sampling of the entire island is needed. I used

information from the Punta Cevallos survey to develop an island-wide sampling plan. I used

simulations to assess the amount of effort required to implement such a plan. Simulations were

conducted across 10,000 iterations, and I used the mean estimate of variance across all iterations

as the expected variance for different sampling strategies. I wanted to determine how many plots

would have to be sampled to produce a coefficient of variation (CV) <= 10%. Given that during

the Punta Cevallos survey, surveys for incubators, walkers, and eggs were conducted on the

same plots and that the variance was largest for estimates of incubators, I did not focus on

walkers or eggs for my simulations.

Island-wide sampling frame

I considered all south-facing aspects on Española Island as part of my sampling frame.

Waved albatross have not been located on north-facing aspects in the past. One possible

explanation is that waved albatross rely on a sea breeze out of the southeast produced by the

Humboldt Current to assist with takeoff and to manage heat loads. Thus, I did not consider north

facing aspects as part of my sampling frame. To help account for hypothesized differences in

waved albatross density on the vegetated part of the island, I suggest two additional strata as well

as extending the two strata from my case study for a total of four strata within the sampling

frame (Figure 1-6). First, I propose to use a stratum to include large, historically occupied inland

breeding colonies (i.e., Radar Colony and Central Colony; Figure 1-1Figure 1-1). Second, I

propose inclusion of an inland vegetation stratum to account for areas where waved albatross

could exist but are not thought to be highly concentrated. Third, the coastal stratum from my

case study should be extended to include Punta Suárez and the South Coast breeding colonies. Lastly, the 100 m vegetation stratum outlined in the Punta Cevallos survey should be extended to include the entire south half of the island. I used Arcmap 10 (ESRI 2011) to divide the area of each stratum located in the vegetation into 50 m x 50 m plots and I divided the coastal stratum into 100 m sections containing everything between the coast and the vegetation line. I calculated the number of available plots on each stratum (0).

Sampling plan

During the Punta Cevallos survey, rapid counts on the coastal stratum were conducted rapidly (mean duration: 7 minutes) resulting in an easily obtained auxiliary variable. The coastal stratum had the highest abundance of waved albatross (77% of individuals in my study) in a relatively small area (3% of the total sampling frame). In addition, the ratio estimator worked well during my study (see Results and Discussion); consequently, for the island-wide survey I suggest obtaining a rapid count on all available plots within the coastal stratum as well as a subsample of intensive counts (i.e., double observer counts). Given the relatively low abundance of birds in the two vegetation strata, their total relatively large size (97% of the sampling frame), and difficulty of travel within the vegetation, I did not consider the use of a ratio estimator on these strata due to the difficulty of obtaining an auxiliary count for all available plots. Instead, I suggest using a simple random sampling plan in combination with double observers to account for detection on all vegetated strata. Therefore, the number of double observer plots allocated to each stratum is the only component affecting the precision of the sampling plan in the simulations.

Simulated population

To propose an allocation of sampling effort for future studies, I simulated a population and compared precision of different sample sizes (i.e., sampling effort in terms of double observer plots) for each of the four proposed strata. Because animals are often not randomly distributed across the landscape (e.g., due to resource selection, social interactions, weather), I chose to model a spatial distribution based on my observed counts from the Punta Cevallos survey rather than assume a random distribution. To test hypotheses about the spatial distribution of waved albatross, I fit four variations of the negative binomial distribution using a nonlinear mixed effects model (Proc NLmixed) implemented in SAS (v.9.2, SAS Institute, Cary, North Carolina) to counts on the coastal and the 100 m vegetation strata from my study. To assess the fit of each distribution and to rank them, I used Akaike's Information Criterion adjusted for small sample size (AICc; Burnham and Anderson 2002) and chose the highest ranked distribution of the four to use in simulations of the population.

The first distribution I considered was the basic negative binomial. The basic negative binomial distribution models count data using two parameters: the mean (m), and a scaling parameter (k). The k parameter is a measure of overdispersion or clumping. As overdispersion increases, k goes to 0 and, as overdispersion decreases, k goes to infinity (i.e., albatross are randomly distributed across the habitat and the distribution approaches a Poisson distribution; White and Bennetts 1996). The second distribution I considered was a zero-inflated negative binomial distribution that adjusts the negative binomial with an additional parameter: the probability of obtaining a zero count (π_{zero}). Biologically, this adjustment may be needed when animals are clumped around a certain habitat type and are not found in other areas as may be the case if albatross are found in openings in the vegetation, but not in thick, dense vegetation.

Third, I considered a mixture of a negative binomial distribution and a Poisson distribution

allowing for partial clumping in the spatial distribution of animals (Joe and Zhu 2005). This

mixture model allows for the estimation of the amount of non-clumping in the data (the

probability of being a Poisson distribution, π_{pois}) and the average number of animals on a plot

(the mean and variance parameter of the Poisson distribution, λ). This adjustment allows for

some degree of clustering in an otherwise random distribution of animals across the landscape.

Lastly, I fit a mixture of a zero-inflated negative binomial combined with a Poisson distribution

that contains all five parameters described above. No data were available for the historic stratum

so I assumed that this stratum had the same distribution as the 100 m vegetation stratum. I also

did not have data to inform the inland stratum so I used a Poisson distribution based on the

hypothesis that, for every 10 plots surveyed, 1 bird would be found and that birds are randomly

distributed. This hypothesis was based on experience navigating through the inland strata

(personal observation; D. J. Anderson, personal communication).

Results

Punta Cevallos

Using equation 1-2, I estimated a total of 4324 (SE 361) breeding pairs and 1647 (SE

157) walkers for the Punta Cevallos colony across the entire breeding season (Table 1-2). These

estimates suggest a continued decline in the number of breeding pairs using this colony since

1994 (Figure 1-5). The coastal stratum contained 77% of the breeding pairs and 23% were found

in the vegetation stratum.

Coastal Stratum

The rapid counts on all 69 plots resulted in a total count of 2416 incubating albatross, 108 abandoned eggs, and 1153 walkers. On the intensive plots, detection probabilities were 0.996 for incubators, 0.957 for walkers, and 0.923 for abandoned eggs. I estimated a ratio between rapid counts and adjusted intensive counts of 1.29 for incubators, 1.02 for walkers, and 2.01 for abandoned eggs. I estimated 228.16 (SE 104.70) abandoned eggs suggesting that 93% of the breeding pairs were available to be detected during the time of the survey. I estimated abundance over the entire breeding season to be 3340 (SE 329.08) breeding pairs and 1204 (SE 89.86) walkers in the coastal stratum.

Vegetation Stratum

On the 100 m vegetation stratum, I surveyed 28 plots out of 276 available plots resulting in a proportion of the area surveyed of 0.10. I counted 45 walkers, 80 incubating albatross, and 20 abandoned eggs resulting in a probability of being available of 0.80 for incubators. I observed a detection probability of 1.00 for incubators, walkers, and for abandoned eggs on all 15 plots sampled with a double observer. This resulted in an estimate of 984.08 (SE 148.98) breeding pairs and 442.84 (SE 129.31) for the 100 m vegetation stratum.

Extension to an island-wide survey

When fitting distributions to the results from my study, I found the most parsimonious model fit a standard negative binomial distribution with a mean of 44.93 and a k parameter of 1.01 on the coastal stratum (Table 1-3). When fitting models to the estimates from the vegetation stratum I found that a zero-inflated negative binomial distribution fit slightly better than the standard negative binomial distribution with a ΔAICc of 0.80. The maximum likelihood estimate of the mean was 3.77, $k = 5.26$, and the probability of obtaining a zero was 0.24. For

the proposed island-wide survey, I simulated a breeding population of 7221 birds on the coastal stratum, 2382 on the 100 m vegetation stratum, 1629 on the historical stratum, and 824 on the inland stratum, for a total of 12096 breeding pairs available for detection distributed across the entire island (Figure 1-6).

My simulations showed that the inland stratum had the highest expected variance followed by the 100 m vegetation, historical, and lastly, the coastal stratum (Figure 1-7). The expected variance on the coastal stratum (with the entire rapid count auxiliary variable) was minimal compared to the rest of the estimates. A total sampling effort of 148 rapid counts and 40 additional double observer plots allocated with 3 double observer plots on the coastal, 14 on the 100 m vegetation stratum, 9 on the historical stratum, and 14 double observer plots on the inland vegetation stratum (Figure 1-8), respectively, resulted in an expected CV of 10.3%, approaching the desired 10% CV (Figure 1-9).

Discussion

Punta Cevallos survey

This study is the first to test the utility of a probability-based sampling design, while simultaneously accounting for variability in detection, animal availability, and movement of individuals to estimate waved albatross abundance. While my estimates cannot be extrapolated to the entire island, limited comparisons of breeding pairs can be made between estimates of the coastal stratum and estimates by Harris (1973), Douglas (1997), and Anderson et al. (2002, 2008) from the Punta Cevallos breeding colony. My estimates suggest a continued decline in waved albatross numbers since 1994 (Figure 1-5). Previous estimates accounted for availability by tracking the number of eggs laid in a subsection of the colony across the entire breeding

season. By timing my surveys late within the laying season and by counting abandoned eggs, I was able to account for variable animal availability given a one week survey. In addition, previous estimates did not account for variability in detection. If corrected for detection, the difference between my 2011 estimate and the three previous estimates would be higher, further exacerbating the degree of the apparent decline of the Punta Cevallos breeding colony.

The methods used for conducting counts were designed to be as close as possible to those used by Anderson et al. (2002, 2008), with the addition of a dependent double observer method to account for detection. The dependent double observer approach worked well and detection was high (>0.92) for birds and eggs on plots. These high detection probabilities suggest that previous estimates of waved albatross abundance (Harris 1973, Douglas 1998, Anderson et al. 2002, Anderson et al. 2008) probably had high detection probabilities as well because I mimicked those field protocols. Many methods for estimating detection exist (e.g., mark-recapture, distance sampling), and no one method will work best for all studies examining abundance of wildlife species. Hegg et al. (2012) used an independent double observer approach to estimate detection when counting Yellow-eyed Penguin (*Megadyptes antipodes*) nests. While this method worked well in this application, the method required marking the nest and conducting a separate count by a different observer. This process could be time consuming in dense seabird colonies, but could be useful for applications where the organism of interest is stationary and found in relatively low densities.

On the 100 m vegetation plots I was expecting detection to be lower than on the coastal stratum due to the dense vegetation. However, I found that detection was 1 for incubating birds, walkers, and eggs within the vegetation plots. One possible explanation for the high detection probability is that the small plot size allowed thorough searching. Observers insured that plots

were searched thoroughly by examining survey tracks on a hand held GPS unit as the plot search was being conducted. Another possible explanation is that far fewer birds were found on the vegetation plots than on the coastal plots, and it is easier to overlook a bird when they occur in high densities as they do on the coast.

The plot size of both strata allowed sampling to be conducted in a short time frame and I was able to make the assumption that the probability of being on a plot was 1. Some seabird breeding colonies provide a convenient opportunity to fully meet this assumption because birds are easily detected and are relatively stationary. With other animals, this assumption cannot be made because individuals are not stationary and surveys cannot be conducted quickly enough to restrict movements. With these sampling designs, if movement on and off of plots is not accounted for, the resulting abundance estimate will be biased high (Kendall et al. 2009, McClintock et al. 2009, Ivan et al. 2013a). Recent studies incorporating movements on and off the plot while estimating abundance were conducted on flat-tailed horned lizards (Grant and Doherty 2007) and snowshoe hares (Ivan et al. 2013a) using a combination of radio telemetry and a mark-recapture framework. In these cases, the movement on and off of the plots can be minimized by keeping the time frame as short as possible, while still allowing adequate detection.

I estimated the total number of breeding pairs by correcting counts using the probability of being available (the $\hat{P}_a$ term). I adjusted the counts for the number of breeding pairs that had already left the study area by estimating the number of abandoned eggs. To do this, I made two assumptions. The first was that every bird that was going to breed had already done so. Variation among years and a small number of individuals laying eggs after my counts were conducted (Figure 1-2, Anderson et al. 2008) could lead to bias associated with this assumption.

This bias could have been minimized by conducting surveys even later in the laying period. However, conducting surveys later might increase bias associated with the assumption that the egg remains intact and is not moved or destroyed once abandoned. A study addressing the persistence of abandoned eggs would allow us to solidify this assumption and could help optimize the timing of surveys. Although no predators on the island exist, I believe that eggs may occasionally disappear (e.g., washed away with a big wave) or be moved by temporary adoptive parents (K.P. Huyvaert, personal communication). Overall, I think the bias associated with these two assumptions is minimal and that the egg counts did well in accounting for the superpopulation across time.

Uncertainty in the biological definition of walkers did not allow for such an easy correction of the $\hat{P}_a$ term. If a walker is an individual who has arrived at the colony to relieve their mate of incubation responsibilities, the walker would already have been accounted for in estimating the number of breeding pairs. Another possibility is that a walker could be a bird who is skipping a breeding attempt. Although skipped breeding is not thought to be common in the smaller albatross species such as the waved albatross, skipping does occur at some level (K.P. Huyvaert, unpub. data; Chapter 2). Lastly, a walker could be a pre-breeder who has not attempted to breed. For the Laysan albatross, VanderWerf and Young (2011) suggest that all skipped breeders and most pre-breeders will visit the breeding colony, even in a year they decide not to breed. The application of telemeters to apparent walkers would allow us to better describe their availability patterns and to extend this knowledge to our operational definition of walkers. This information could better inform estimates of the $\hat{P}_a$ term for walkers, and, in turn, improve adjusted estimates of the number of birds using the colony. For these reasons, I report number of walkers and the combined number of albatross "using" the colony as metrics of interest, but I

recognize that the total number of breeding pairs is the most biologically meaningful metric and represents the breeding population in the year the survey was conducted.

My estimates do not account for skipped breeders or pre-breeders that did not attend the colony during the survey. One way to address estimation of these birds is with a robust design mark-recapture study where transition probabilities between breeding states could be estimated (Pollock 1982, Kendall and Bjorkland 2001), but would require the marking of individuals. More specifically, by estimating the proportion of birds that skip breeding in the year of the survey, an adjustment to the $\hat{P}_a$ term of birds detected as incubators could be made (Kendall et al. 2009). Similarly, if chicks were marked and the proportion of the population that was in a pre-breeder state was known, the $\hat{P}_a$ term could be adjusted to account for pre-breeders. These two adjustments would allow me to account for birds that could be detected as walkers and birds that were at sea and unavailable to be detected, thus eliminating the need to count walkers. Additionally, by making these two adjustments, the abundance metric changes from the breeding population to the entire population of waved albatross.

To address P_{area}, I used a stratified design incorporating a 100 m vegetation and a coastal strata. In general, many other designs could be considered to address this parameter and many books have been written on probability-based designs (e.g., Cochran 1977, Thompson 2002). The coastal stratum was easy to navigate and includes most of the breeding pairs, while the 100 m vegetation stratum was very difficult to work in and contains a smaller proportion of the breeding population. For these reasons, attempts to estimate the number of waved albatross breeding in the vegetation since the eradication of feral goats in 1978 have been limited. Douglas (1997) and Anderson et al. (2002, 2008) attempted to count the number of waved albatross at historic breeding colonies in the interior of the island. These counts had no estimates

of precision and one problem encountered was that the boundaries of historic colonies were not well defined and have probably changed since Harris's (1973) counts. Gibbs and Woltz (2010) attempted to count the number of birds using the Central Colony. However, they did not incorporate a probability-based sampling design, instead focusing on birds encountered opportunistically along trails associated with the Galápagos giant tortoise. With the changing vegetation, some colonies may have disappeared (e.g., Douglas 1998) or birds may have dispersed over a wider vegetated area. This is not thought to be the case because albatross are known for their breeding site fidelity (e.g., Bried et al. 2003) and breeding site movements of more than a few meters between years have been reported as uncommon for the waved albatross (Huyvaert 2004). My probabilistic sampling design did well (CV 8%) when estimating abundance of the Punta Cevallos breeding colony and could be extended to an island-wide survey.

Extension to an island-wide survey

A probability-based island-wide sampling design could be a useful tool to assess the status of waved albatross, and, while the logistics of conducting such a survey would be challenging, they are not impossible. Travel between the three main breeding colonies on the island (Punta Cevallos, Punta Suárez, South Coast; Figure 1-1) is difficult and requires the use of a boat. High cliffs carved by the intense swells of the Humboldt Current on the south side of the island and dense vegetation between breeding colonies are mostly responsible for the difficult travel. The easiest access to the South Coast breeding colony is to land a boat on the north side of the island and bushwhack across the island, through the Central Colony, taking advantage of any trails made by tortoises. I suggest using the three main breeding colonies (i.e., Punta Suárez, South Coast, and Punta Cevallos) as starting points for the surveys and traveling to plots in the

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other three strata from the nearest coastal breeding colony. From my study, I was not able to assess the amount of time it requires to travel between the breeding colonies or to travel between plots on the historical and inland strata. However, exploratory treks to the Radar and Central Colonies suggest that such travel is possible (unpub. data). As better estimates of the time required traveling between plots are obtained, an estimate of cost could be built into simulations to allocate effort.

To test the feasibility of an island-wide survey, I explored the effects of different sample sizes (in terms of the number of double observer plots required) on the variance associated with an estimate of abundance where samples (plots) were distributed amongst the four proposed strata. Through simulation I found that the variance associated with the coastal stratum was minimal compared to that of the three strata located within the dense vegetation. This was not surprising as the auxiliary rapid counts in this stratum approached true censuses where every individual is counted. During my study, rapid counts were done by the same experienced observer on all plots, and little difference between the rapid counts and intensive counts existed. If the same protocol were used for the island-wide survey, relatively few intensive plots would be needed to achieve the desired precision in this stratum. However, my surveys were conducted by experienced investigators with close to 40 years of combined waved albatross research experience between the primary and secondary observers. If different observers were used to conduct the rapid counts, or if counts were performed by an inexperienced observer, I suggest allocating more effort to intensive counts on this stratum to account for additional sampling variance caused by the observational process.

Despite having the fewest birds, the inland stratum was allocated the highest number of plots due to its large size. Similarly, the 100 m vegetation stratum received more plots than the

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historical stratum. Because the same distribution of breeding birds was assumed for the 100 m vegetation and historic strata, area was the only factor affecting differences in variance between the two. If an island-wide survey were conducted, a better estimate of the distribution associated with each stratum could be obtained and effort could be allocated more efficiently. Given the difficulties associated with sampling each stratum, I think that these simulations could be a useful tool for future attempts to estimate waved albatross abundance.

Conclusions

Estimating abundance is a common focus of many monitoring plans and studies. Although much has been written on abundance estimation (e.g., Seber 1973, Eberhardt and Thomas 1991, Borchers 2002) and the parameters I discussed are not novel, I have not seen all of these parameters emphasized and represented in a single framework, although I build on work by Skalski (1994) and Pollock (2004). Not all of the above parameters will be needed for each sampling situation, but my general approach allows for an organized thought process and strategy for planning a sampling scheme. Sampling designs are a mixture of field biology and statistical theory (design-based and model-based estimators) and I found my organizational approach useful when designing and implementing an abundance survey for the waved albatross.

With the exception of a few breeding pairs, the critically endangered waved albatross breeds exclusively on Española Island. My results suggest a continued decline in one of this island's three major breeding colonies since 1994. My estimate accounts for a large portion of the breeding population and further conservation and management may be needed for the persistence of this species. Given uncertainty in previous island-wide estimates caused by the difficulty of sampling the vegetation, availability of birds to be detected, movement of birds during the survey period, and detection of birds, I believe that a critical step to direct

conservation and management is to obtain an unbiased and precise estimate of abundance for the

entire species' breeding area. Future island-wide estimates using the strategy developed here

could serve as a baseline for future comparisons and would be useful to assess the effects of

management activities as well as the current status of the species. With threats ranging from

bycatch in fisheries to climate change, this information would be useful for national

governments, conservation organizations, and other stakeholders involved in the conservation of

this species (ACAP 2008, Anderson et al. 2008, IUCN 2013).

Table 1-1. The number of plots available for a sampling scheme to estimate abundance of waved albatross on Española Island, Galápagos Archipelago, Ecuador. I suggest using a stratified sampling design to account for variation caused by different habitats and breeding colonies. I suggest four strata because I expect to find different densities of birds breeding on each stratum. I suggest a coastal stratum, surveying all open areas found on the coast to encompass all large breeding colonies. Observers on the coastal stratum survey the entire area between the coast and the dense vegetation in 100 m stretches. The plot size of all other strata is 50 m x 50 m. I suggest a 100 m stratum as a buffer to the open coastal stratum to account for the majority of birds venturing into the vegetation to breed. I also suggest a historical stratum to account for historical breeding colonies found in the interior of the island. Lastly, I suggest the inclusion of an inland stratum to account for areas were waved albatross could be found, but are not breeding in high densities.

Stratum	Size	Plots available
Coastal	77ha	143
100 m	207ha	828
Historical	153ha	610
Inland	1995ha	7981

Table 1-2. Abundance estimates of the waved albatross from my survey in 2011 of the greater Punta Cevallos colony, Espanola, Galapagos, Ecuador. The counts column provides raw or adjusted counts and the $\hat{N}$ column is the estimated abundance. Abundance estimates are reported for the coastal and 100 m vegetation strata. The last two rows of the table are the total abundance estimates for both breeding pairs and walkers.

	Counts	$\hat{N}$	$\widehat{SE}$	Lower 95% CL	Upper 95% CL
Coastal stratum (22 ha)					
Breeding pairs adjusted for availability	2524	3340.13	329.08	2753.59	4051.60
Breeding pairs unadjusted for availability	2416	3111.97	311.97	2556.83	3787.65
Abandoned eggs	108	228.16	104.70	92.81	560.87
Walkers	1153	1204.43	89.86	1040.58	1394.08
100 m vegetation stratum (69 ha)					
Breeding pairs adjusted for availability	100	984.08	148.98	692.08	1276.09
Breeding pairs unadjusted for availability	80	787.27	136.38	1062.83	511.70
Abandoned eggs	20	196.82	59.96	314.35	617.59
Walkers	45	442.84	129.31	698.42	175.86
Total (91 ha)					
Breeding pairs	2496	4324.21	361.23	3616.21	5032.22
Walkers	1198	1647.27	157.46	1338.64	1955.90

Table 1-3. Model selection results of fitting 4 variations of the negative binomial distribution to counts of waved albatross on the coastal stratum and the vegetation stratum used during the 2011 Punta Cevallos survey. For each model, I provide the Akaike information criterion with small sample size correction (AICc), difference in the AICc compared to the lowest AICc (ΔAICc), the AICc weight (w), and the number of parameters.

Coastal stratum

Model	AICc	ΔAICc	w	# of parameters
Negative binomial	668.80	0.00	0.60	2
Zero inflated negative binomial	671.00	2.20	0.20	3
Zero inflated negative binomial and Poisson	671.70	2.90	0.14	5
Negative binomial and Poisson	673.20	4.40	0.07	4

Vegetation stratum

Model	AICc	ΔAICc	w	# of parameters
Zero inflated negative binomial	127.10	0	0.52	3
Negative binomial	127.90	0.8	0.35	2
Zero inflated negative binomial and Poisson	130.70	3.6	0.09	5
Negative binomial and Poisson	132.10	5	0.04	4
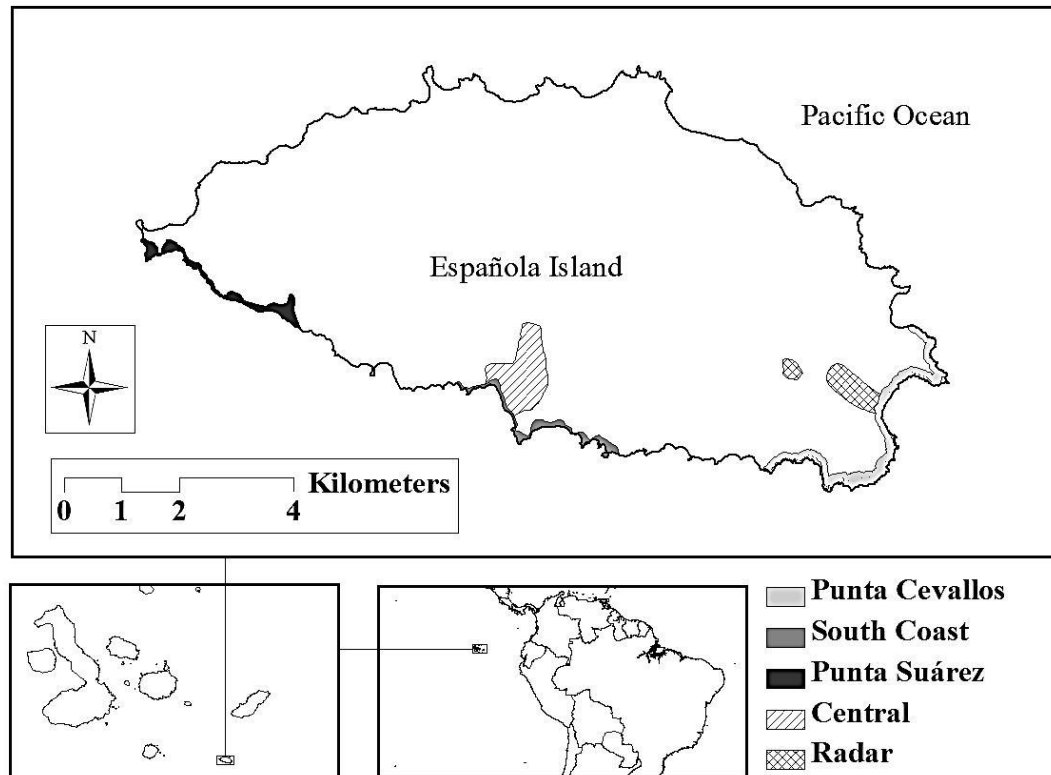
Figure 1-1. Locations of major waved albatross breeding colonies on Española Island, Galápagos Archipelago, Ecuador. Waved

albatross have not been located on north facing aspects of the island in the past.
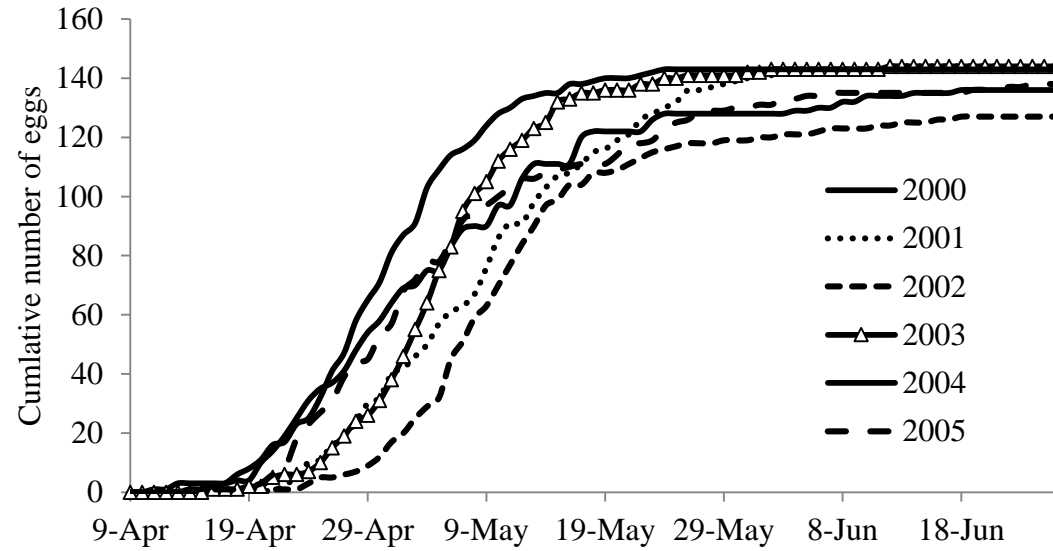
Figure 1-2. Cumulative number of eggs laid by waved albatross in a subsection of the Punta Cevallos breeding colony from 2000

to 2005 on Española Island, Galápagos Archipelago. Data from Anderson et al. (2008).
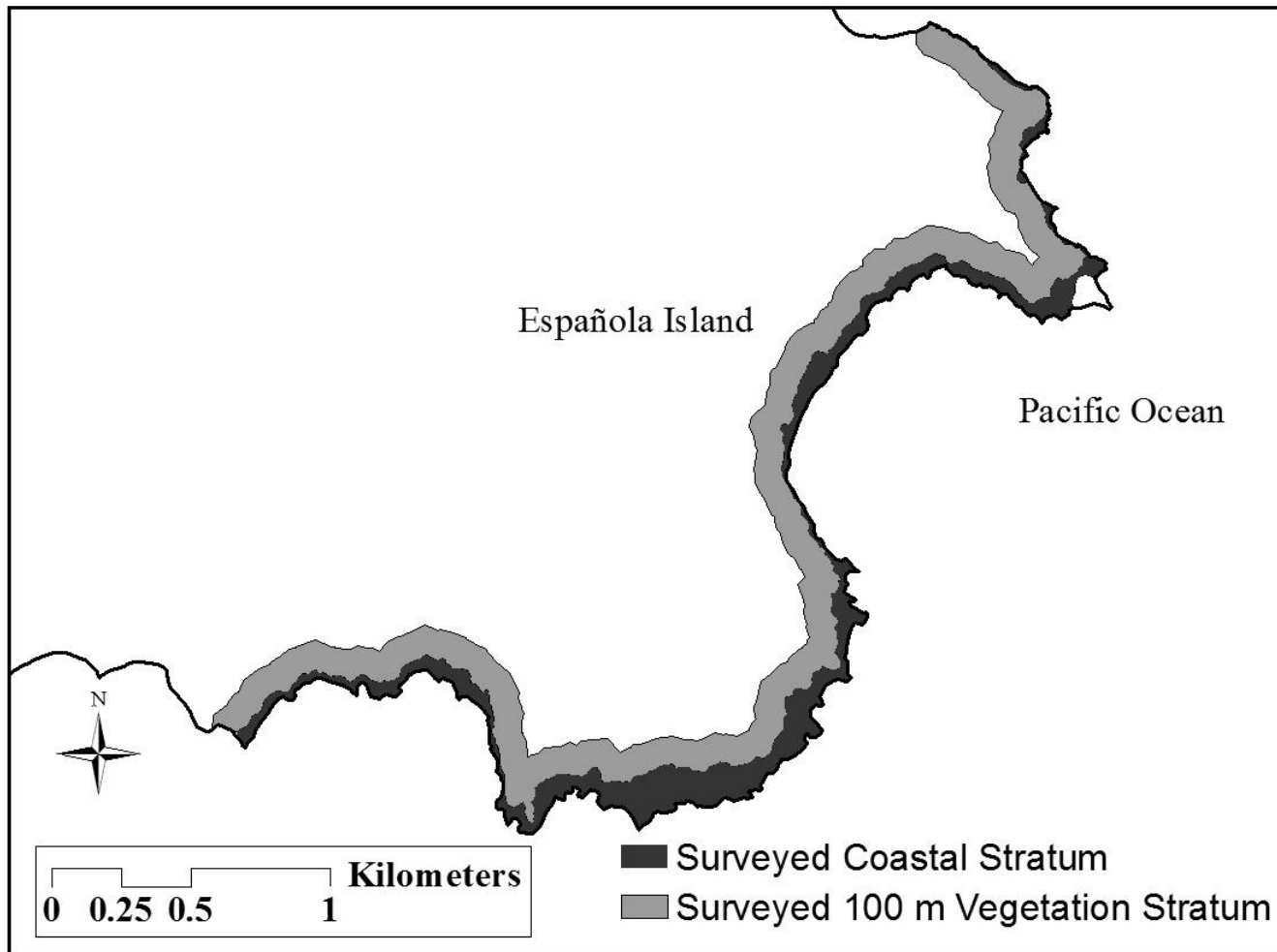
Figure 1-3. The greater Punta Cevallos breeding colony on Española Island, Galápagos Archipelago, Ecuador. The study area consisted of two strata (coastal and 100 m vegetation).
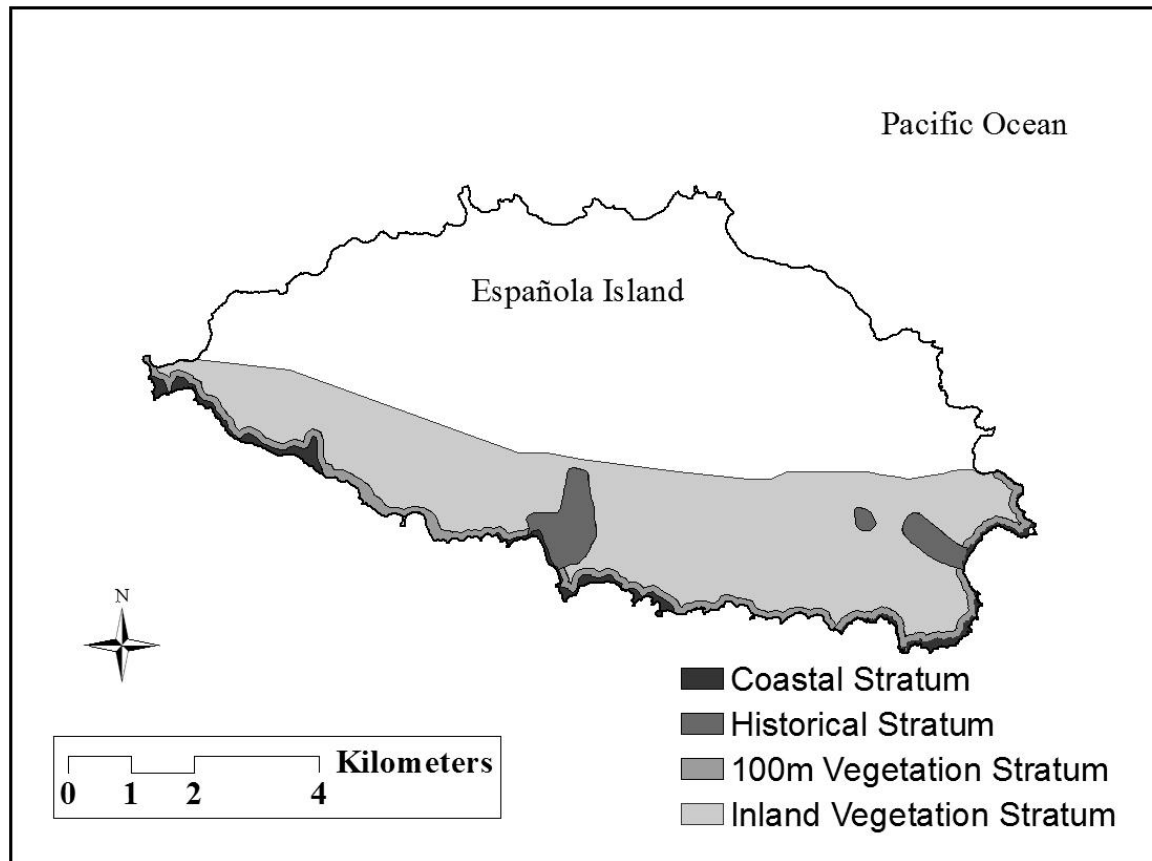
Figure 1-4. Española Island, Galápagos Archipelago, Ecuador delineated into 4 strata for the proposed island-wide survey. The proposed strata include coastal, historical, 100 m vegetation, and inland vegetation. I suggest a coastal stratum to encompass all large breeding colonies. To account for historical breeding colonies found in the interior of the island I suggest the addition of a historical stratum. The purpose of the 100 m vegetation stratum is to serve as a buffer to the open coastal stratum and to account for the

Figure 1-4 (continued) majority of birds venturing into the vegetation to breed. Lastly, I suggest the inclusion of an inland stratum to account for areas were waved albatross could be found, but are not breeding in high densities.
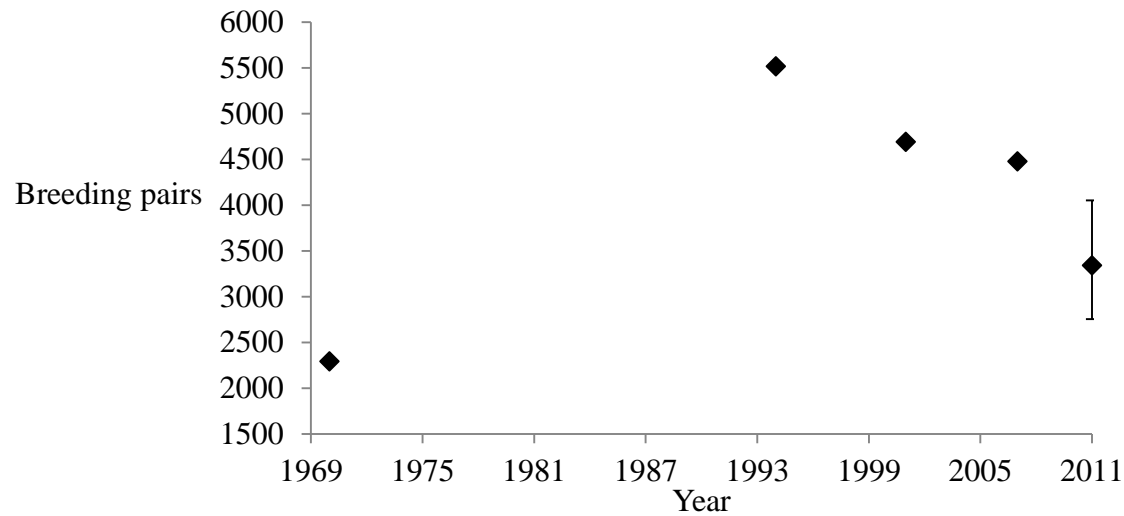
Figure 1-5. Estimated number of breeding pairs of waved albatross on the Punta Cevallos breeding colony for years 1970 (Harris 1973), 1994 (Douglas 1998), 2007 (Anderson et al. 2008), and my survey in 2011. The error bars represent the 95% confidence interval around the 2011 estimate. The previous estimates were unable to estimate variance.
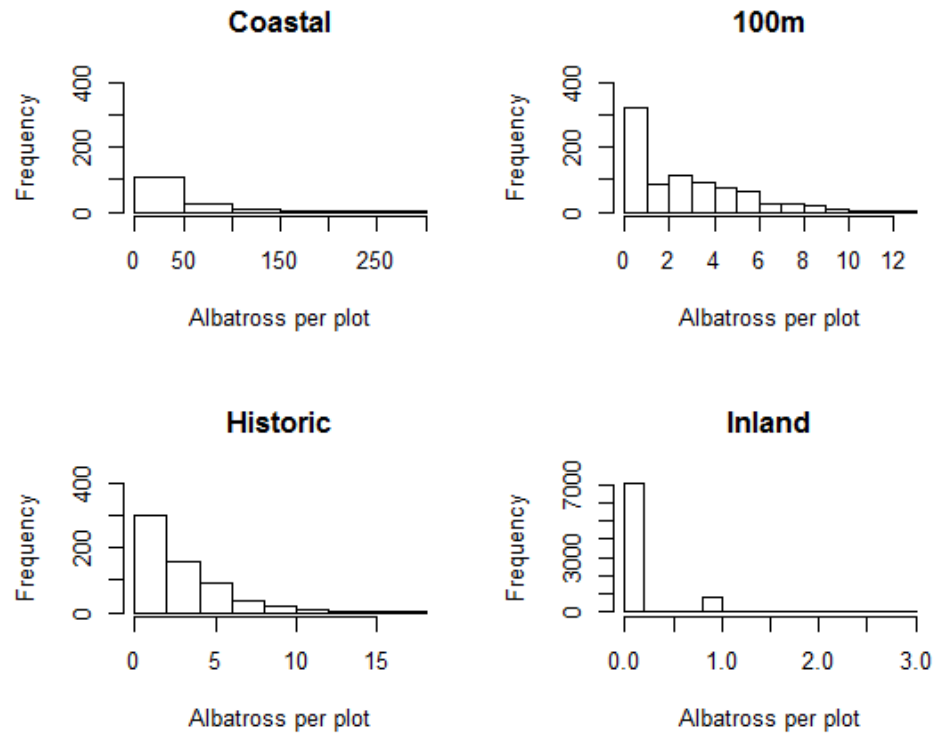
Figure 1-6. Histograms of counts of plots on four strata of a simulated population based off of counts from the Punta Cevallos breeding colony, Española Island, Galapagos Archipelago. The frequency of plots is on the y-axis and the true number of albatross per plot is on the x-axis. Note that the y-axis scale is different for the inland stratum and each x-axis has a different scale due to the variable density of birds on the different strata.
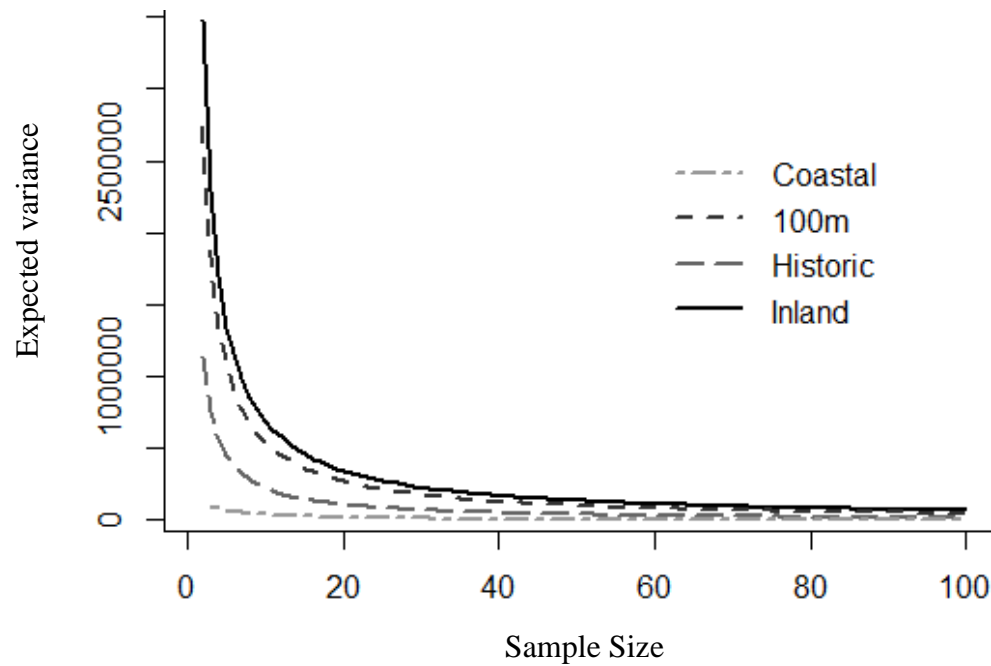
Figure 1-7. Expected variance associated with a simulated population of waved albatross breeding on Española Island, Galápagos Archipelago, consisting of four proposed strata. The simulated population was based off of estimates of abundance from the Punta Cevallos breeding colony. The sample size is the number of double observer plots surveyed on each stratum in addition to the 168 single observer plots conducted on all available plots on the coastal stratum.
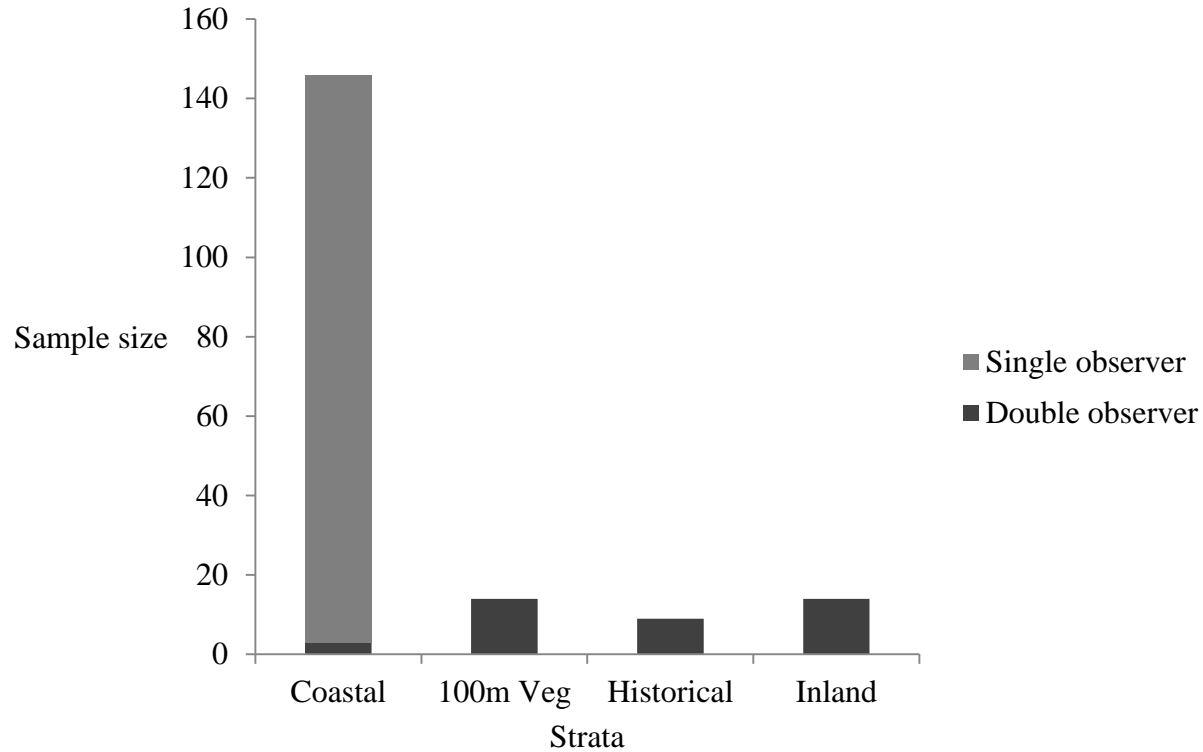
Figure 1-8. The allocation scheme of 143 single observer and 40 double observer plots provided by a simulation exercise intended to provide an island-wide estimate of abundance with a 10% CV on Española Island, Galápagos Archipelago. The coastal stratum was assumed to be surveyed using double sampling scheme consisting of a rapid single observer count on all plots and an intensive double observer count on a subset of available plots. On all other strata, the plots are placed using a simple random sampling scheme and a double observer to account for detection.
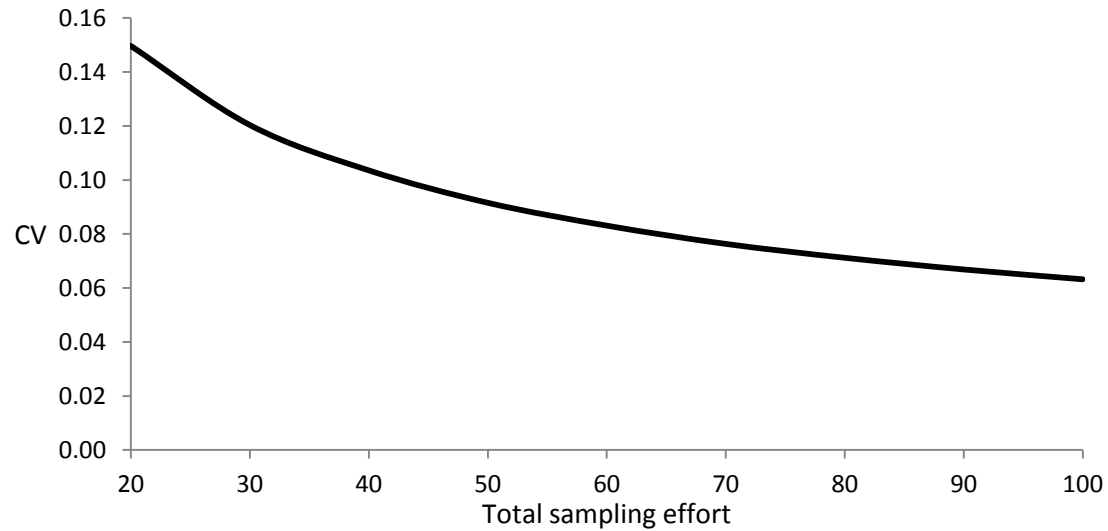
Figure 1-9. The predicted coefficient of variation (CV) for different sample efforts of 20 to 100 double observer plots, optimally allocated in terms of precision, to four strata of a simulated population of waved albatross. The simulated population was based on estimates of abundance from the Punta Cevallos breeding colony of waved albatross, Española Island, Galapagos Archipelago.

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Chapter 2:   Survival and breeding probabilities of the critically endangered waved albatross

(*Phoebastria irrorata*)

Summary:

Bycatch from fisheries and extreme weather events have influenced survival and

breeding probabilities of many pelagic seabird species worldwide. Declines in adult survival of

the critically endangered waved albatross (*Phoebastria irrorata*) are thought to be associated

with bycatch in the small-scale fishery located off of the coasts of Peru and Ecuador as well as El

Niño Southern-Oscillation events. This observation is thought to explain recent declines in

breeding population size. Previous efforts to document this decline have not formally considered

that a variable proportion of the population does not breed every year or that different life history

stages may have different survival rates. I used multistate mark-recapture methods to address

these concerns while estimating apparent pre-breeder survival, first-time age-specific breeding

probabilities, adult survival, and adult breeding probabilities from a historic (1969-1979) and a

contemporary (1999-2012) mark-recapture dataset. The majority of birds bred for the first time

between the ages of 5 and 8 years. The probability of transitioning from a breeder to a skipped

breeder was similar for birds in both datasets and ranged from 0 to 0.574. However, the historic

dataset showed some evidence that more birds are skipping breeding during years with higher

sea surface temperature while sea surface temperature had little effect on estimates from the

contemporary dataset. Similarly, the probability of transitioning from a skipped breeder to a

breeder was best modeled as a constant probability during the time covered by the historic

dataset, but in the contemporary dataset, this transition probability was positively associated with

annual sea surface temperature. This contrast promotes the need for research addressing

foraging strategies, prey availability, and other factors that could be driving a bird's decision to

transition to a breeding state from a skipped breeding state. I found no discernible difference in average survival probabilities between the historic and contemporary datasets. However, I did find evidence for a negative trend in apparent adult survival across the years in the contemporary dataset. This trend suggests that the relatively recent increase of longline fishing in the foraging zone of waved albatrosses could be an important source of mortality. An assessment of the magnitude and impacts of bycatch in this fishery may be critical for the conservation and management of this species.

Introduction

Background

Declines of albatross populations worldwide are garnering increasing attention by the conservation community. The International Union for Conservation of Nature (IUCN) considers 22 of the world's 24 albatross species at risk of extinction to some degree (IUCN 2013), in large part because of mortality via bycatch in fisheries (Phillips 2013), but threats such as the impacts of climate change and pollution may also contribute to declines in albatrosses (Croxall and Gales 1998). The impact of such anthropogenic activities on albatross populations is compounded by their life history, which is characterized by a long lifespan and delayed and irregular breeding patterns. A long lifespan results in numerous opportunities to breed, and, when forced to make a tradeoff between survival or a successful breeding attempt, natural selection will select for investment in survival (Stearns 1992, Pfister 1998). Thus, if anthropogenic threats are leading to relatively lower survival, this may also lead to fewer attempts at reproduction. As a result, albatrosses are thought to comprise the most threatened family of seabirds (Diomedeidae) in the world (Croxall and Gales 1998). Given this outlook, research quantifying the impact anthropogenic threats have on different life history parameters is crucial to best direct management and mitigation actions affecting albatrosses.

Waved albatross life history

With the exception of a small number of pairs, the waved albatross (*Phoebastria irrorata*) breeds exclusively on Española Island, in the Galápagos Archipelago, Ecuador. Adults return to colonies on Española in late-March and early April to breed (Huyvaert et al. 2006), followed by incubation and several months of chick provisioning. Between incubation bouts, adults forage at sea and are susceptible to mortality in artisanal fisheries (Awkerman et al.

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2006). Fledglings typically depart the colony in November or December, remaining at-sea until they reach breeding age (Figure 2-1). Estimates of survival during this pre-breeder stage have never been made for this species, and little is known about waved albatross first-time age-specific breeding probabilities, though this species is thought to breed for the first time between the ages of four and ten (Harris 1969).

After a waved albatross becomes an established breeder, apparent annual adult survival ranges from 0.86 to 0.93 (Anderson et al. 2008) and comparisons with historic estimates suggest that apparent survival has declined since 1971 when average annual adult survival was estimated as 0.95 (Harris 1973). Extrinsic factors that may contribute to observed variation in adult survival in this species include environmental variation (Awkerman et al. 2006; Anderson et al. 2008), variation in fishing effort (Alfaro-Shigueto et al. 2010), as well as factors contributing to their availability to be detected in the colony. In other albatross species, the loss of a mate and the cost of previous breeding attempts (Weimerskirch 1992, Veran and Lebreton 2008, Cubaynes et al. 2011) have been associated with an adult albatross's decision to breed in a given year. If an albatross does not breed, it may not appear at the breeding colony and will be unavailable for detection.

Extrinsic threats

Incidental bycatch of albatross in longline fisheries is the greatest immediate threat to albatrosses. Worldwide, individuals of 21 of the 24 species are known to have been caught and killed on longline hooks (Gales 1998) and incidental bycatch in fisheries is thought to be a primary threat to the waved albatross, contributing to its current listing as critically endangered (IUCN 2010). Anderson (2003) determined that the tropical Peruvian Upwelling off of the coasts of Peru and Ecuador comprises the primary foraging area for breeding waved albatrosses

(Figure 2-2). Small boats with only a few fishermen each constitute the fishing fleets in this zone so this fishery is considered artisanal or small-scale (Alfaro-Shigueto et al. 2011). As a result, quantifying fishing effort for the entire zone is difficult, although data collected from 30 harbors along the coast of Peru show a 54% increase in the number of vessels deployed from 1995 to 2005. In addition, a concomitant shift from less-invasive to more-invasive longlining techniques has occurred, with a 357% increase in the number of vessels deploying longlines from 1995 to 2005 (Alfaro-Shigueto et al. 2010). Despite being considered small-scale, these Peruvian fisheries are estimated to be equivalent to one-third of the global longline swordfish industry (Alfaro-Shigueto et al. 2010), and could have a detrimental impact on marine vertebrates, such as the waved albatross. In addition to incidental bycatch, intentional catch of waved albatross for human consumption has been documented in this fishery (Awkerman et al. 2006).

Stochastic environmental changes such as weather events have been shown to decrease survival and breeding success in several albatross species (Awkerman et al. 2006, Nevoux et al. 2010, Rolland et al. 2010). The waved albatross is the only tropical albatross species making them particularly vulnerable to the impacts of El Niño-Southern Oscillation (ENSO) events (Awkerman et al. 2006, Anderson et al. 2008) due to ENSO-mediated influences on the ecosystem in the foraging zone and breeding colonies (Urban et al. 2000, Waluda et al. 2006). ENSO events are characterized by higher sea surface temperatures, warmer average daily air temperatures, and increased rainfall (NOAA 2012), which could result in higher costs of incubating an egg (Awkerman et al. 2005), a decreased prey base (Rodhouse 2001), and an increase in pathogen vectors (e.g., mosquitoes) on the breeding grounds (Anderson and Fortner 1988). Hypotheses related to climate change predict that the frequency and intensity of ENSO

events will increase in the future (Timmermann et al. 1999). Thus, quantifying the influence of ENSO events on waved albatross survival and breeding probabilities may help direct management in the future.

Analytical approaches

Quantifying the influence of fishing intensity and ENSO events on the demographic parameters of albatrosses can be challenging given sampling constraints. Individuals are most easily observed at colonies during the breeding season although a variable proportion of the population may not breed and is, therefore, unavailable for detection (Kendall et al. 2009). Albatrosses also have delayed breeding with first-time breeding probabilities varying among individuals and species (e.g., Weimerskirch 1992, Nevoux et al. 2010). Individuals who do not breed, either because they have not reached breeding age or are skipping a year, often remain at sea, and are unobservable. If not accounted for, these behaviors can produce biased demographic parameter estimates (Fujiwara and Caswell 2002). One way to address this issue is through the use of multistate mark-recapture modeling (Kendall et al. 1997). These models improve estimation of transitions between life history stages by allowing for unobservable states (Kendall and Nichols 2002).

A standard mark-recapture approach (e.g., Cormack-Jolly-Seber, multistate, Cormack 1964, Jolly 1965, Seber 1965, Brownie et al. 1993) models parameters as fixed effects and the variance associated with a parameter is the combination of both process and sampling variance. Sampling variance is a result of the observation process and has little biological meaning. Process variance, linked to environmental variation, can be separated from sampling variance by modeling parameters as random effects around a biologically meaningful model, a variance components approach (Burnham and White 2002).

Below, I consider multistate mark-recapture modeling of a historical dataset, collected from 1960 to 1981, and a contemporary dataset, collected from 1999 to 2012, of the waved albatross. I estimate pre-breeder survival, adult survival, detection, first-time age-specific breeding probabilities, and adult breeding probabilities using a traditional mark-recapture approach. When the dataset is sufficient to support inclusion of time variation on all parameters in the models (excluding pre-breeder survival and first-time age-specific breeding probabilities, see Methods), I separate process variance from sampling variance using a variance components approach on each parameter. I predict that adult survival and adult breeding probabilities for the waved albatross will be negatively associated with the intensity of ENSO events. Because no reliable measure of fishing effort is available for the entire area where waved albatross forage, I will investigate linear trends in adult survival over time as a possible proxy for fishing effort with the assumption that fishing effort has increased over time (Alfaro-Shigueto et al. 2010). For the waved albatross, I expect bycatch in fisheries and extreme weather events to negatively influence adult survival and adult breeding probabilities to be negatively associated with SST anomalies, which are associated with the occurrence of ENSO events.

Methods

Study area

Española is the oldest and southeastern most island in the Galápagos Archipelago, Ecuador. Waved albatross breed only on southern aspects of the island (Harris 1969), possibly due to the need of a sea breeze produced by the Humboldt Current for takeoff and management of heat loads. The historic dataset (1960-1981) was collected from the Punta Suárez, Radar, and Punta Cevallos breeding colonies (Figure 2-3), while the contemporary dataset (1999-2012) was

collected from a well-studied portion of the Punta Cevallos breeding colony (Subcolonies 1-3 Figure 2-4; Huyvaert and Anderson 2004).

Surveys

Surveys were designed to take place during the breeding season. M.P. Harris began banding waved albatross in 1960 to estimate the age of first-breeding and survival (Harris 1969, 1973). Harris and his teams banded 3528 chicks and 2443 adults for a total of 5971 marked individuals between the years of 1960 and 1981 (Table 2-2). However, between the years of 1960 and 1968, few to no individuals were recaptured. Similarly, no birds were recaptured in 1980. Given that the data were sparse for several years, I only considered years 1969 to 1979 for multistate mark-recapture analyses reported here. I used mark-recapture data for 2285 individually marked chicks and 2446 individually marked adults for my analysis of the historic dataset. Adults and chicks were banded with field-readable plastic and metal bands starting in 1999 at the large colony of Punta Cevallos; a total of 1488 individual chicks and 3423 individual adults were banded between the years of 1999 and 2012 (Table 2-1).

While both chicks and adult birds were marked during both efforts, some birds in the historic dataset were only marked with a metal band and some birds were only marked with a field-readable plastic band. In the contemporary dataset, all birds were marked with both a metal band and a field-readable plastic band. For both efforts, chicks were banded just before fledging (November-December). Observations of adult birds for each dataset were categorized as either "breeders" or "walkers". Birds were known to be breeders if they were observed caring for an egg or a chick. Walkers were birds that were not observed caring for an egg or a chick. Biologically, walkers could belong to 1 of 3 possible categories. First, a walker could be a pre-breeder that is not attempting to breed. Second, a walker could be a skipped breeder not

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attempting to breed. Third, a walker could be a breeder that has not relieved their mate yet. The walker status was recorded, but because their exact biological status was unknown, these observations were not included in the analyses.

Multistate mark-recapture structure

When implementing a multistate mark-recapture model, defining states that accurately reflect the life history stages of the target species is critical (Fujiwara and Caswell 2002). For this analysis, I considered two life history stages (pre-breeder and adult) represented by three biological states (Figure 2-5). Individuals that were marked as chicks were considered in a pre-breeder state (P). Birds that were observed breeding were considered to be in a breeder state (B). Lastly, individuals who were known to be breeders in previous years, but were unavailable to be detected as a breeder in a subsequent year, were classified as being in a skipped breeder state (S). In the case of the waved albatross, breeders are in an observable state, while both skipped breeders and pre-breeders (except for the initial marking of chicks) are in an unobservable state.

I applied a statistical model that best accounts for the transitions to and from each life history stage of the waved albatross (Figure 2-5, Nichols et al. 1992). In this case, the biological parameters of primary interest are survival, first-time breeding probabilities, and the transitions of adults between breeding and skipped breeding states. Specifically, I focused on pre-breeder survival (S^P) and between season (annual) apparent adult survival (S_i^A) for each time interval (i). Given an individual survives time interval i, it can either transition from (ψ) or remain in its current state. I also allowed pre-breeder transition probabilities to vary with age (a). The transition probabilities I considered are ψ_a^{PB}, ψ_i^{BS}, and ψ_i^{SB}. Because I could not detect breeders perfectly, I modeled the detection probability of breeders (p_i) as a function of time. Waved

albatross can transition from a pre-breeder state to a breeder state and between breeder and skipped-breeder states (Figure 2-5).

I applied several constraints in order for the model to make biological sense or for the parameters to be identifiable (Kendall and Nichols 2002). Because pre-breeders and skipped breeders were unobservable, I set the detection probabilities for these states to zero. Biologically, individuals that have transitioned from a pre-breeder state to a breeder state cannot transition back to a pre-breeder state. Similarly, individuals can only become skipped breeders after they have bred at least once. Thus, transitions to a pre-breeder from either a breeder or skipped breeder state were fixed to zero. The last age-specific transition (between age 7 and 8) from a pre-breeder to a breeder was constrained to one in order to estimate survival of pre-breeders (Clobert et al. 1994). The maximum age that I considered was 8 years because the time series was not sufficiently long to consider older ages. Because the pre-breeder state was unobservable, interval-specific pre-breeder survival probabilities were not estimable. Thus, I modeled pre-breeder survival as a constant probability. Lastly, because skipped breeders were unobservable, survival for this state was not uniquely estimable. This parameter was constrained to equal survival of breeders (Kendall and Nichols 2002). I referenced this mutual survival probability as adult survival (S_i^A).

I used sea surface temperature (SST) anomalies (deviation of monthly sea surface temperature from the mean monthly sea surface temperature from the years 1981 to 2010) collected in ENSO zones one and two (NOAA 2012) as an index of the occurrence of ENSO events. As SST increases, so does the intensity of ENSO events (Timmermann et al. 1999). Zones one and two encompass known waved albatross foraging locations during the breeding season (Anderson et al. 2003). I considered the hypothesis that annual SST, averaged from the

first day of April to the last day of March (SST_a), would be negatively associated with annual

adult survival and would be associated with an increased probability of skipping a breeding

attempt in the following breeding season. I also considered that an individual's decision to breed

might be influenced by SST during the non-breeding season which includes the three months

prior to the breeding season (January through March, SST_n), when adult waved albatross are

foraging at sea. Lastly, because life history theory predicts that environmental stressors should

affect measures of reproductive success more than survival in long-lived species (e.g., Pfister

1998), I expected SST_a to have more of an effect on the breeding probabilities of waved albatross

than it would have on adult survival. The historic dataset could not support time variation on

adult survival or adult transition probabilities so these factors were only considered in my

analysis of the contemporary dataset. For the historic dataset, I ran a balanced model set of 36

fixed effects models using the temporal covariates described above. For the contemporary

dataset, I ran 160 fixed effects models consisting of all possible combinations of the temporal

covariates described above, or time. Each parameter was either modeled as time-specific or with

one temporal covariate, but not both. I also considered an additive model for adult survival

incorporating a linear trend and SST_a together.

Because the contemporary dataset could support time variation on S_i^A, ψ_i^{BS} and ψ_i^{SB}, I

used a variance components approach to evaluate if environmental covariates could explain a

portion of the temporal variation observed in these parameters. To do this, I fit random effects

models to the maximum likelihood time-varying parameter estimates in an attempt to explain a

portion of the temporal variation in S_i^A, ψ_i^{BS}, and ψ_i^{SB} (Burnham and White 2002). I modeled

process variance (σ^2) in adult survival (S_i^A) as an intercept-only model, as a linear trend, as a

function of SST_a, and as a linear trend plus SST_a. I modeled process variance in ψ_i^{BS} and ψ_i^{SB} as

an intercept-only model, as a function of SST_a, and as a function of SST_n. To rank the fit of each

model, I used an information-theoretic approach based on a quasi-likelihood AICc adjusted for

overdispersion in the data (QAICc, Burnham and Anderson 2002). To test for overdispersion in

the data, I used a median $\hat{c}$ procedure (Cooch and White 2012). All data analyses were

conducted in Program MARK (White and Burnham 1999). For the traditional fixed effects

approach, I model averaged parameter estimates to account for model selection uncertainty. I

built all possible combinations of biologically meaningful temporal covariates and used

cumulative model weights to rank the fit of each covariate, as described by Doherty et al. (2012).

When using a variance components approach, I used the proportion of the process variance (from

the intercept-only random effects model (σ^2_{int}) explained by the predictor variable (h), which I

calculated as: $\frac{(\sigma^2_{int} - \sigma^2_{int+h})}{\sigma^2_{int}}$, to quantify the utility of each predictor variable.

Results

Historic dataset

Based on the median $\hat{c}$ procedure, I estimated overdispersion as 1.573 (SE 0.019) for the

historic dataset. This dataset could not support time variation in S_i^A, ψ_i^{BS}, or ψ_i^{SB}. Thus, I was

not able to use a variance components approach, such that evidence for each hypothesis was

evaluated using a traditional fixed effects approach. Of the 36 models, the model that allowed

adult survival to vary with SST_a, time variation on detection, age-specific first-time breeding

probabilities, the probability of transitioning from a breeding to a skipped breeding state varying

with SST_a, and the probability of transitioning from a skipped breeding state to a breeding state

as constant over time, held 100% of the QAICc weight (Table 2-2), and I relied solely on this

model for parameter estimates. Pre-breeder survival was modeled as a constant probability between the years 1969 to 1979 and was 0.842 (SE 0.018). Adult survival estimates from this historic dataset ranged from 0.850 (SE 0.040) to 0.945 (SE 0.013) and was negatively associated with SST_a ($\hat{\beta}$ = -0.408, SE 0.149, Figure 2-6). Very few pre-breeders transitioned to a breeding state until age five with the majority (0.606, SE 0.141) of individuals transitioning at age six (Figure 2-7). However, the resolution at age 7 was weak due to the relatively short 10 year time frame. The probability of transitioning from a breeding state to a skipped breeding state ranged from 0.003 (SE 0.04) to 0.223 (SE 0.035) and was positively affected by sea surface temperature averaged across the nonbreeding season ($\hat{\beta}$ = 2.451, SE 0.917, Figure 2-8). The probability of transitioning from a skipped breeder to a breeder was estimated as a constant probability of 0.054 (SE 0.026). Detection ranged from 0.038 (SE 0.006) in 1978 to 0.715 (SE 0.026) in 1973 (Table 2-4).

Contemporary dataset

Based on the median $\hat{c}$ procedure, I estimated overdispersion as 2.045 (SE 0.003) for the contemporary dataset. This dataset did support time variation on S_i^A, ψ_i^{BS}, and ψ_i^{SB}. Of the 160 models, 10 had a QAICc weight greater than 0.010 (Table 2-5). Model-averaged constant pre-breeder survival was 0.847 (SE 0.013). Detection ranged from 0.464 to 0.971 (Table 2-6). First-time age-specific breeding probabilities increased with age (Figure 2-9). Model-averaged estimates of apparent adult survival ranged from 0.927 to 0.953 (Figure 2-10). Cumulative model weights for temporal covariates suggested that they had little explanatory ability; however of the variables I evaluated, a linear trend across time had the most cumulative weight (Table 2-7). The model-averaged estimates of the probability of transitioning to a skipped breeder from a breeder ranged from 0.014 to 0.654 (Figure 2-11). Cumulative model weights suggested that

time variation (Table 2-7) was important when modeling this parameter. The model-averaged estimates of the probability of transitioning to a breeding state from a skipped breeding state ranged from 0.118 (SE 0.148) to 0.613 (SE 0.181, Figure 2-12). A constant term had the most cumulative model weight for this transition (Table 2-7).

Due to the large amount of variability in the model-averaged estimates from the fixed effects approach (Figures 2-10, 2-11, and 2-12), I investigated hypotheses related to adult survival and adult breeding probabilities with a variance components approach using temporal covariates to explain temporal variation (Table 2-8). In all cases the random effects models were improvements over the most general fixed effects model in terms of QAICc (Table 2-9). Each random effects model addressing adult survival contained a portion of the QAICc weight. Of the predictor variables of interest influencing adult survival, a negative trend across time ($\hat{\beta}$= -0.006, SE 0.003) explained the most process variance (22%). The estimates of adult survival from this model ranged from 0.895 (SE 0.020) to 1.0 (Figure 2-13). A negative trend across time plus SST_a as an additive effect (Figure 2-14) explained 9% of the process variance. Temporal process variation in the probability of transitioning from a breeder to a skipped breeder was best modeled as an intercept-only random effect around a constant mean transition probability of 0.202 (SE 0.067, Table 2-9). The estimates for this probability ranged from 0 to 0.574 (SE 0.039, Figure 2-15). Of the predictor variables of interest, none explained a portion of the process variance beyond the intercept-only model (Table 2-8). Variation in the probability of returning to a breeder from a skipped breeder was best modeled as an intercept-only random effect around a constant transition probability of 0.439 (SE 0.098) given its QAICc value (Table 2-9). However, the predictor variable SST_a was associated with a higher probability of returning to a breeder from a skipped breeder state ($\hat{\beta}$ = 0.753, SE 0.244), and explained 55% of the process variance

from the intercept-only model (Table 2-8). Estimates from this model ranged from 0 to 0.880 (SE 0.178, Figure 2-16).

Discussion

Worldwide, the conservation of albatrosses is of concern because of extrinsic threats and the influence of these threats on vital rates. This study provided a unique opportunity to compare breeding and survival probabilities of pre-breeders and adults between a historic dataset (1969 to 1979) and a contemporary dataset (1999 to 2012). Estimates of first-time age-specific breeding probabilities exhibited the same pattern for both datasets, but the point estimates suggest that relatively fewer birds transition to a breeding state at ages five and six in the contemporary dataset. This could be due to differences in the type and amount of prey available while foraging at sea now compared to 40 years earlier. If less prey is available or if the quality of prey is not as good, it may take longer for birds to reach sexual maturity (e.g., Vincenzi et al. 2013). Similarly, mean pre-breeder survival estimates were almost identical for the historic dataset (0.842, SE 0.015) and the contemporary dataset (0.843, SE 0.013). The estimates for mean adult survival showed no apparent difference between the historic (0.916, SE 0.018) and more recent years (0.934, SE 0.011). From the variance components approach, I detected evidence of a negative trend in adult survival for the contemporary dataset (Figure 2-13), suggesting a recent decrease in adult survival. This recent decrease could be due to increases in small-scale longline fishing effort in the waved albatross's foraging zone (Alfaro-Shigueto et al. 2010).

The point estimates for the mean probability of transitioning from a breeder to a skipped breeder were lower in the historic dataset (0.050, SE 0.017) than the contemporary dataset (0.145, SE 0.057); however, the confidence intervals for the two estimates did overlap. Similarly, the mean probability for transitioning from a skipped breeder to a breeder was lower

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in the historic dataset (0.054, SE 0.026) than in the contemporary dataset (0.457, SE 0.085). One possible explanation for the observed differences in the adult breeding probabilities is that data collected in the later years of the historic dataset included very little resighting information; these years had generally lower detection probabilities. The combination of this observation and the short time frame of the historic dataset could also translate to poorly estimated probabilities. For this reason, I ran an a posteriori model that considered no transitions to or from the breeding state (i.e., no temporary emigration), with all other parameters estimated as a constant probability. For both datasets, this model contained none of the QAICc weight when compared to models that considered variation in these transition probabilities with all other parameters held constant. Alternatively, if a bird decided to breed but arrived at the colony before or after the surveys, it may have been considered a skipped breeder when in fact it was a breeder. Therefore, any differences in the length of the survey period or data collection methods between the two datasets could have resulted in the observed difference in these adult breeding parameters.

Several additional differences between the historic and contemporary datasets exist in terms of the data collection as well as study design and these need to be acknowledged. Most of the data collection for the historic dataset took place at the Punta Suárez breeding colony while the contemporary dataset was collected from a well-studied portion of the Punta Cevallos colony. Given that 99% of the world's waved albatross breed on Española Island and that these two colonies are at most only 10 km apart, I believe that any bias associated with comparing the two different colonies is minimal. Nevertheless, the data collection process was much more intensive for the contemporary dataset than the historic. The specifics of the data collection process for the historic dataset are unknown, but generally resulted in an individual being marked and/or resighted only once or twice within a given year. Alternatively, the contemporary dataset

includes multiple observations of individuals within a given year. The data collection for this

dataset began with a behavioral study in Subcolony 1 (Figure 2-4) that resulted in individuals

being resighted many times over several months. In 2004, banding efforts were expanded to

include birds in Subcolonies 2 and 3 (Figure 2-4); an additional 1436 individuals were banded in

this expansion and resights from 2005 to 2012 took place over a week to ten days. This

expansion in banding effort may have caused some bias in the estimated demographic

parameters for this dataset due to different sampling frames, but, given the high site fidelity of

the waved albatross, this bias is likely to be minimal.

Extrinsic threats

Bycatch

Concern has grown about albatross bycatch rates in the last 15 years (e.g., Croxall and

Gales 1998, Gales 1998, Rolland et al. 2010). Examples of conservation and mitigation actions

to decrease this bycatch include seasonal and area closures, reducing the number of longlines,

submerging hooks to depths inaccessible to albatross, increasing the rate at which the hooks are

submerged to deter boat-following behavior, and setting hooks at night (Bull 2007). While these

methods are effective, they are often targeted at large-scale industrial fisheries. The small-scale

fishery located in the Peruvian upwelling zone has caused recent concern because of bycatch of

seabirds, sea turtles, marine mammals, and other pelagic megafauna, including the waved

albatross (Awkerman et al. 2006, Mangel et al. 2010, Alfaro-Shigueto et al. 2011). In addition to

bycatch, intentional catch of seabirds and sea turtles for human consumption have been

documented in this fishery (Awkerman et al. 2006, Alfaro-Shigueto et al. 2011). This zone is the

main foraging area for the waved albatross during the breeding season (Anderson et al. 2003)

and take, either intentional or from bycatch, may be driving the negative trend in adult survival I

observed in the contemporary dataset. My study, combined with recent studies on bycatch in the Peruvian Upwelling, suggest that this small-scale fishery could be a major sink for some marine vertebrates, including the waved albatross. This area has the highest documented bycatch rate for sea turtles in the world and is likely one of the world's principal areas of concern for cetacean bycatch (Wallace et al. 2010). Minimizing the take from this fishery may be critical to the persistence of not only the critically endangered waved albatross but other marine vertebrates as well.

My results show that pre-breeder survival estimates were similar for the historic and contemporary datasets suggesting that the recent increase in longline fishing may not be dramatically affecting this life history stage. In other albatross species, pre-breeders exhibit different strategies for foraging at sea and these strategies may be linked to survival. In wandering albatross, pre-breeders and adult females forage in similar zones and may be more susceptible to being caught in longline fisheries than adult males (Weimerskirch and Jouventin 1987). Little is known about waved albatross foraging zones for pre-breeders or adults outside of the breeding season. Awkerman et al. (2006, 2007) suggest that adult males are more susceptible to bycatch, while immature individuals and adult females are captured at a lower rate for waved albatross. This observation combined with the similar estimates of pre-breeder survival despite the recent increase in long line fishing, may suggest that females and pre-breeders are foraging in zones less susceptible to longline fishing than adult males. Phillips et al. (2005) suggest that foraging strategies are influenced by breeding status, success of breeding attempts, and sex in black-browed albatross. This information could be gained for the waved albatross through the use of satellite transmitters (e.g., Weimerskirch et al. 1993) and/or geolocators (e.g., Mackley et al. 2010), and could contribute to a better understanding of the

interactions between waved albatross and fishing operations throughout the species' foraging zone off of the coast of South America. This information would be useful to help direct conservation and management within this fishery.

El Niño-Southern Oscillation events

In addition to incidental bycatch and intentional catch in fisheries, previous work has shown evidence of lower adult survival during ENSO events for the waved albatross (Anderson et al. 2008). Given this, I predicted that ENSO events modeled as a function of SST would have a greater impact on adult breeding probabilities than on adult survival. However, some evidence exists suggesting that SST_a was negatively associated with adult survival in both the historic and contemporary datasets. In the contemporary dataset, evidence was strongest when SST_a was modeled as an additive effect compared to a trend over time (Figure 2-14). The influence of SST on adult breeding probabilities was less consistent for the two datasets. As expected, in the historic dataset adults were more likely to skip breeding attempts in years with high SST_n and individuals were less likely to return to a breeding state from a skipped breeding state in years with high SST_n. In contrast, the contemporary dataset yielded little evidence that the probability of transitioning from a breeder to a skipped breeder was associated with either SST_a or SST_n and the probability of transitioning from a skipped breeder to a breeder was positively affected by SST_a. Cubaynes (2011) suggests that nonbreeding red-footed boobies (*Sula sula*) may benefit from lower competition at the breeding colony during ENSO years. If waved albatrosses are attempting to breed during ENSO years but abandoning their nest, this lower competition hypothesis may explain why more birds transition to a breeding state from a skipped breeding state in years with higher SST_a. If this is this case, a survey period that lasted throughout the breeding season may allow detection of birds transitioning to a breeder state and replacing birds

that breed and abandon earlier in the season. The continued marking of chicks over a longer time frame may lead to better evaluation of hypotheses relating SST and bycatch to the life history traits of the waved albatross. Pardo et al. (2012) showed that younger and older black-browed albatross are much more susceptible to environmental variation than middle-aged individuals. The first cohort of waved albatross chicks in the contemporary dataset are just now entering the middle-aged class (10 to 30 years) defined by Pardo et al. (2012) and a similar analysis in the future may provide useful information for future conservation and management of this species.

Other factors

Worldwide, bycatch in fisheries is considered to be the greatest threat to albatross populations (Croxall and Gales 1998); however, other factors may also be contributing to lower population numbers, including the waved albatross. Several recent studies describe the presence of novel pathogens in naïve populations of other seabirds in Galápagos including *Toxoplasma gondii* in the critically endangered Galápagos penguin (Deem et al. 2010) and Haemoproteus spp. blood parasites in several seabirds (Levin et al. 2011). Also, Weimerskirch (2004) suggested that outbreaks of avian cholera have resulted in declining trends in the large yellow-nosed albatross population on Amsterdam Island; this disease may be an important threat for other albatross species.

For the waved albatross, habitat loss from encroachment of dense vegetation that has grown since the eradication of goats in 1978 may also be important to consider. Douglas (1998) observed the apparent disappearance of two breeding colonies on Española since Harris' (1973) surveys and, in 2011, no birds were observed breeding in the interior of the island where the Radar Colony had been described in the past (P.A. Street and K.P. Huyvaert; unpublished data).

If nesting space is a limiting factor for this species then continued encroachment by vegetation may further impact population growth via reduced reproduction and concomitant declines in recruitment.

Alheit and Niquen (2004) documented regime changes in the Humboldt Current where the waved albatross forages. More specifically, the Humboldt Current was characterized by sardine dominance throughout the majority of the years when the historic dataset was collected, while it was characterized by an anchovy regime during the years of the contemporary dataset. These changes could also be contributing to the negative trend in survival observed in the contemporary dataset of the waved albatross if albatross prey species mirror the patterns shown for anchovies and sardines. Nonetheless and despite these other potential sources of mortality, I believe bycatch in fisheries is the leading cause of the observed negative trend in adult survival in the contemporary dataset due to the directly observed mortality of albatrosses in the form of band recoveries from fishermen (Awkerman et al. 2006) coupled with the drastic increase in the number of vessels deploying longlines since 1995 (Alfaro-Shigueto et al. 2010).

Assumptions

Because the waved albatross has a protracted life history lasting several decades, some ages and stages of birds are not observable in the colony during the breeding seasons when the data analyzed here were collected. Three major assumptions were made in order to address these unobservable states. First, pre-breeder survival and first-time age-specific breeding probabilities were assumed to be the same across cohorts and over time. Chicks have been marked every year since 2008. If this monitoring effort continues, future research will be able to address hypotheses relating time, cohort-specific survival, and transition probabilities to ENSO events and bycatch (Cubaynes et al. 2011). Second, pre-breeders who have not bred by age seven were

assumed to breed at age eight with a probability of 1. Age eight was the oldest age that these

datasets could support due to the short length of the time series. In reality, some individuals

might choose to start breeding at a later age. Continued monitoring efforts will be able to

address this concern as additional years are added to the time series. Finally, survival of skipped

breeders is assumed to be the same as survival of breeders. If this assumption is true, skipping a

breeding attempt has no benefit in terms of fitness; I expect this assumption may be false. The

use of additional information such as GPS transmitters or radio telemetry could help to reduce

any bias associated with all three assumptions by making these unobservable states observable

(Kendall et al. 2009). Despite limitations imposed by these assumptions, my results provide

useful information that was not previously known for this species.

Conclusions

I was able to expand the current knowledge of waved albatross by revisiting a historic

and contemporary dataset and applying the same analytical methods and assumptions to both.

Using multistate mark-recapture models, I simultaneously tested hypotheses relating ENSO

events and temporal trends, as a proxy for bycatch in small-scale fisheries, to adult survival.

Estimates of adult breeding probabilities and pre-breeder survival were obtained for the first time

in this species by incorporating unobservable states into this multistate mark-recapture

framework.

My results suggest that take, either from bycatch or intentional catch, may be

contributing to the recent decline in adult survival of the waved albatross. Because this species

is long-lived, any decrease in adult survival will result in population-level impacts that may

eventually result in extinction. The small-scale fishery that overlaps to a large extent with

known waved albatross foraging grounds is a major economic and food source for people in this

region (Alfaro-Shigueto et al. 2010); management may best be directed at promoting the sustainability of this fishery for continued economic benefits while reducing waved albatross mortality. Alfaro-Shigueto et al. (2011) suggest that one way to accomplish this goal is through initiatives that recognize and work towards minimizing the environmental impacts, including non-target species catch, of fishing in this zone. Such community-based conservation efforts could include promoting education of local fisherman and seabird bycatch mitigation. For example, for vessels less than 35 feet in length, ACAP (2011) recommends using a single scare line, seasonal closures, and retaining used baits as possible bycatch mitigation. While my results suggest a recent decline in adult survival may be due to increased fishing effort, the results do not inform where or how to concentrate mitigation efforts. Future research focusing on identifying critical foraging areas could help to best direct bycatch mitigation efforts. Continued monitoring of the waved albatross at Española Island focusing on the estimation of demographic parameters may allow us to address the effectiveness of these efforts by quantifying direct changes in vital rates. As more information is gained, mitigation can be better directed and may be critical for the persistence of the waved albatross.

Table 2-1. Number of waved albatross banded and recaptured between the years 1999 and 2012 on the Punta Cevallos breeding colony, Española Island, Galápagos Archipelago, Ecuador. Combined banding effort is the sum of the number of chicks banded and the number of adults banded.

Year	Number chicks banded	Number adults banded	Number of individuals recaptured
1999		136	0
2000	30	99	66
2001	199	153	149
2002	121	28	111
2003		93	237
2004	253	1183	284
2005		294	705
2006		392	914
2007		427	1287
2008	199	215	1137
2009	313	88	848
2010	174	90	638
2011	199	131	876
2012		94	575
totals	1488	3423	7827
combined banding effort		4911	

Table 2-2. Number of waved albatross banded and recaptured between the years 1960 and 1981 on Española Island, Galápagos Archipelago. Combined banding effort is the sum of the number of chicks banded and the number of adults banded. Ninety-six percent (96%)of the birds were banded in the Punta Suárez breeding colony while the other 4% where banded at the Punta Cevallos and Radar breeding colonies.

Year	Number chicks banded	Number adults banded	Number of individuals recaptured
1960		31	0
1961	519	483	11
1962	109		2
1963	99	5	7
1964	100		2
1965			4
1966	231	78	82
1967		5	4
1968		86	0
1969	50	76	36
1970	709	662	572
1971	635	246	296
1972	183	373	609
1973	200	166	847
1974		49	606
1975		52	674
1976		1	101
1977	499	56	366
1978			57
1979	9	43	364
1980	185		0
1981		31	116
totals	3528	2443	4756
combined banding effort		5971	

Table 2-3. Multistate mark-recapture model selection results from a traditional fixed effects modeling approach of waved albatross breeding on Española Island, Galápagos Archipelago between the years 1969 to 1979. Each model provides a maximum likelihood parameter estimate of apparent pre-breeder survival (S^P), apparent adult survival (S^A), probability of detection (p), first-time age-specific breeding probabilities (ψ^{PB}), probability of transitioning from a breeding state to a skipped breeding state (ψ^{BS}), and the probability of transitioning from a skipped breeding state to a breeding state. Models are ranked based on their quasi-Akaike Information Criterion with small sample size correction (QAICc). Annual sea surface temperature (SST_a) and sea surface temperature during the nonbreeding season (SST_n) were modeled as temporal covariates. A period (.) represents a constant probability. Models were ranked using the QAICc difference (ΔQAICc) between each model and the most parsimonious model in terms of precision and the number of parameters (k). The QAIC value for the highest ranked model was 11323.325.

Model	Δ QAICc	QAICc Weights	k
S^P (.)S^A (SST$_a$) p(time) ψ^{PB} (age) ψ^{BS} (SST$_n$) ψ^{SB} (.)	0.000	1	24
S^P (.)S^A (SST$_a$) p(time) ψ^{PB} (age) ψ^{BS} (SST$_a$) ψ^{SB} (SST$_n$)	28.647	0	23
S^P (.)S^A (SST$_a$) p(time) ψ^{PB} (age) ψ^{BS} (SST$_a$) ψ^{SB} (.)	28.715	0	24
S^P (.)S^A (SST$_a$) p(time) ψ^{PB} (age) ψ^{BS} (.)ψ^{SB} (SST$_a$)	29.177	0	23
S^P (.)S^A (SST$_a$) p(time) ψ^{PB} (age) ψ^{BS} (.)ψ^{SB}(SST$_n$)	30.503	0	23
S^P (.)S^A (SST$_a$) p(time) ψ^{PB} (age) ψ^{BS} (SST$_a$) ψ^{SB} (SST$_a$)	30.694	0	23
S^P (.)S^A (.) p(time) ψ^{PB} (age) ψ^{BS} (SST$_a$) ψ^{SB} (.)	37.820	0	24
S^P (.)S^A (.) p(time) ψ^{PB} (age) ψ^{BS} (SST$_a$) ψ^{SB} (SST$_n$)	38.848	0	22
S^P (.)S^A (.) p(time) ψ^{PB} (age) ψ^{BS} (.)ψ^{SB} (SST$_n$)	94.214	0	23

Table 2-4. Estimated detection probabilities (p_i), associated standard error (SE), and 95% confidence intervals of waved albatross detected on Española Island, Galápagos Archipelago between the years 1969 to 1979.

Year	p_i	SE	Lower 95% CL	Upper 95% CL
1970	0.703	0.056	0.583	0.801
1971	0.245	0.015	0.216	0.276
1972	0.540	0.023	0.494	0.585
1973	0.720	0.027	0.664	0.769
1974	0.467	0.020	0.429	0.505
1975	0.500	0.021	0.458	0.542
1976	0.066	0.008	0.052	0.084
1977	0.244	0.019	0.208	0.283
1978	0.038	0.007	0.027	0.053
1979	0.250	0.024	0.207	0.300

Table 2-5. Multistate mark-recapture model selection results from waved albatross breeding on Española Island, Galápagos Archipelago between the years 1999 to 2012 and analyzed using a traditional fixed effects modeling approach. Each model provides a maximum likelihood parameter estimate of apparent pre-breeder survival (S^P), apparent adult survival (S^A), probability of detection (p), first-time age-specific breeding probabilities (ψ^{PB}), probability of transitioning from a breeding state to a skipped breeding state (ψ^{BS}), and the probability of transitioning from a skipped breeding state to a breeding state. Models are ranked based on their quasi-Akaike Information Criterion with small sample size correction (QAICc). The table only includes models that contained AICc weight >= 0.01. Annual sea surface temperature (SST_a) and sea surface temperature during the nonbreeding season (SST_n) were modeled as temporal covariates. I also considered a linear trend on survival (trend) and modeled parameters as a constant probability (.). Models were ranked using an adjusted information theoretic approach that measures the distance (ΔQAICc) from the most parsimonious model in terms of precision and the number of parameters (K).

Model	ΔQAICc	QAICc Weights	k
S^P (.)S^A (trend) p(time) ψ^{PB} (age) ψ^{BS} (time) ψ^{SB} (.)	0.000	0.254	36
S^P (.)S^A (trend) p(time) ψ^{PB} (age) ψ^{BS} (time) ψ^{SB} (SST_a)	0.640	0.185	37
S^P (.)S^A (.) p(time) ψ^{PB} (age) ψ^{BS} (time) ψ^{SB} (.)	0.894	0.163	35
S^P (.)S^A (time) p(time) ψ^{PB} (age) ψ^{BS} (time) ψ^{SB} (SST_n)	2.150	0.087	48
S^P (.)S^A (time) p(time) ψ^{PB} (age) ψ^{BS} (time) ψ^{SB} (SST_a)	2.757	0.064	48
S^P (.)S^A (SST_a) ψ^{PB}(age) ψ^{BS} (time) ψ^{SB} (.)	2.916	0.059	36
S^P (.)S^A (.) p(time) ψ^{PB} (age) ψ^{BS} (time) ψ^{SB} (SST_n)	2.976	0.057	36
S^P (.)S^A (trend+SST_a) p(time) ψ^{PB} (age) ψ^{BS} (time) ψ^{SB} (.)	4.348	0.029	38
S^P (.)S^A (trend) p(time) ψ^{PB} (age) ψ^{BS} (SST_a) ψ^{SB} (time)	6.196	0.011	36

Table 2-6. Model-averaged estimates of detection probability (p_i), associated standard error (SE), and 95% confidence intervals of waved albatross detected on Española Island, Galápagos Archipelago between the years 1999 to 1979. Albatross were marked at subcolonies 1-3 (Figure 2-4; Huyvaert and Anderson 2004).

Year	p_i	SE	Lower 95% CL	Upper 95% CL
2000	0.672	0.234	0.204	0.943
2001	0.778	0.109	0.504	0.923
2002	0.464	0.074	0.326	0.608
2003	0.900	0.114	0.430	0.991
2004	0.971	0.088	0.073	1.000
2005	0.527	0.051	0.427	0.625
2006	0.564	0.046	0.473	0.651
2007	0.676	0.069	0.529	0.794
2008	0.659	0.099	0.449	0.821
2009	0.585	0.109	0.368	0.774
2010	0.707	0.157	0.353	0.915

Table 2-7. Cumulative model weights of temporal covariates affecting adult survival (S^A), the probability of a breeder transitioning to a skipped breeder (ψ^{BS}), and the probability of a skipped breeder transitioning to a breederf (ψ^{SB}) of waved albatross breeding on Española Island, Galápagos Archipelago between the years 1999 and 2012. The temporal covariates considered were a linear trend over time (trend), time, intercept-only (constant), and annual sea surface temperature (SST_a).

Parameter	Temporal covariate	Cumulative model weight
S^A	trend	0.463
S^A	constant	0.249
S^A	time	0.172
S^A	SST_a	0.116
ψ^{BS}	time	0.934
ψ^{BS}	SST_a	0.028
ψ^{BS}	SST_n	0.021
ψ^{BS}	constant	0.017
ψ^{SB}	constant	0.507
ψ^{SB}	SST_a	0.260
ψ^{SB}	SST_n	0.185
ψ^{SB}	time	0.049

Table 2-8. Variance components analysis of apparent adult survival (S^A), the probability of transitioning from a breeder to a skipped breeder (ψ^{BS}), and the probability of transitioning from a skipped breeder to a breeder (ψ^{SB}) for waved albatross breeding at Punta Cevallos on Española Island, Galápagos Archipelago, Ecuador. Percentages represent the portion of the total process variance obtained by the intercept-only model explained by the predictor variable of interest. Models are ranked by the portion of the variation explained. The explanatory variables considered were annual sea surface temperature (SST_a), sea surface temperature during the nonbreeding season (SST_n), and a linear trend over time.

Parameter	Model	% variation explained
S^A	trend	21.98
S^A	trend + SST_a	9.08
S^A	SST_a	0
ψ^{BS}	SST_n	0
ψ^{BS}	SST_a	0
ψ^{SB}	SST_a	54.96
ψ^{SB}	SST_n	0

Table 2-9. Model selection results of the random effects models ranked by ΔQAICc for waved albatross breeding at Punta Cevallos on Española Island, Galápagos Archipelago. Variance components analysis of apparent adult survival (S^A), the probability of transitioning from a breeder to a skipped breeder (ψ^{BS}), and the probability of transitioning from a skipped breeder to a breeder (ψ^{SB}). Trend represents a linear trend over time. SST_a represents the annual sea surface temperature averaged across the years included in the analysis. SST_n represents the sea surface temperature during the three months prior to the breeding season (January-March) averaged across the years included in the analysis.

Parameter	Model	ΔQAICc	QAICc Weights	# Parameters
S^A	trend + SST_a*	0.000	0.281	50.738
S^A	intercept	0.004	0.280	50.398
S^A	trend	0.301	0.242	50.243
S^A	SST_a	0.803	0.188	50.736
S^A	General fixed effect	6.758	0.010	54.000
ψ^{BS}	intercept	0.000	0.358	50.676
ψ^{BS}	SST_a	0.232	0.319	50.860
ψ^{BS}	SST_n**	0.291	0.310	50.853
ψ^{BS}	General fixed effect	6.549	0.014	54.000
ψ^{SB}	intercept	0.000	0.387	49.723
ψ^{SB}	SST_n	0.378	0.321	49.181
ψ^{SB}	SST_a	0.602	0.287	50.054
ψ^{SB}	General fixed effect	8.546	0.005	54.000
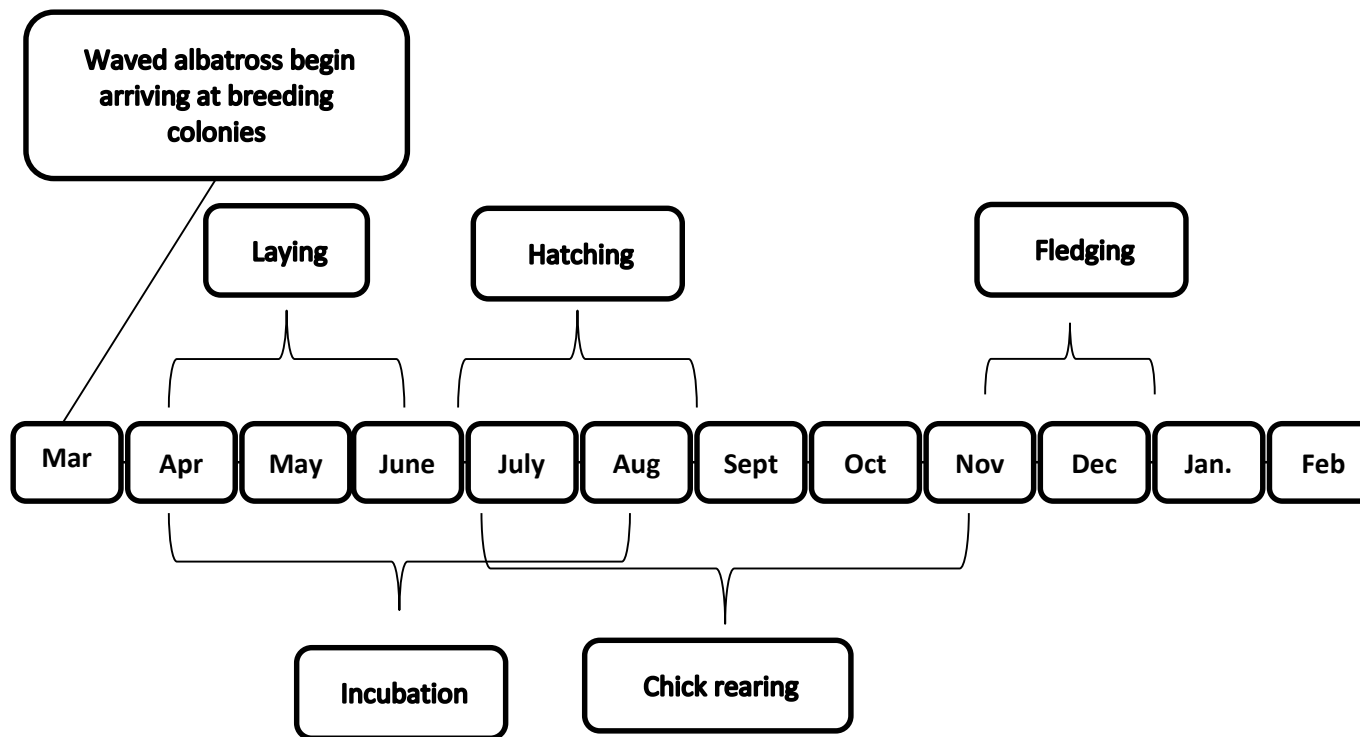
Figure 2-1. Annual timeline of the breeding biology of the waved albatross on Española Island, Galapagos Archipelago, Ecuador. Reproduction begins in late March or early April each year with arrival of males to the breeding colony, followed shortly by females. Egg-laying begins in late April and most birds will have laid an egg by the middle of June. Incubation takes ~2 months and incubation duties are shared by both parents. After hatching, the chick is brooded for several weeks followed by several months of provisioning by adults until the chick fledges, typically in December. Once a chick fledges it will remain at sea for several years before it returns to the breeding colony and attempts to breed.
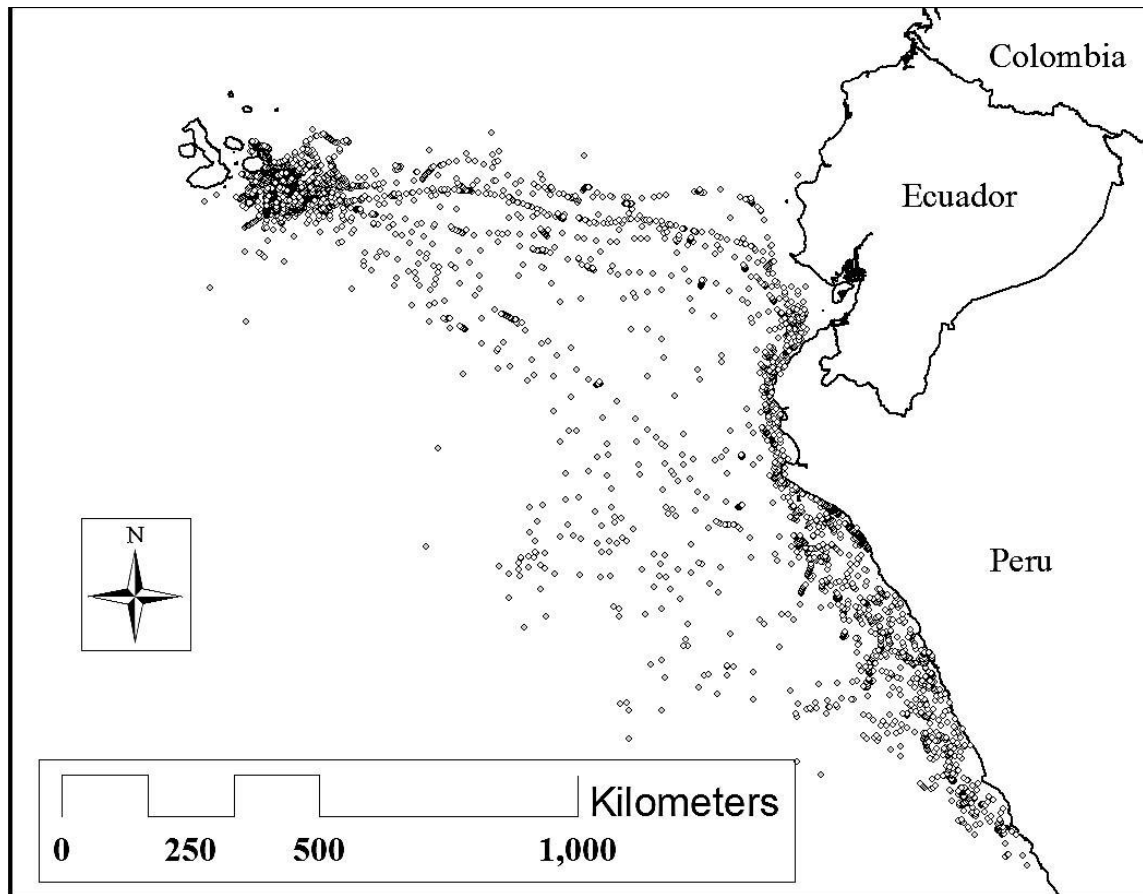
Figure 2-2. At-sea foraging locations of adult breeding waved albatrosses, determined from bird-mounted Platform Transmitter

Terminals (PTTs) in 1995, 1996, 2000, and 2001, and from Global Positioning System (GPS) units deployed on birds between 2003

and 2005 (Anderson et al. 1998, 2003, Fernández et al. 2001, Mouritsen et al. 2003, Awkerman et al. 2005, Anderson et. al 2008).

This figure includes position data for 47 birds over 57 observed trips.
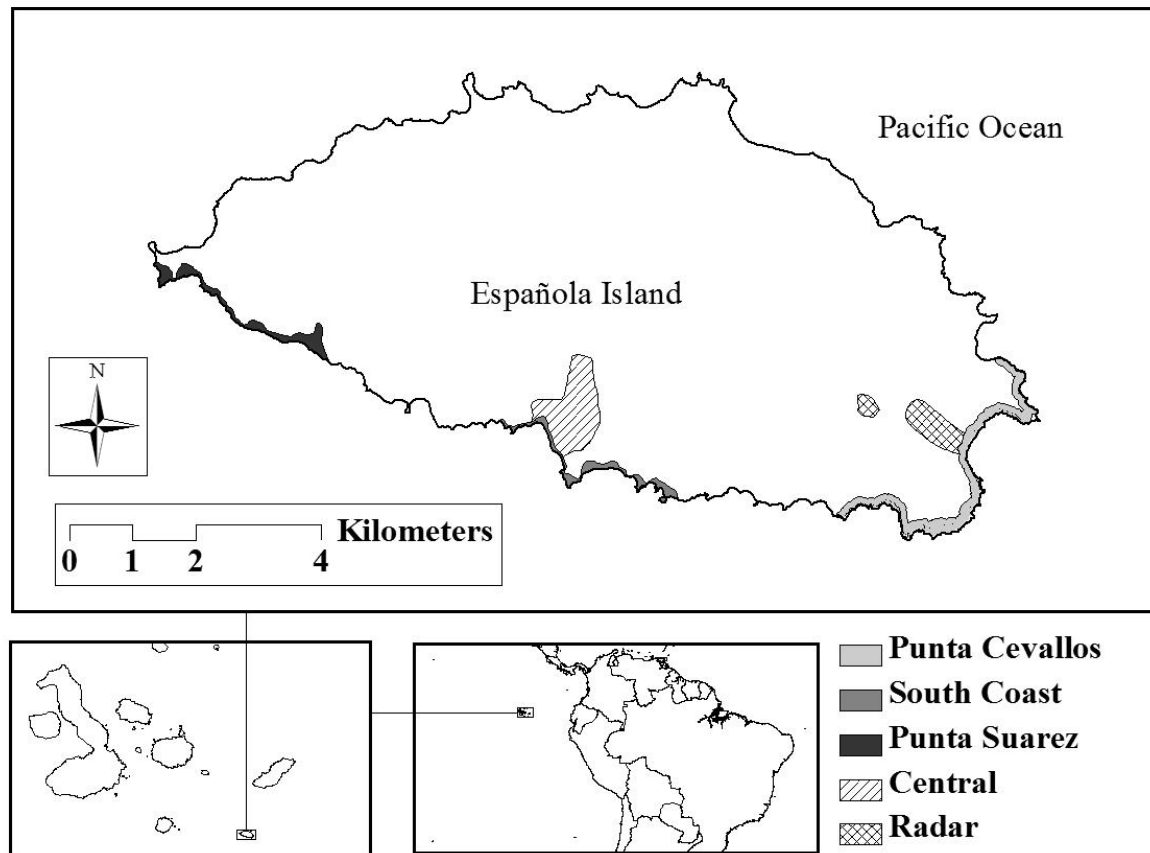
Figure 2-3. Major waved albatross breeding colonies located on Española Island in the Galápagos Archipelago, Ecuador. The majority of the historic dataset (1969-1979) was collected from the colony at Punta Suárez, but a small portion was collected from the Punta Cevallos and Radar breeding colonies. The contemporary dataset (1999-2012) was only collected from the Punta Cevallos breeding colony.
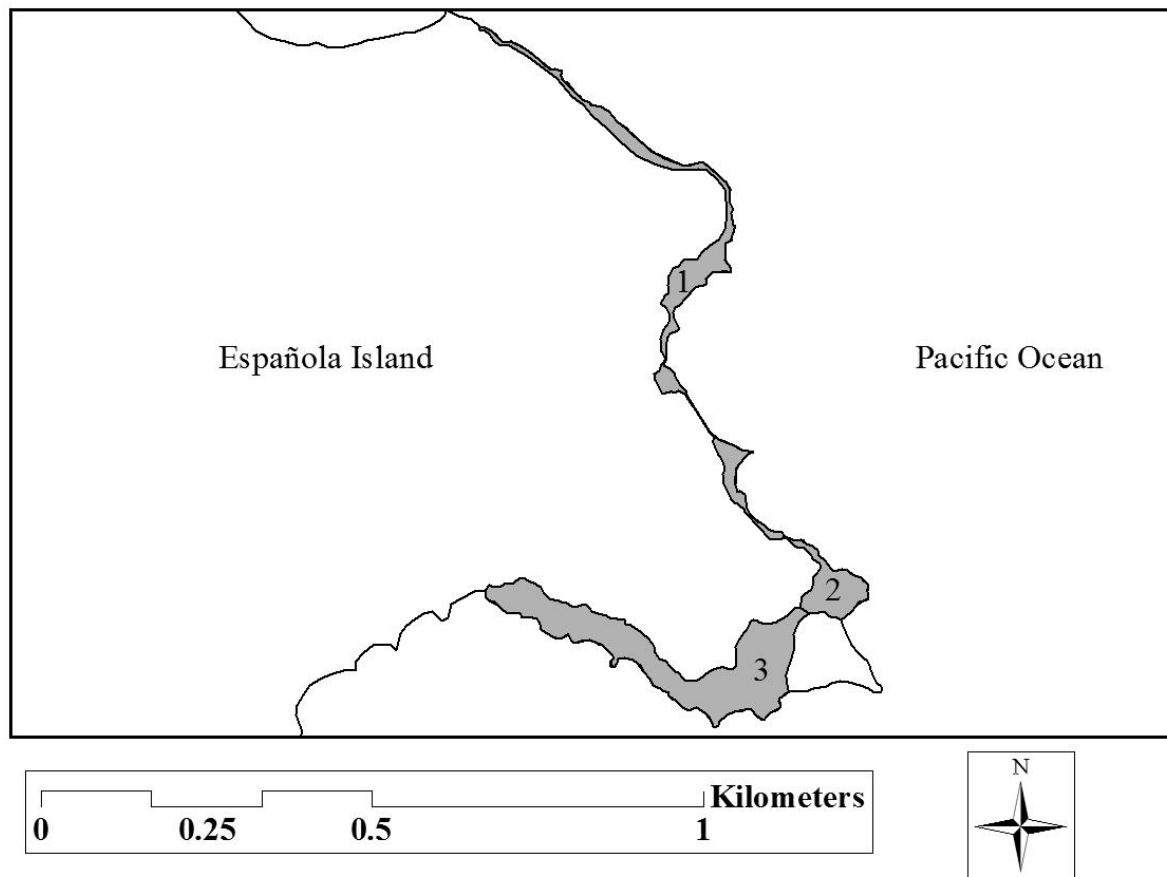
Figure 2-4. The Punta Cevallos breeding colony truncated to well-surveyed subcolonies of breeding waved albatross on Espanola

Island in the Galápagos Archipelago. The contemporary dataset was collected from subcolonies 1 – 3 (Huyvaert and Anderson 2004).

4% of the historic dataset was collected from this colony, but the specific locality is unknown.
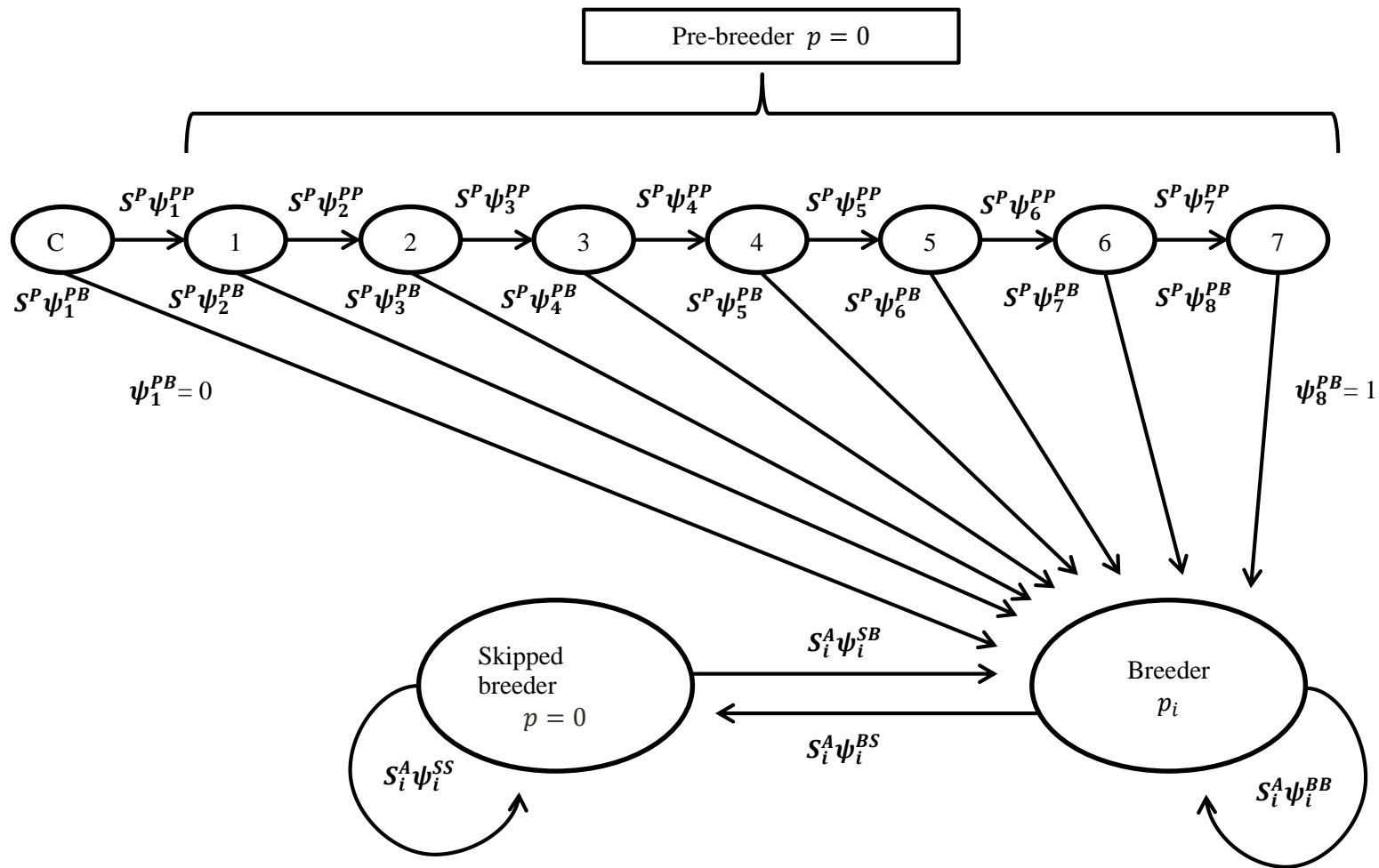
Figure 2-5. Model structure representing pre-breeding and adult life history stages of the waved albatross. Pre-breeders survive with a constant probability through time (S^P), remain in an age-specific pre-breeder state (ψ_{age}^{PP}), or transition to a breeding state with a

Figure 2-5 (continued) first-time age-specific breeding probability (ψ_{age}^{PB}). Adults were allowed to survive time interval i with

probability (S_i^A) and transition between two breeding states, breeder and skipped breeder. An individual in a breeder state could

remain as a breeder (ψ_i^{BB}) or transition to a skipped breeder state (ψ_i^{BS}). Individuals in a skipped breeder state were allowed to remain

as a skipped breeder (ψ_i^{SS}) or transition to a breeding state (ψ_i^{SB}). Birds were captured as chicks and breeders, but could only be

recaptured as breeders with a time-specific detection probability (p_i). Pre-breeder and skipped breeder states were unobservable and

detection was fixed at 0 for these states. Pre-breeders that had not attempted to breed by age 8 were assumed to attempt breeding with

probability 1. Lastly, no individuals were observed as breeders the year after being captured as a chick and this transition probability

was set to 0.
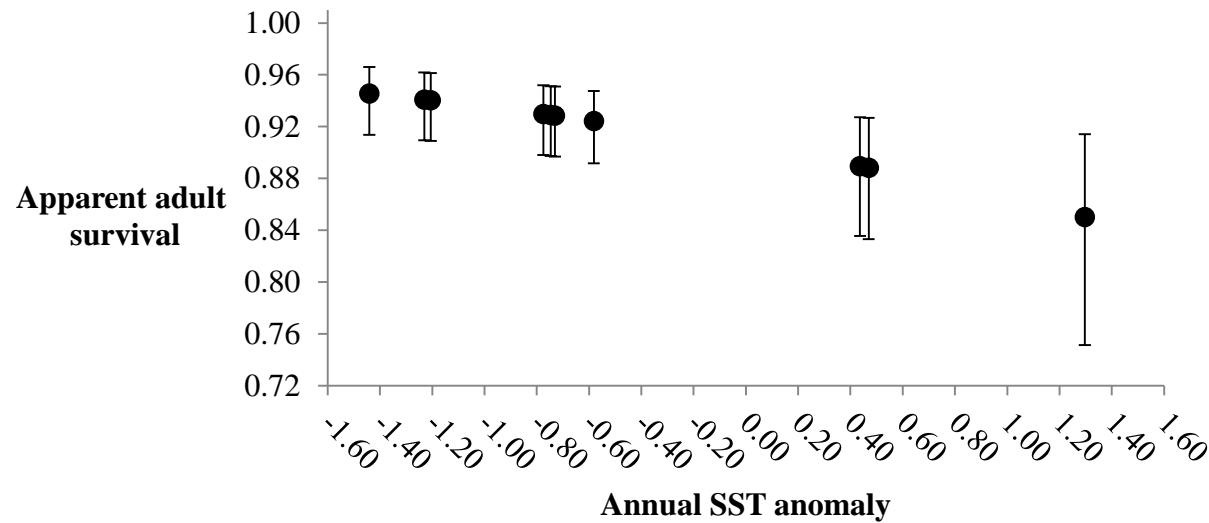
Figure 2-6. Estimates of apparent adult survival and 95% confidence intervals from a traditional fixed effects model for mark-recapture data collected between the years 1969 and 1979 for waved albatross breeding on Española Island. Estimates were obtained from modeling adult survival as a function of annual sea surface temperature anomalies, time variation on detection, age-specific first-time breeding probabilities, and adult breeding probabilities as a function of sea surface temperature averaged over nonbreeding months.

Figure 2-7. Apparent first-time age-specific breeding probabilities and 95% confidence intervals of waved albatross breeding on Española Island, Galápagos Archipelago, between the years 1969 and 1979.
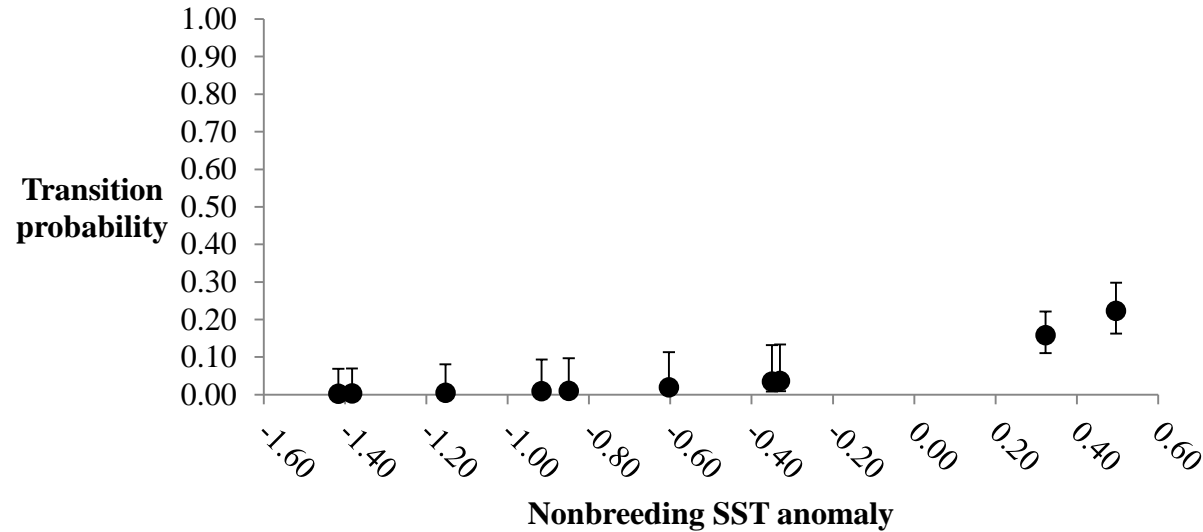
Figure 2-8. Probability and 95% confidence intervals of transitioning from a breeder to a skipped breeder from a traditional fixed

effects modeling approach between the years 1969 and 1979 for waved albatross breeding on Española Island, Galápagos

Archipelago. Estimates were obtained from modeling adult survival as a function of annual sea surface temperature anomalies, time

variation on detection, age-specific first-time breeding probabilities, and adult breeding probabilities as a function of sea surface

temperature averaged over nonbreeding months.
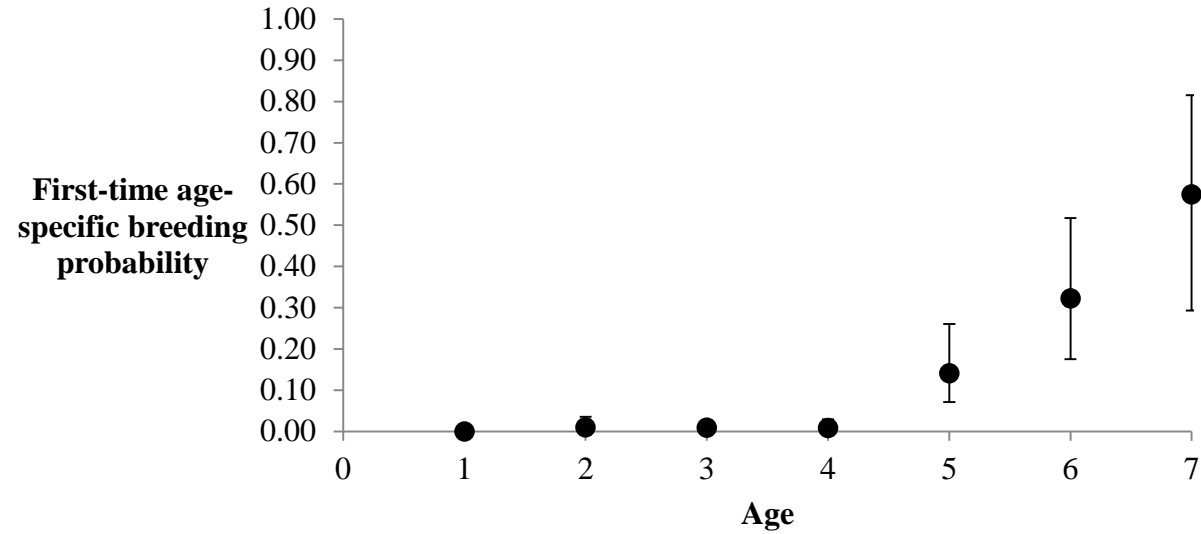
Figure 2-9. Model-averaged estimates of first-time age-specific breeding probabilities and 95% confidence intervals of waved albatross marked as chicks on Española Island, Galápagos Archipelago between the years 1999 and 2012.
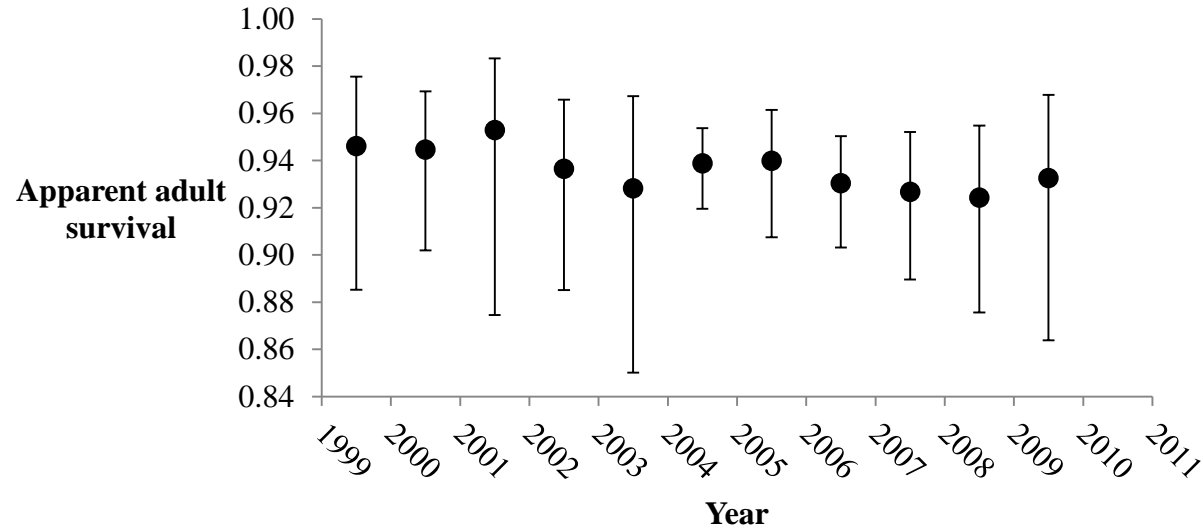
Figure 2-10. Model-averaged estimates and 95% confidence intervals of annual apparent adult survival of waved albatross breeding

on Española Island, Galápagos Archipelago, between the years 1999 and 2012. Estimates were obtained using a traditional fixed

effects modeling approach.
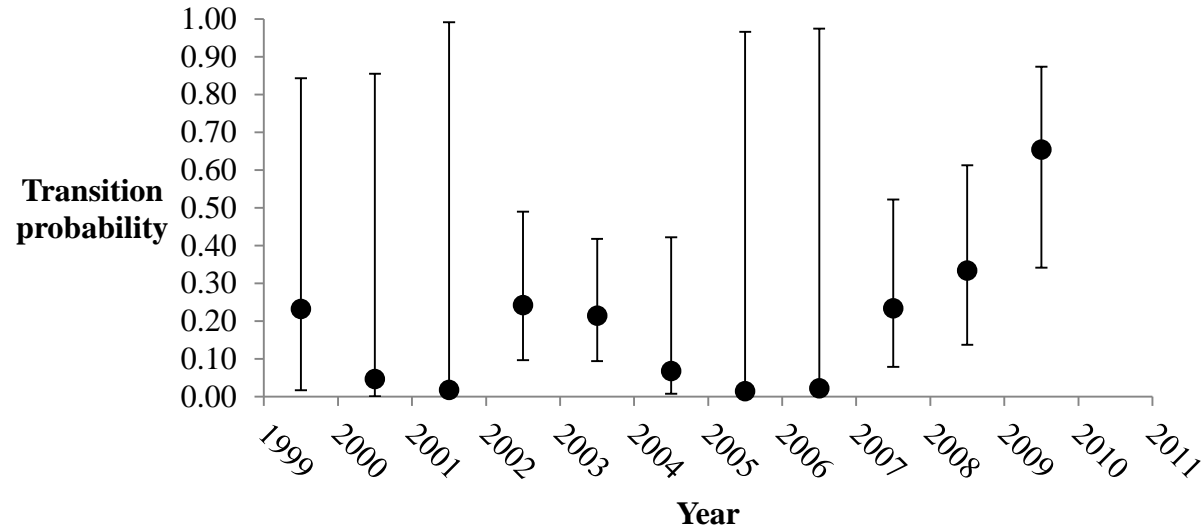
Figure 2-11. Model-averaged estimates and 95% confidence intervals of the probability of waved albatross breeding on Española Island, Galápagos Archipelago, transitioning to a skipped breeder state for the years 1999 and 2012. Estimates were obtained using a traditional fixed effects modeling approach.
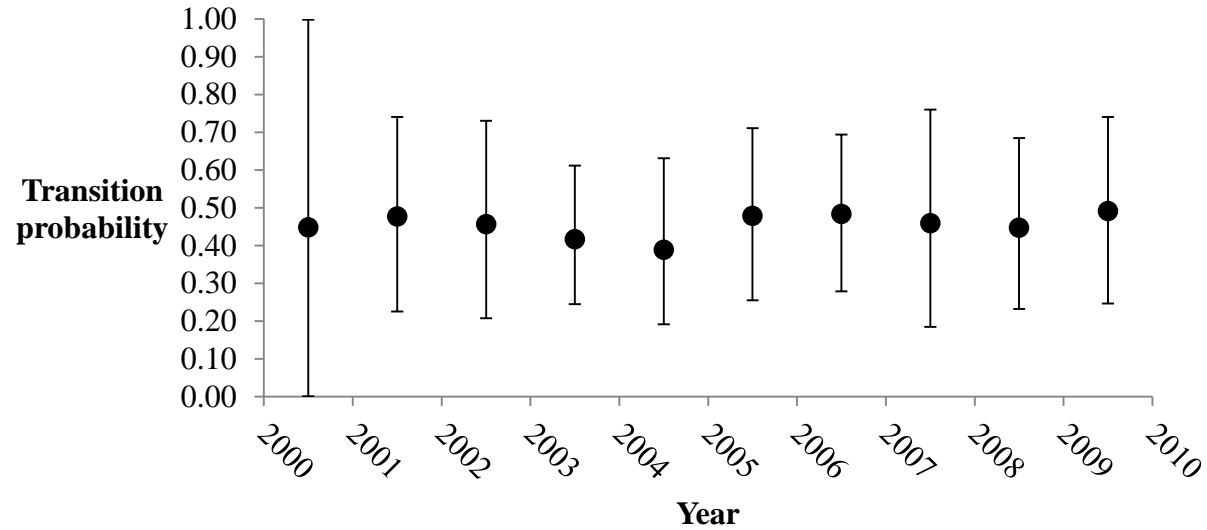
Figure 2-12. Model-averaged estimates and 95% confidence intervals of the probability of waved albatross on Española Island,

Galápagos Archipelago, transitioning from a skipped breeder to breeder state for the years 1999 and 2012. Estimates were obtained

using a traditional fixed effects modeling approach.

The plot shows apparent adult survival on the y-axis (ranging from 0.76 to 1.00) versus year interval (i) on the x-axis (1999 to 2010). Data points with 95% confidence intervals show adult survival, with a model estimate line showing a negative trend.

$$S_i^A = 0.973 - 0.006(i)$$

Legend:
- ● Adult Survival
- — Model estimates
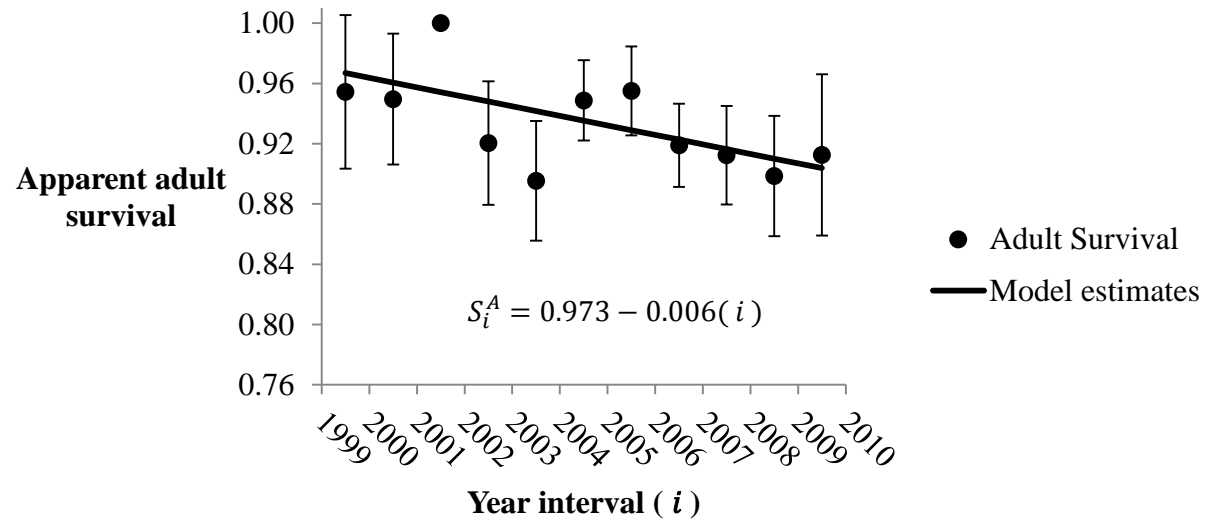
Figure 2-13. Apparent adult survival and 95% confidence intervals of waved albatross breeding on Española Island, Galápagos Archipelago, modeled as a random effect around a negative trend over time. This model explained 22% of the process variance.

The chart shows:
- Y-axis: Apparent adult Survival (0.76 to 1.00)
- X-axis: Year interval (i), 1999–2010
- Legend: ● Adult Survival, — Model estimates
- Equation on chart:

$$S_i^A = 0.965 - 0.005(i) - 0.007(\text{SST}_a)$$
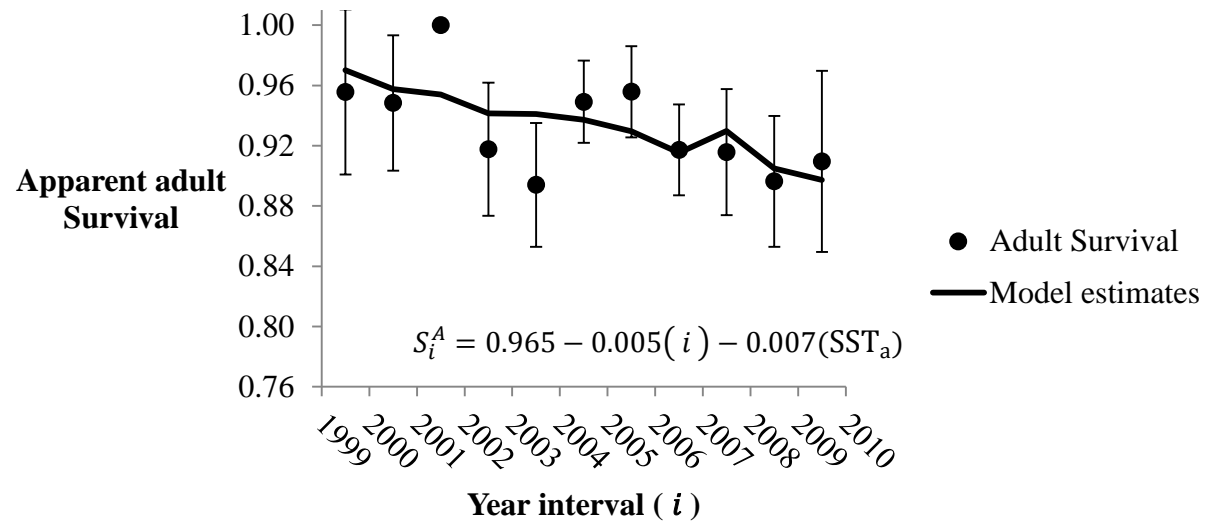
Figure 2-14. Apparent adult survival and 95% confidence intervals of waved albatross breeding on Española Island, Galápagos Archipelago, modeled as a random effect around a negative trend over time and SST_a. This model explained 9% of the process variance.
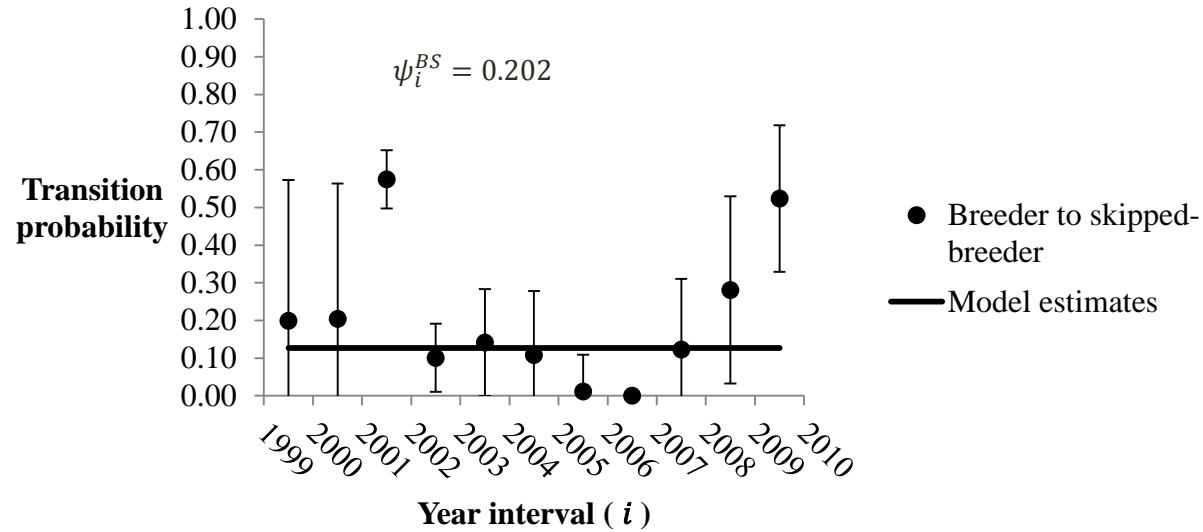
Figure 2-15. The probabilities of a breeding waved albatross breeding at Punta Cevallos, Española Island, Galápagos Archipelago, Ecuador, transitioning to a skipped breeder, as well as the 95% confidence intervals, obtained from an intercept-only random effects model.
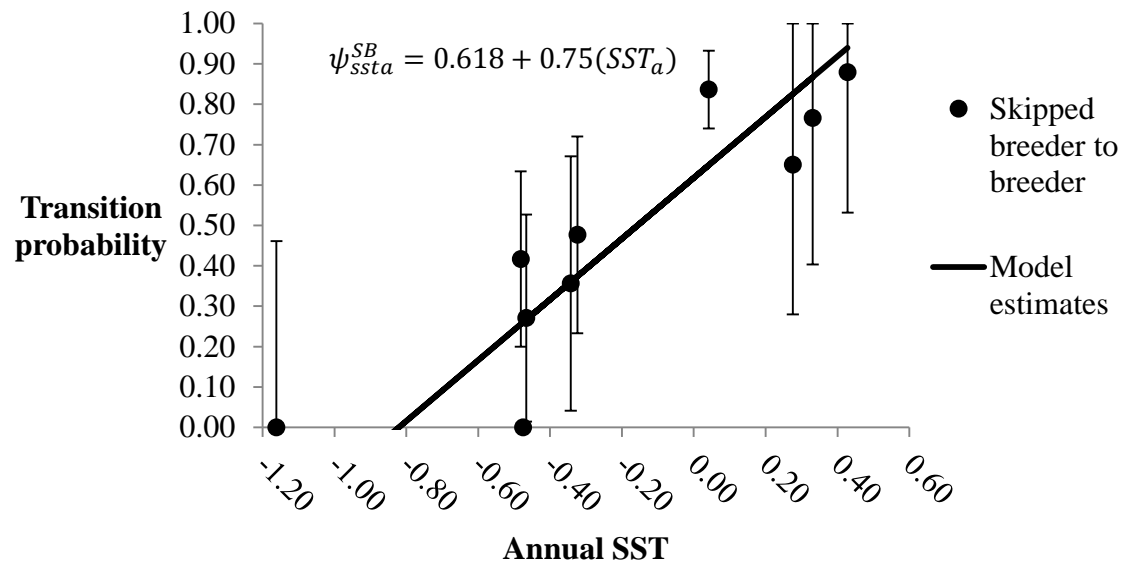
Figure 2-16. The probability and 95 % confidence intervals of waved albatross transitioning from a skipped breeder state to a breeder state. This transition probability was positively affected by annual sea surface temperature. This model explained 54.96% of the process variance from the intercept only random effects model. Note that the y-axis does not intersect the x-axis at zero.

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