Ecology and Conservation of Magellanic and Galápagos Penguins in a Changing World

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Abstract

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Climate change is rapidly altering the environment that wildlife experience, influencing their performance, ecological interactions, and population dynamics. Penguin species are threatened across the Southern Hemisphere and serve as indicators of environmental change and charismatic ambassadors for conservation. Focusing on two species of South American penguins, I leveraged field studies and remote sensing to test ecological hypotheses surrounding wildlife responses to global change as well as to ask applied questions with the aim of informing the management of threatened species.

First, I examined the consequences of climate-driven delays in breeding in Magellanic penguins (*Spheniscus magellanicus*). Changes in phenology (i.e., the timing of important life events like growth, migration, and breeding) are widespread organismal responses to climate change that have been observed across taxa worldwide. Elucidating the impacts of these shifts is difficult yet essential for predicting how populations will be affected by global change. I explored the interaction between

the timing of egg laying and subsequent breeding-season events like fledging at a large colony of Magellanic penguins at Punta Tombo, Argentina (Chapter 1). I found that differential shifts in events within the breeding season—hatching delayed while fledging dates did not—led to a shortened nestling period and reduced growth in chicks, with implications for their survival. Next, I tested for increasing temporal mismatch between penguin breeding and the window of optimal oceanographic conditions and resource availability (Chapter 2). I found evidence that Magellanic penguins cope with high environmental variability by matching long-term averages of resource phenology instead of tracking yearly conditions. As breeding delayed, however, fewer penguins bred at this optimal time. Together these chapters reveal the mechanisms by which climate-driven phenological shifts affect individuals and populations. The chapters highlight the importance of examining phenology across multiple annual-cycle events as well as considering how environmental variability and natural history together shape the outcomes of phenological shifts.

My other dissertation chapters focused on the rare and endangered Galápagos penguin (*Spheniscus mendiculus*). These chapters aimed to reveal components of Galápagos penguin natural history, behavior, and demography that will aid in designing effective management strategies. First, I tested the accuracy of less invasive methods (i.e., measuring morphological features) for determining the sex of individual penguins (Chapter 3). Next, using this newly established method for sexing Galápagos penguins, I developed the first Bayesian, hierarchical mark-recapture model to estimate survival probabilities of male and female Galápagos penguins (Chapter 4). This analysis accounted for imperfect detection of individuals, tag loss, and transience, which can each result in biased survival estimates. I found low estimates of survival and detection for this species, highlighting the challenges of data collection and the need for cutting-edge quantitative tools to accurately estimate demographic rates and population trends for this rare and endangered seabird.

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DEDICATION

I dedicate this dissertation my parents

and to my grandmother, Beverly Stevens Waite, who loved birds.

Chapter 1.

CONSEQUENCES OF PHENOLOGICAL SHIFTS AND A COMPRESSED BREEDING PERIOD IN MAGELLANIC PENGUINS

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Abstract

Phenological shifts may ameliorate negative effects of climate change or create carry-over effects and mismatches that decrease fitness. Identifying how phenological shifts affect performance is critical for understanding how individuals and populations will respond to climate change, but requires long-term, longitudinal data. Using 34 years of data from the Magellanic penguin (*Spheniscus magellanicus*) colony at Punta Tombo, Argentina, we examined the consequences of the delayed onset of breeding (i.e., arrival and egg-laying dates) that has occurred at the colony since 1983. To understand how the delay propagates through the rest of the reproductive cycle, we identified phenological trends in hatch and fledge dates. Median hatch dates were 0.29 days later each year, amounting to a 10-day shift over the course of the study. Median fledge dates did not shift over the 34-year period however, thus shortening the median nestling period duration by 14%. We tested several predictions regarding performance outcomes of the compressed nestling period, finding that later-hatched chicks fledged significantly younger than earlier-hatched chicks, and that younger fledglings left the colony with smaller bills and with more chick down. Interestingly, although younger chicks fledged significantly lighter and in worse body condition than older fledglings early in the study, this trend reversed over time, with younger chicks actually fledging heavier and in better body condition in more recent years. Smaller and lighter fledglings were less likely to recruit to the colony as adults. We find that delayed breeding has significantly compressed nestling periods at Punta Tombo, influencing chick growth and fledgling condition. These findings highlight the importance of studying phenology across multiple life events to fully understand the consequences of phenological shifts for organismal fitness.

Keywords: phenology; compressed phenology; climate change; migratory bird; fledging traits; recruitment; Magellanic penguin; *Spheniscus magellanicus*

1.1 INTRODUCTION

Changes in the timing of recurring life-history events (i.e., phenology) are documented across taxa worldwide (Parmesan and Yohe 2003). As environmental conditions frequently determine the timing of such events, changes in phenology are among the most apparent responses populations have to climate change. Directional phenological shifts, wherein annual events like reproduction or migration take place earlier or later than typical, occur in terrestrial, freshwater, and marine organisms (Walther et al. 2002). For example, plants flower earlier when exposed to warmer spring temperatures (Walther et al. 2002), whereas cetaceans may delay their autumn migration in years with later sea ice freeze-up dates (Hauser et al. 2017). Because the timing of such events determines the environment that individuals and their offspring experience, shifts in phenology may have consequences for individual performance and fitness. Discerning the specific ecological and evolutionary consequences of these changes, however, requires detailed, long-term, and longitudinal data (Moyes et al. 2011). Such datasets, particularly those that include individual-level information on performance metrics like growth and survival, are rare (Reed et al. 2013, Youngflesh et al. 2018).

One commonly studied outcome of phenological shifts is trophic mismatch, which occurs when the magnitude or direction of shifts vary across trophic levels (Cushing 1990, Keogan et al. 2018, Kharouba and Wolkovich 2020). Few studies, however, have examined the consequences of differential phenological shifts within a species (Visser and Gienapp 2019, Hällfors et al. 2020), which may expand or compress life history stages and have demographic and evolutionary outcomes separate from those deriving from shifts at a single stage (e.g. expanded and compressed first flower to last flower: CaraDonna et al. 2014, compressed flower to seed transition: Sethi et al. 2020, compressed migration to onset of breeding: Tomotani et al. 2018). Phenological expansion or compression can occur when multiple events respond to the same environmental cue at varying intensities (Tomotani et al. 2018) or when life-cycle events respond to different environmental cues.

For example, the timing of some events track dynamic drivers such as temperature, while other events are constrained by temporally fixed drivers like photoperiod (Körner and Basler 2010). In migratory species, shifts in the timing of environmental cues may differ between breeding and non-breeding habitats. Therefore, while shifts at certain stages may buffer against the effects of climate change, how these shifts propagate across subsequent stages will determine demographic outcomes.

In bird populations, there are many examples of changes in arrival and clutch initiation dates in the spring, but there are few studies of autumn phenology (Gallinat et al. 2015), and even fewer that address these questions in the Southern Hemisphere (Chambers et al. 2013, 2014). Timing of events near the end of the breeding season, like fledging and juvenile dispersal, determines the environment that fledglings face during their post-fledging period and first year. Juvenile survival rates are often low and can vary drastically with environmental conditions (Gaston 2004, Dehnhard et al. 2014, Gownaris and Boersma 2019). Because population growth rates in birds can be highly sensitive to changes in juvenile survival (e.g., in terns *Sterna hirundo*: Ezard et al. 2006, in raptors *Milvus migrans*: Sergio et al. 2011), it is important to consider fledgling condition and the timing of late breeding-season events in studies of phenological shifts. Here, we leverage a long-term dataset to examine shifts in the timing of multiple reproductive events in a migratory bird.

Background: Delayed Onset of Breeding in a Magellanic Penguin Colony

Arrival and egg-laying dates have become later at the Magellanic penguin (*Spheniscus magellanicus*) colony at Punta Tombo, Argentina, with median egg-laying dates occurring nine days later than in the early 1980s (Boersma and Rebstock 2014, Rebstock and Boersma 2018). Egg laying is later when arrival dates are later, which is likely a carry-over effect of limited food availability during the non-breeding season (Rebstock and Boersma 2018). In years when food is limited or more difficult to find in their winter range, adults likely take longer to reach sufficient body condition for breeding and delay their migration to the breeding colony (Rebstock and Boersma 2018).

Though egg-laying dates have shifted later over the last 35 years, it is unclear if the timing of other breeding-season events are as plastic. The timing of molting in birds, for example, is likely driven by photoperiod as well as local food availability (Wingfield and Farner 1993). Photoperiod controls the timing of reproductive events in several high-latitude penguin species (citations in Otsuka et al. 2004), but the strength of photoperiod as a cue for more temperate species is less understood (Otsuka et al. 2004). At Punta Tombo, nutrient-rich tidal fronts near the colony dissipate in the late austral summer and early autumn when chicks are fledging and adults begin gaining weight for the post-breeding molt. Delaying fledging or molting beyond the period of high ocean productivity and food availability could increase the risk of starvation for fledglings and adults. Additionally, adults with very late-fledging chicks may need to balance feeding their chicks with gaining weight for the energy-intensive molt. Some penguin species with fixed molting periods after breeding are known to abandon late-fledging chicks rather than delay molting (African *Spheniscus demersus:* Sherley et al. 2014; Adelie *Pygoscelis adeliae:* Ainley et al. 1983). If fledging dates are inflexible among Magellanic penguins at Punta Tombo, the delayed onset of breeding could force a shortening of the nestling period. A compressed nestling period may result in chicks fledging smaller, lighter, in worse body condition, or with more chick down. Identifying when phenological compression or expansion of life-cycle stages occurs and how it influences individual performance is key for assessing the ecological and evolutionary consequences of phenological shifts widely documented in individual stages.

We evaluated how delayed arrival and laying dates at Punta Tombo (as shown in Rebstock and Boersma 2018) carry through the breeding season to interact with hatch and fledge dates and to impact fledgling condition and survival. We first determined whether median colony hatch and fledge dates and nestling period duration changed since the 1980s. When preliminary analyses showed that the nestling period duration shortened over time, we tested several predictions on the consequences of this shift for individuals, analyzing performance metrics including chick age, bill, flipper, and foot size, and body condition at fledging as well as post-fledging survival.

1.2 MATERIALS & METHODS

Study System

Magellanic penguins are long-lived, Southern Hemisphere seabirds that time migration and reproduction to track the availability of prey throughout the year (Boersma et al 1990). We followed banded individuals and their nests, eggs, and chicks at the Punta Tombo colony in Chubut, Argentina (44.03 W, 65.21 S) from 1983 to 2017. Punta Tombo is a declining colony, with the number of active nests at Punta Tombo decreasing 36% between 1987 and 2014, from around 314,000 to 201,000 nests (Rebstock et al. 2016).

This population winters off the coast of northern Argentina, Uruguay, and southern Brazil and aligns breeding with the peak of resource availability at Punta Tombo in the austral spring (Stokes et al. 2014). During the breeding season, the penguins' primary prey species, anchovy and juvenile hake, aggregate in tidal mixing fronts that form close to the colony (Boersma et al. 2009).

Male Magellanic penguins begin arriving at the colony each year in September, and females arrive one to two weeks later (Boersma et al. 1990). Egg laying begins in October, with females laying one clutch of two eggs. Eggs hatch after 38 to 42 days, with males and females alternating incubation duties (Boersma et al. 2013). The chick nestling period typically lasts 65 to 75 days, but chicks have been observed fledging as young as 49 or as old as 112 days old (Boersma et al. 2013, Gownaris and Boersma 2021). Fledging at Punta Tombo begins in January of each year and peaks between 24 January and 17 February (Boersma et al. 1990, Boersma et al. 2013). Once chicks leave the nest to go to sea, they receive no further care from their parents. Mortality during this first year is high, with survival of juvenile cohorts ranging from 0 to 44%, depending on the year (average female survival: 16% ± 11 SD, average male survival: 19% ± 14 SD; Gownaris and Boersma 2019). Carcasses found in the penguins' wintering range are highly biased toward juveniles (Vanstreels et al. 2013). Some juveniles that survive their first winter return to Punta Tombo the following year to molt into adult plumage, while others are not seen again until they are breeding adults (Boersma et al. 2013). Fifty percent of females begin breeding by age six, and 50% of males begin breeding by age seven (Boersma et al. 2013, Gownaris and Boersma 2019).

Data Collection

Nest checks:

We arrived at Punta Tombo in September or October of each year from 1983 to 2017 except 2011, when permit issues prevented fieldwork. We searched for banded birds and checked their nests regularly throughout nest establishment and egg laying. Beginning eight to twelve days before estimated egg hatch dates, we visited nests daily so that we knew chick hatch dates within one day. We marked chicks with temporary, fiber-tape bands labeled with chick ID and/or colored chicks with semi-permanent marker to be certain of chick identity. Once chicks had feet over 8 cm long, we applied a numbered, stainless-steel tag to the outer webbing of the left foot (Boersma and Rebstock 2010). We checked chicks every ten days or less until they died, fledged, or the field crew left near the end of the breeding season. We considered a chick to have fledged if it was seen after 10 January and weighed over 1.8 kg at its last weighing (Boersma et al. 1990). We defined a chick's fledge date as the day it was last seen in its nest. If a chick had not fledged by the time the field season ended, we did not assign it a fledge date. Similarly, if more than five days elapsed between when the chick was last seen and when its nest was next checked, we did not assign the chick a fledge date.

Chick measurements:

To examine how nestling duration influences chick mass and size at fledging, and how fledging mass and size relate to post-fledging survival, we weighed and measured chicks every 1-10 days (depending on the year and area of the colony) until they fledged. In penguins, the size of their flippers and feet can influence their dive depths, agility, and speed in the water (Davis and Renner 2003, Walker and Boersma 2003, Koehn et al. 2016), while their bill size determines the size of prey they can catch (Holmes and Pitelka 1968, Koehn et al. 2016). We weighed chicks with spring scales (100, 200, 300, 1000, 2500, 3000, or 6000 g) and measured their bill length (length of exposed culmen), bill depth (vertical thickness, measured at the nares), flipper length (elbow joint to the tip), and foot length (heel to the tip of the middle toe) with Vernier calipers (±0.1 mm) and a zero-stop ruler (±1 mm) (as in Boersma 1974). Magellanic penguin chicks often fledge with some of their chick down remaining over their juvenile plumage. This may increase their drag or alter their buoyancy in the water, which is known to reduce dive depth, duration, and swim speeds in other diving seabirds (Elliott et al. 2007). To quantify down cover, we estimated the percentage of down remaining on each chick at the time of measurement, rounding to 100, 75, 50, 25, or, 0% (note: when we recorded 0%, there were often small down patches on the head or neck).

Statistical Approach

Colony trends:

We determined the median hatch and fledge dates for each year between 1983 and 2017 (except 2011) using a marked sub-area of the colony that we checked daily from when we arrived until we departed every year. Because the timing of second-egg hatching is strongly correlated with the timing of the first egg, often hatching two days later (Boersma 1992, Rebstock and Boersma 2011), we excluded second eggs from the hatch-date analysis. We calculated median as the 50th percentile of hatch and fledge dates, excluding years where the field crew left before 50% of the chicks fledged (two years: 1989 and 2014). We fit multiple linear models with median hatch date and median fledge date as the response variables and year as the fixed effect. We included hatch dates for 1,876 first-hatched eggs, with number of eggs varying among years between 13 and 108. We included fledge dates for 916 fledglings, with the number of fledglings each year varying between 9 and 97. Because the number of eggs and fledglings varied among years, we weighted the median-date observations in our model by including the natural log of each year's sample size in the 'weights' argument in *lm* in R. In our analysis of median fledge dates, we excluded years with extremely low reproductive success where fewer than nine study chicks fledged (six years: 1984, 1990, 1999, 2000, 2002, and 2012).

Fledging age:

To understand the impact of delayed breeding on individual chicks, we first tested the prediction that chicks with later hatch dates fledge younger. We used a Cox proportional hazards model with mixed effects using the *coxme* package in R (Therneau 2015). Using a survival regression allowed us to include chicks that did not fledge before we left at the end of the field season (i.e., right-censored cases; n = 515 out of 1,605 chicks). The response variable was a survival variable indicating fledging status and age. We included hatch date as a continuous fixed effect and nest ID as a random effect to account for non-independence between siblings.

Morphology:

We determined chick body condition at fledging using the scaled mass index (SMI). Following Peig and Green (2009), we calculated a condition score for each chick as

$$SMI_i = M_i \left[\frac{FL_0}{FL_i}\right]^b$$

where M_i is the chick's mass at fledging, FL_i is its flipper length at fledging, FL_0 is the mean flipper length at fledging of all study chicks, and b is the slope of a standardized major axis regression (SMA) on log-transformed mass over log-transformed flipper length at fledging.

To test for morphological consequences of fledging at a younger age, we used linear mixed effects models to examine the relationship between fledging age and mass or size at fledging. Because we were interested in morphology at the time of fledging, we only included chicks that had a measurement recorded within five days of their fledge date. We built separate sets of models for seven response variables: bill length, bill depth, flipper length, foot length, mass, body condition, and down cover. We included age at last measurement, year, and their interaction (because the relationship between age and condition at fledging may have changed across years) as continuous fixed effects. In the model with down cover as the response variable, we built a generalized linear mixed-effects model (GLMM) with the same fixed and random effects but treated down as a binomially distributed outcome variable giving a down score out of 4. Because Magellanic penguin morphological features develop at different rates (e.g., flippers and feet generally reach adult size before fledging, whereas the bill generally reaches adult size after fledging; Gownaris and Boersma 2021), we used model selection to find the predictor variables with the best explanatory power for each response variable. We used AIC to compare the full model, the model without the interaction term, each fixed effect, and a null, intercept-only model for each response variable. When ΔAIC was < 2 between the most competitive nested models, we focused our interpretation on the model with the fewest parameters (Arnold 2010). To account for non-independence between siblings, we included nest ID as a random-intercept term. We ran the analyses using the *lme4* package in R (Bates et al. 2015) and plot estimates from the best performing models in Figure **1.2**.

Likelihood of return after first winter:

We analyzed whether morphological characteristics at the time of fledging predicted recruitment, which we define as an individual returning to the colony, having survived its first winter at sea. We used a subset of study chicks that received a stainless-steel flipper band (see Boersma and Rebstock 2010) before fledging (n = 879) and built GLMMs with returned to the colony as a Bernoulli-distributed response variable. Individuals could be resighted as a juvenile (age one) but are more likely to be resighted as an adult (age two or older) and were treated the same in the model. Using a smaller subset of banded chicks for which we had measurements at the time of fledging (n = 542), we tested fledgling mass, scaled mass index, bill length, bill depth, flipper length, and foot length as predictor variables. Because of collinearity among some of the predictor variables, we considered each variable individually in separate models and compared the AICs of each model to determine which morphological feature best described fledgling return. We tested three additional predictor variables in separate models including down cover (n = 312 chicks), fledge date (n = 879), and fledge age (n = 879). We included hatch year as a random-intercept effect in all models due to the variability in cohort survival among years (Gownaris and Boersma 2019). We excluded chicks that fledged after 2010 to allow sufficient time for chicks to return to the colony as breeders, thus increasing our likelihood of sighting them (as in Koehn et al. 2016). Because chicks banded at Punta Tombo are only rarely found recruiting to other colonies, we assumed that those that did not return were dead (Koehn et al. 2016). We performed all analyses using R version 3.6.1 (R Core Development Team 2019).

1.3 RESULTS

Colony Trends

Colony hatch dates were delayed 0.29 days per year, amounting to 9.97 days over the course of the study (n = 34 years (1876 eggs), 95% CI [0.19, 0.40], $P < 0.0001$, $R^2 = 0.51$; Figure **1.1**a). There was no significant trend in fledge dates among years (n = 26 years (916 chicks), 95% CI [-0.29, 0.19], $P = 0.69$, $R^2 = 0.01$; Figure **1.1**b). Taken together, the length of the chick nestling period, or, the days between median hatch and median fledge dates, decreased over the course of study by more than 12 days (n = 26 years, coef = -0.37, 95% CI [-0.59, -0.14], $P = 0.002$, $R^2 = 0.33$; Figure **1.1**c).

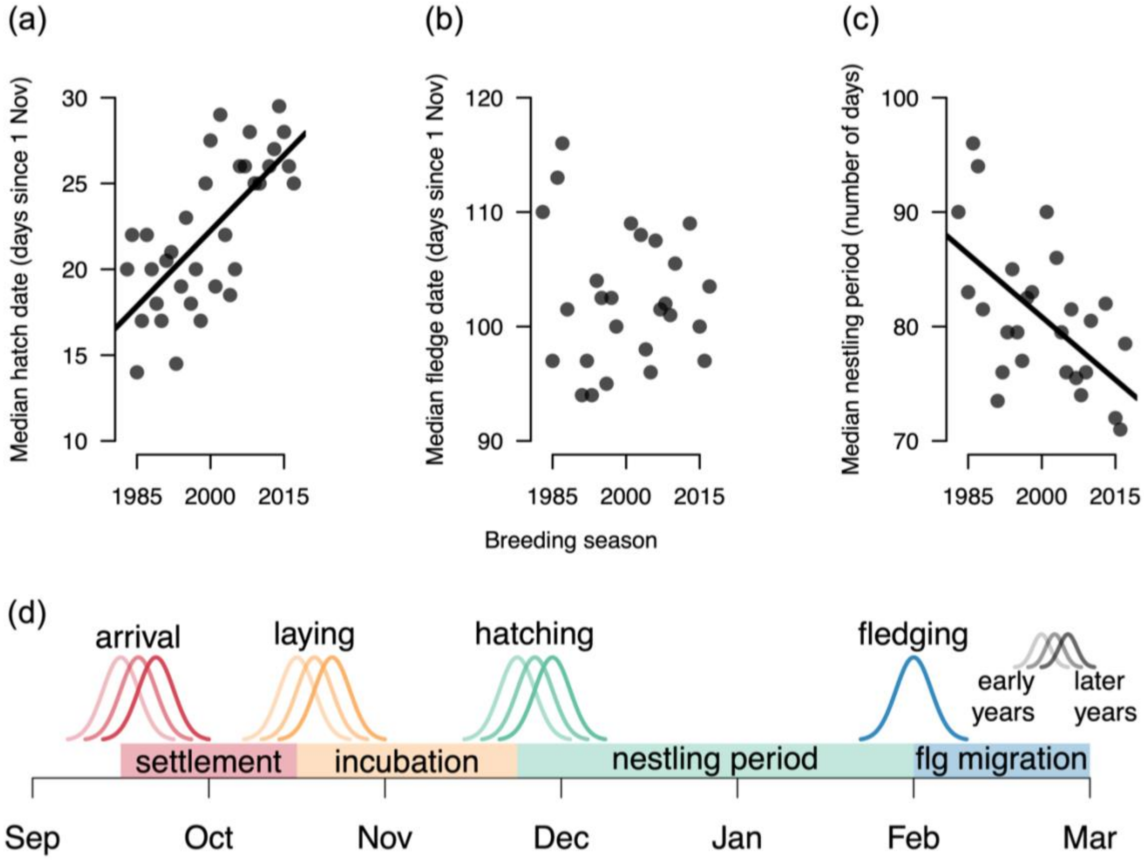

Figure 1.1: (a) Median hatch dates, (b) median fledge dates, and (c) median nestling duration between 1983 and 2017. Hatch dates grew later (n = 34 years (1876 eggs), $P < 0.0001$, $R^2 = 0.51$), fledge dates showed no significant trend (n = 26 years (916 chicks), $P = 0.69$, $R^2 = 0.01$) and median nestling duration shortened (n= 26 years (916 chicks), $P = 0.002$, R^2=0.33) over the course of the study. (d) Conceptual figure showing the annual reproductive cycle and trends in arrival, lay, hatch, and fledging dates over the course of the study. All are delayed except for fledge dates, which show no significant trend (arrival and lay trends Rebstock and Boersma 2018; hatch and fledge trends this study). Fledgling migration is abbreviated as flg migration.

Fledging Age and Morphology

Later hatched chicks fledged younger than earlier hatched chicks (Cox regression, coef = 0.050, SE = 0.008, P = < 0.0001, n = 1605 chicks). Mass, body condition, and foot length at fledging were best explained by the full model, which included age at fledging, year, and the interaction between age and year as fixed effects (n = 662; Table 1); in the early years of the study, chicks that spent more days in the nest fledged heavier, in better body condition, and with longer feet than other chicks. This trend reversed over the course of the study, with younger chicks now fledging in better condition, at greater mass, and with longer feet than older fledglings (Table **1.1**, Figure **1.2**a, 2b, 2f, Appendix S1: Table S1). Age and breeding year, without the interaction term, best explained bill length at fledging (n = 662; Table **1.1**, Appendix S1: Table S1), with older chicks fledging with longer bills (Figure **1.2**c). Age alone best explained bill depth at fledging (n = 662; Table **1.1**, Appendix S1: Table S1); older chicks fledged with deeper bills (Figure **1.2**d). No model explained flipper length better than the null model (Table **1.1**, Figure **1.2**e, Appendix S1: Table S1). Younger chicks fledged with more down than older fledglings (coef = -0.08, 95% CI [-0.10, -0.07], P < 0.0001, n = 415; Table **1.1**, Figure **1.2**g).

Table 1.1: Summary of models describing mass and size of chicks at fledging over various ages and breeding seasons. Age:Year is the interaction between age at fledging and breeding season.

Response	Predictors	AIC	ΔAIC
Mass	Age + Year + Age:Year	913.0	--
	Year	925.3	12.3
	Age + Year	927.1	14.1
	Age	935.0	22.0
	Intercept only	937.9	24.8
Bill length	Age + Year	181.0	--
	Age + Year + Age:Year	183.0	2.0
	Age	186.6	5.6
	Intercept only	226.3	45.3
	Year	227.9	46.9
Bill depth	Age	-968.5	--
	Age + Year	-966.7	1.7
	Age + Year + Age:Year	-965.1	3.3
	Year	-961.4	7.1
	Intercept only	-959.3	9.2
Flipper length	Intercept only	1256.9	--
	Age	1257.7	0.8
	Year	1258.7	1.8
	Age + Year	1259.7	2.8
	Age + Year + Age:Year	1261.3	4.4
Foot length	Age + Year + Age:Year	1047.2	--
	Year	1051.8	4.6
	Age + Year	1053.8	6.6
	Intercept only	1056.1	8.9
	Age	1056.6	9.3
Scaled mass index	Age + Year + Age:Year	1126.3	--
	Year	1138.5	12.2
	Age + Year	1140.5	14.1
	Intercept only	1143.9	17.6
	Age	1144.8	18.5
Down	Age + Year + Age:Year	966.4	--
	Age	966.7	0.4
	Age + Year	967.3	0.9
	Intercept only	1066.8	100.4
	Year	1068.8	102.4

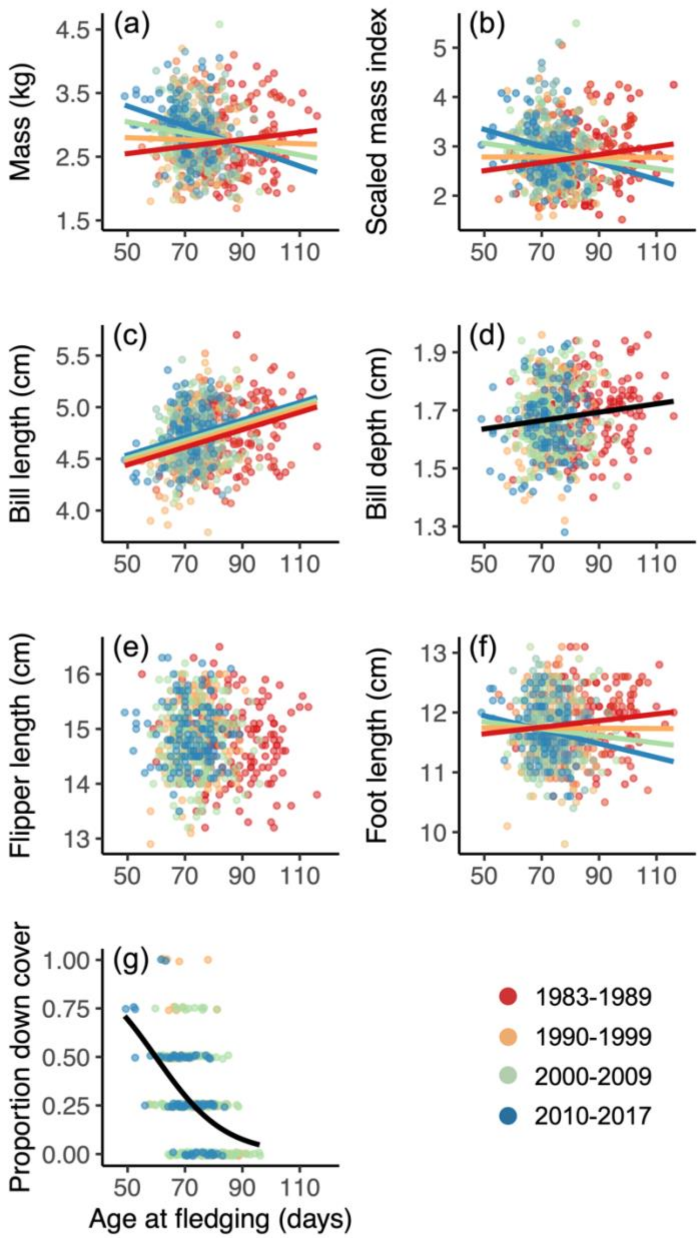

Figure 1.2: Relationship between age at last measurement and (a) mass, (b) body condition (scaled mass index), (c) bill length, (d) bill depth, (e) flipper length, (f) foot length, and (g) proportion down cover ($n_{a,b,c,d,e,f}$=662, n_g=415). Points represent each study chick and are colored by decade. Lines show best fit model estimates. When year was not a significant predictor, we draw one black line. When year was a significant predictor, lines represent an example year from each decade and are colored by the encompassing decade: 1985 (red), 1995 (orange), 2005 (green), and 2015 (blue).

Return after First Winter

Forty-six of 542 banded fledglings returned to Punta Tombo as juveniles (having survived their first year at sea; n = 4) or adults (two years of age or older; n = 45, 3 of which were first seen as juveniles). Thirty-one of the returning penguins were male, 8 were female, and 7 were not sexed. Mass and all four morphological measurements were significant predictors of the likelihood of fledgling return (Figure **1.3**). Heavier fledglings were more likely to return as juveniles or adults (coef = 1.49, 95% CI [0.83, 2.20], $P < 0.0001$), as were chicks with longer bills (coef = 2.02, 95% CI [0.90, 3.19], $P < 0.001$), deeper bills (coef = 5.48, 95% CI [2.68, 8.44], $P < 0.001$), longer flippers (coef = 0.66, 95% CI [0.12, 1.22], $P = 0.019$), and longer feet (coef = 1.04, 95% CI [0.42, 1.68], $P = 0.001$). Mass and bill depth best described the likelihood of fledgling return (Appendix S1: Table S2). Scaled mass index did not predict fledging return (95% CI [-0.17, 0.93], $P = 0.171$), nor did down cover (n = 312, 95% CI [-0.41, 0.42], $P = 0.927$). In the two models including fledge date and fledge age as the predictor variables, 74 of 879 banded fledglings returned as juveniles or adults. Neither fledge date (coef = -0.02, 95% CI [-0.05, 0.01], $P = 0.178$) nor fledge age (95% CI [-0.06, 0.003], $P = 0.070$) predicted recruitment.

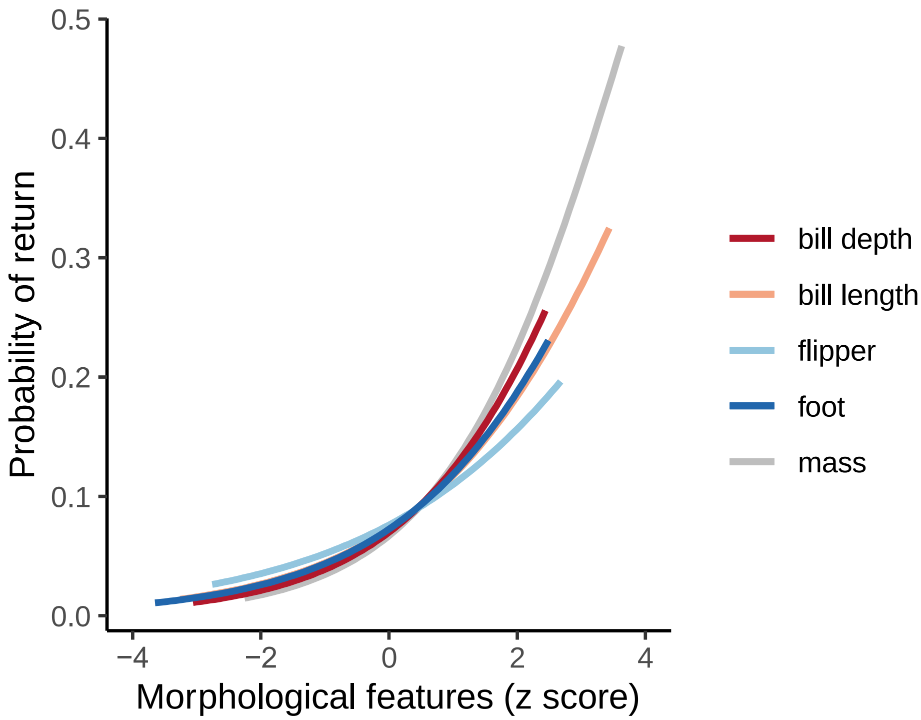

Figure 1.3: Generalized linear mixed effects models giving the probability of re-encountering a fledgling as an adult or juvenile given its mass (gray), bill length (red), bill depth (orange), flipper length (light blue), and foot length (dark blue) at fledging (n=542), with features presented as z scores. Heavier fledglings and those with larger bills, flippers, and feet were more likely to be seen in the colony as juveniles or adults. We found no significant relationship between body condition (scaled mass index) or down cover at fledging and a chick's probability of returning to the colony.

1.4 Discussion

Climate change has altered the phenology of organisms worldwide but has done so unequally across key life-history events within the same species. We found that though median hatch dates in Magellanic penguins at Punta Tombo became later over the last 34 years, median fledge dates remained consistent on average over time, albeit with high interannual variability (**Figure 1.1**). This compression of the nestling period has implications across performance axes including chick age, size, and condition at fledging, as well as post-fledging survival.

Unequal within-species phenological shifts influence time to fledging

Median hatch dates at Punta Tombo shifted 10 days later over the 34-year study. This tracks the delayed arrival of females to the colony and delayed egg laying reported in Rebstock and Boersma (2018). Changes in the timing of egg laying and chick hatching have occurred in several seabird families including Laridae, Hydrobatidae, Procelliariidae, and Spheniscidae, with breeding trending earlier or later, depending on the species and family (Chambers et al. 2014, Keogan et al. 2018). Rather than the delay in breeding we see at Punta Tombo however, most observations of penguin species show advancement or no change in the timing of breeding (reviewed by Chambers et al. 2014). The delay at Punta Tombo is driven by oceanographic conditions in their non-breeding range. Specifically, later arrival dates for females correlate with the strength of the Rio de la Plata Plume (Rebstock and Boersma 2018). In years when the plume is strong, water is more turbid and penguin prey are likely spread over a wider area along the coast, decreasing visibility and prey encounter rates and delaying penguins in reaching a sufficient body condition to begin spring migration (Rebstock and Boersma 2018). Females that arrive late to the colony are generally in worse body condition than females that arrive earlier (Rebstock and Boersma 2018).

Our finding that the timing of fledging did not change over the last 34 years likely reflects constraints imposed by the timing of food availability close to the colony. Chlorophyll-a levels, a proxy for forage fish abundance (Afán et al. 2015), peak in the southwest Atlantic in late November and are declining in January and February when chicks are fledging (Rivas et al. 2006, Boersma at al. 1990, Boersma et al. 2013) and adults begin traveling farther to forage (Boersma et al. 1990, Boersma and Rebstock 2009). Though the proximate causes of fledging are unknown, fledging when the ocean is still productive would likely increase prey encounter rates for recent fledglings and reduce their risk of starvation through trophic mismatch (Cushing 1990). Chicks therefore likely time fledging based on a combination of evolved responses to photoperiod and the quantity and quality of food being brought to the nest. These factors are decoupled from the conditions in the non-breeding range that determine the arrival and onset of breeding in adults, and this decoupling has likely contributed to the differential shifts in the timing of reproductive events, resulting in the compression of the nestling period.

Fledging age and condition at fledging

Chicks that fledged younger left the colony with shorter and narrower bills, but we found no relationship between age and flipper length. These results match our predictions based on what we understand about chick growth in this species—while chicks typically reach adult flipper size before fledging, their bills do not grow to adult size until after they fledge (Gownaris and Boersma 2021).

We found a more complex relationship between age at fledging and three of the morphological measurements: mass, body condition, and foot length (Figure **1.2**a, Figure **1.2**b,Figure **1.2**f). In each of these analyses, there was a significant interaction between age at fledging and year. Early in the study, chicks that remained in the nest longer fledged heavier, in better body condition, and with longer feet. In later breeding seasons however, the trend reversed, with younger chicks fledging with a higher mass, body condition, and foot length. One possible explanation for this is that in the 1980s, chicks of lower quality that would benefit from more time in the nest and more meals from parents were able to extend their nestling period. In present day, low-quality chicks are unable to do the same. Alternatively, density dependence may have been a stronger driver of chick growth at Punta Tombo 30 years ago—with the colony having decreased over 40% since the 1980s (Rebstock et al. 2016, Gownaris & Boersma 2019), there may now be more food available for chicks. Though we do not see evidence of release from density dependence expressed in mean number of chicks fledged per nest, which has not increased with the decrease in density (Gownaris and Boersma 2019), chicks fledging younger and heavier in recent years may indicate that there is more food available for surviving chicks and warrants future studies of density dependence at Punta Tombo.

Smaller and lighter fledglings are less likely to recruit

Magellanic penguin chicks that fledged at a lower mass or with smaller bills, flippers, or feet were less likely to be seen again as juveniles or adults (Figure **1.3**). These findings are consistent with several studies showing that post-fledging survival increases with fledgling traits such as wing-length and mass (Schwagmeyer and Mock 2008, references in Naef-Daenze and Grueble 2016), including findings by Koehn et al. (2016) that Magellanic chicks with longer flippers and feet than those of their sibling were more likely to return to colony as adults. Though sex was not a focus of the study, we do note that we resighted more males than females over the course of the study. Gownaris and Boersma (2019) showed that juvenile female survival was lower than that of juvenile males. We found no significant effect of chick down at fledging on return rates, suggesting that its negative impact on swimming and diving is minor. The down feathers are weakly attached to their follicles at this stage and are easily lost when pulled or rubbed. The fledglings therefore likely shed their remaining down quickly as they move through the water. Though we found a signal for indirect consequences of shortening the nestling period via mass and skeletal size at fledging, we did not find that fledge date or fledge age predicted the likelihood of return directly. This could mean that our statistical power was insufficient to capture the comprehensive signal (i.e., sample of returned fledglings was not large enough) or that other determinants of fledgling survival overwhelmed the effects of fledging age.

Mortality during the post-fledging period is high for many birds because younger individuals are less effective at foraging and less capable of avoiding predators (Orians 1969, Lescroël et al. 2019). Nevertheless, juvenile survival can be an important determinant of population growth, even in long-lived populations where adult survival is considered the major factor in population dynamics (Gaillard et al. 1998, Dehnhard et al. 2014, Naef-Daenze and Grueble 2016). In fact, sex-biased mortality of juvenile Magellanic penguins at Punta Tombo contributed to the skewed adult sex ratio more than mortality in any other age class (Gownaris and Boersma 2019, Gownaris et al. 2020). By deepening our understanding of the linkages between breeding phenology, fledging condition, and recruitment, we gain insight into the factors driving survival of individuals in this difficult-to-study, yet demographically important, age class.

Conclusions

Magellanic penguins, along with other top marine predators, are sentinel species (Boersma 2008), informing us of changes in the marine environment. The changes in phenology that we observe in this population inform us not only of the fate of the species, but of broader environmental changes in their ocean habitat. It is clear that the impacts of climate-driven phenological shifts on species performance are complex. While some effects of environmental change can be buffered by phenological plasticity, like the onset of reproduction and the duration of the nestling period in this study, these changes were made at the cost of chick growth, which may indirectly reduce the likelihood of these chicks surviving their first year at sea. Fledging dates did not shift over the last 34 years, suggesting not only that the drivers of phenology differ among key life-history events, but that these drivers are impacted unequally by global change. As the body of literature documenting phenological shifts in plant and animal species grows, so too must our understanding of the nuances of these shifts. This study highlights the importance of examining how phenological shifts propagate across the annual cycle, revealing phenological stretching or compression that impacts performance and survival.

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1.7 Data Availability Statement

Data are available on Zenodo: http://doi.org/10.5281/zenodo.4658311

1.8 Supplementary Material

Supporting Information. Cappello, C. D., and P. D. Boersma. 2021. Consequences of phenological shifts and a compressed breeding period in Magellanic penguins. Ecology.

APPENDIX S1

Table S1 Parameter estimates for best supported linear mixed effects models testing the effect of age at fledging (age) and breeding season, presented as years since 1900 (year), on six morphological features. For model comparisons, see Table 1.1.

Response	Predictors	coef	STE	*t*
Mass	intercept	-2.85	1.30	-2.19
	age	0.07	0.02	3.94
	year	0.06	0.01	4.47
	age:year	-0.0007	0.0002	-4.04
Bill length	intercept	3.75	0.18	21.28
	age	0.01	0.00	7.14
	year	0.003	0.001	2.76
Bill depth	intercept	1.56	0.03	46.11
	age	0.0015	0.0004	3.36
Flipper	--	--	--	--
Foot	intercept	8.08	1.44	5.61
	age	0.05	0.02	2.94
	year	0.04	0.01	2.59
	age:year	-0.0006	0.0002	-2.95
Scaled mass index	intercept	-3.84	1.54	-2.50
	age	0.08	0.02	4.04
	year	0.07	0.02	4.38
	age:year	-0.0008	0.0002	-4.04

Table S2 Comparison of models describing the probability of returning to the colony as a juvenile or adult considering mass or size at fledging.

Predictors	AIC	ΔAIC
Mass	294.50	--
Bill depth	299.28	4.8
Bill length	301.88	7.4
Foot	303.29	8.8
Flipper	308.68	14.2
Scaled mass index	312.63	18.1

Chapter 2.

TROPHIC MISMATCH IN A VARIABLE ENVIRONMENT: EFFECTS OF CLIMATE-DRIVEN PHENOLOGICAL SHIFTS IN A MIGRATORY SEABIRD

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Abstract

Climate-driven phenological shifts may result in mismatches between consumers and resources, decreasing consumer fitness. Although evidence of phenological shifts across many organisms suggests the potential for widespread trophic mismatch, the magnitude of these shifts can be much smaller than the degree of environmental variability to which organisms are already adapted. The degree of environmental variability, and how consumers cope with it, will determine how phenological shifts affect fitness. Leveraging a 34-year field study and 20 years of remotely sensed chlorophyll-a data (a proxy for prey availability), we assessed whether delayed migration and breeding in Magellanic penguins reduced their performance and increased trophic mismatch. Reproductive success was highest when eggs were laid close to the initiation of the local spring chlorophyll bloom. However, chlorophyll phenology was >7 times more variable than egg laying by penguins, and there was no evidence of an increasing mismatch between breeding and annual chlorophyll phenology over the course of the time series. Instead, we found that breeding aligned with the 20-year average of chlorophyll phenology, and that fewer individuals now lay during this window of higher reproductive success. These results suggest that, although penguins may cope with environmental variability by matching long-term averages instead of tracking yearly conditions, this strategy may eventually be an insufficient buffer against climate change as breeding is increasingly delayed. This study emphasizes the need to consider environmental variability and life history together to understand how phenological shifts impact populations.

Keywords: climate change; phenology; trophic mismatch; match-mismatch hypothesis; migration; life history; seabird; Magellanic penguin; *Spheniscus magellanicus*

2.1 INTRODUCTION

Shifts in phenology—the timing of important life events such as growth, migration, or reproduction—are among the best documented organismal responses to global change (Walther et al. 2002, Parmesan 2006). Because the timing of such events determines the environment that individuals and their offspring experience, shifts in phenology have the potential to impact individual performance, population demography, and selection (Visser and Gienapp 2019).

Considerable variation in phenological responses exists within and across trophic levels, with species at higher levels being, on average, slower to respond to environmental change than species at lower levels (Thackeray et al. 2016). Such differential shifts can result in a mismatch between the timing of highest energetic need for consumers (e.g. reproduction) and the timing of peak resource availability (Visser et al. 1998, Post and Forchhammer 2008). Such phenological mismatches are hypothesized to reduce consumer fitness, a concept commonly referred to as the Match-Mismatch Hypothesis (MMH) or the Cushing Hypothesis (Cushing 1990). The MMH provides a useful framework for examining the consequences of phenological shifts and addresses a question crucial to ecology and conservation—can species adjust to their rapidly changing environments?

Trophic mismatch may not always be an outcome of climate-driven phenological shifts. For trophic mismatches to occur with climate change, a few conditions must apply. First, resource abundance must be an important driver of consumer fitness (Kharouba and Wolkovich 2020). Second, there must be seasonality in both resource and consumer annual cycles that enables matching or mismatching (Kharouba and Wolkovich 2020). Finally, climate change must cause a differential phenological shift for consumers and resources. In highly variable environments, however, animals and plants may not be closely tracking their resources year to year, instead employing strategies such as bet hedging or adaptive mismatch (Bertram et al. 2001, Kharouba and Wolkovich 2020). In such cases, increasing trophic mismatch may not be the inevitable outcome of climate-change-induced phenological shifts. Thus, how consumers have evolved to cope with environmental variability and unpredictability will shape whether and how phenological shifts affect fitness through trophic mismatch.

To understand when trophic mismatch should occur, and what its outcome will be for individuals and populations, match-mismatch dynamics must be studied across a diversity of life histories (e.g., migratory vs. resident) and systems (e.g., terrestrial vs. marine, variable vs. predictable). Migratory animals are particularly vulnerable to mismatch with peaks in resource availability because environmental conditions in their non-breeding range can be decoupled from those in their breeding range (Both and Visser 2001). Environmental cues to begin pre-breeding migration may be misaligned with the optimal timing for reproduction at the breeding site. Thus, the timing of migration can limit an animal's ability to track environmental changes in their breeding range through phenological flexibility. For example, in a population of migratory pied flycatchers (*Ficedula hypoleuca*), optimal conditions for breeding advanced over a 20-year period, but arrival from migration did not, resulting in differential phenological shifts with climate change (Both and Visser 2001). Though the population was able to advance breeding by shortening the time between arrival and egg laying, the advance was not enough to track environmental conditions at the breeding site (Both and Visser 2001). Trophic mismatch from mistimed spring migration is thought to be a driver of population declines in several migratory passerine species in Europe (Both et al. 2006).

Support for the MMH is mixed, but testing for match-mismatch in natural systems is difficult (Kharouba and Wolkovich 2020). Studies rarely have information on the timing of both the consumer and its resource, and even fewer have data spanning sufficient years or decades to detect trends over time (Kharouba and Wolkovich 2020). To address these issues, we examined the consequences of delayed breeding in a long-lived, migratory seabird to determine whether MMH induced by climate change is affecting this species. We used data from a 34-year longitudinal study following individual Magellanic penguins (*Spheniscus magellanicus*) and their nests at a large but declining colony at Punta Tombo, Argentina (Rebstock et al. 2016; Figure **2.1**). Over time, spring migration and the onset of breeding at Punta Tombo have become delayed, with median egg-laying and hatching dates occurring nine to ten days later on average than in the 1980s (Rebstock and Boersma 2018, Cappello and Boersma 2021). Oceanographic conditions in the population's non-breeding range in northern Argentina, Uruguay, and southern Brazil influence arrival dates; in years when the Rio de la Plata Plume is stronger, food is likely less available to the penguins, resulting in their later arrival to Punta Tombo and females arriving in worse body condition (Rebstock and Boersma 2018). Oceanographic conditions associated with the Rio de la Plata Plume, however, are unlinked from the oceanographic conditions over 1000 km south near Punta Tombo that drive the annual cycle of resource abundance. The timing of optimal ocean conditions for seabirds, when forage fish are most available, is expected to shift with global warming of sea temperatures (Keogan et al. 2021), but local trends in ocean phenology at Punta Tombo have not been examined. If the window for optimal breeding near Punta Tombo is advancing or unchanged, the penguins that return late to the colony risk their chicks hatching outside of the peak of food availability.

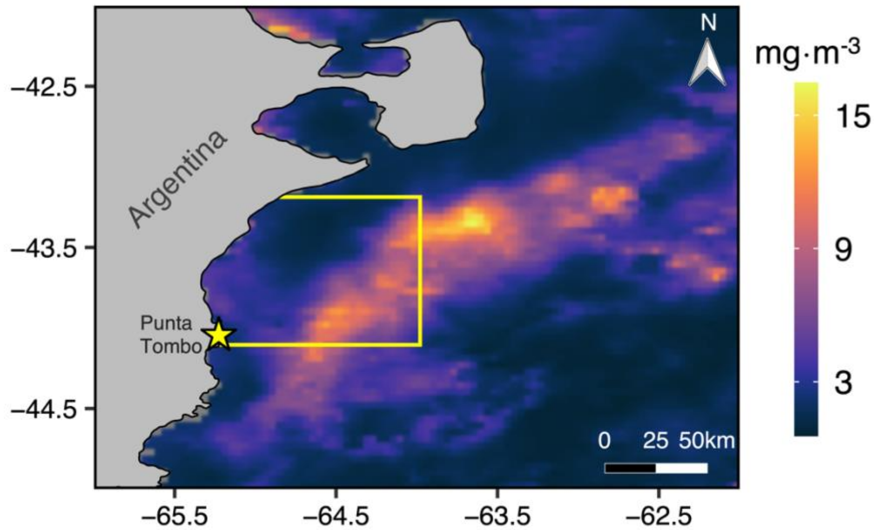

Figure 2.1: Study area showing chlorophyll-a concentration (mg m^{-3}) near Punta Tombo (marked by the star) when the local tidal mixing front is strong and within the penguins' foraging area. The yellow box shows where penguins forage when chicks are under 30 days old and most vulnerable to starvation (Boersma et al. 2015). Data: time-averaged map of 4 x 4 km chlorophyll-a concentration (mg m^{-3}) from MODIS-Aqua from 1 Nov to 1 Dec 2017 (https://giovanni.gsfc.nasa.gov/giovanni/)

To determine whether trophic mismatch is increasing at Punta Tombo and lowering reproductive success, we first tested the prediction that when breeding is later at Punta Tombo, the mismatch between lay dates and optimal ocean conditions increases. Second, we estimated the impact of breeding phenology and its synchrony with oceanographic conditions on reproductive success at the individual level. We tested whether the timing of a common proxy for prey availability, chlorophyll-a concentration (mg m^{-3}, abbreviated CHL), predicted breeding success. We predicted that greater synchrony between penguin laying and CHL bloom initiation dates would correlate with increased reproductive success.

2.2 METHODS

Study System

We studied individually marked Magellanic penguins (*Spheniscus magellanicus*) and their nests at Punta Tombo, Chubut, Argentina (44.03 W, 65.21 S; Figure **2.1**) beginning in 1982. Punta Tombo is a coastal, semi-arid desert and provincial nature reserve. The oceanic waters surrounding Punta Tombo are highly productive in the austral summer as tidal mixing fronts form along the continental shelf (Acha et al. 2004, Rivas et al. 2006). The seasonal front that forms near Punta Tombo in austral spring peaks during the summer and dissipates in the autumn when the water becomes less stratified (Rivas et al. 2006, Rivas and Pisoni 2010). This tidal front is associated with high primary production and fish and seabird feeding (Spinelli et al. 2012, Luzenti et al. 2021) and supports colonies of Magellanic penguins, imperial (*Leucocarbo atriceps*) and Magellanic cormorants (*Leucocarbo magellanicus*), kelp gulls (*Larus dominicanus*), and southern sea lions (*Otaria flavescens*)(Boersma et al. 2013).

Magellanic penguins that breed at Punta Tombo migrate north in the austral winter and spend the non-breeding season on the continental shelf of northern Argentina, Uruguay, and southern Brazil (Stokes et al. 2014). Males return to the colony at Punta Tombo in September to establish nests, and females arrive one to two weeks later (Boersma et al. 1990). Females lay one clutch of two eggs in October, and parents share incubating duties until the eggs hatch 38 to 42 days later (Boersma et al. 1990, Boersma et al. 2013).

Parents rear chicks in the nest for 65 to 75 days on average (Boersma et al. 2013). Chicks less than 30 days old (early chick phase) are continuously guarded by one parent while the other forages at sea, returning with anchovy, juvenile hake, squid, and crustaceans to provision their young (Boersma et al. 2009). During the early chick phase, chicks require meals every 1 to 2 days to survive, and adults forage within 100 km of the colony (Boersma and Rebstock 2009; Figure **2.1**). Chick mortality is highest during this period, particularly within the first ten days (Boersma and Stokes

1995). After 30 days (late chick phase), chicks are frequently left unattended as they are less vulnerable to predation and are able to thermoregulate (Boersma et al. 2013, Gownaris and Boersma 2021). Parents forage farther from the colony during the late chick phase and return to feed their chicks less frequently (Boersma and Rebstock 2009). Chicks fledge in January and February. The primary cause of chick mortality is starvation, with an average of 39% of chicks starving each year (Boersma and Rebstock 2014). Most starvation occurs within 10 days after hatching (Boersma and Stokes 1995, Boersma and Rebstock 2014).

Penguin Data

Beginning in 1982, we followed individual Magellanic penguins, marked with either stainless-steel flipper bands or web tags (Boersma and Rebstock 2010a). In September and October of each year, we searched for banded birds and their nests, marking eggs with permanent marker. Starting eight to twelve days prior to estimated egg hatch dates, we checked the nest every 24 hours until all eggs hatched. If eggs were laid before the first nest check of the season, we estimated the clutch initiation date by subtracting 41 days from the hatch date of the first chick (incubation period: Rebstock and Dee Boersma 2011, Boersma et al. 2013). We marked chicks with temporary, fiber-tape bands and/or colored them with semi-permanent marker to identify first and second-hatched chicks. We then checked the study nests every 1 to 10 days, recording the presence and absence of adults and the condition of chicks until the nest either failed or all the chicks fledged. When chicks' feet were over 8 cm long, we applied a stainless-steel web tag (Boersma and Rebstock 2010a). We considered a chick to have fledged if it was seen after 10 January and weighed over 1.8 kg at its last weighing (Boersma et al. 1990). We did not collect data in 2011 because of permit issues.

Oceanographic Data

We used remotely sensed chlorophyll-a concentration (mg m^{-3}, abbreviated CHL) as a proxy for ocean primary production and penguin prey availability. Because of the difficulty in determining the abundance and distribution of forage fish, and because forage fish feed at a low trophic level, CHL is frequently used as a proxy for food availability in studies of marine predators (Afán et al. 2015). We obtained CHL data from the European Space Agency Ocean Color Climate Change Initiative (OC-CCI) (http://www.esa-oceancolour- cci.org). This product merges data from NASA's Sea-viewing Wide Field-of-view Sensor (SeaWiFS), NASA's Aqua Moderate Resolution Imaging Spectroradiometer (MODIS), and ESA's Medium Resolution Imaging Spectrometer (MERIS). We downloaded five-day composites (v4.2) at 4x4 km resolution from 1998 through 2017 and converted netCDF-formatted files to raster images and rectangular data frames using the *ncfd4* package in R (Pierce 2019). We selected our area of study based on data from satellite transmitters deployed on Magellanic penguins at Punta Tombo between 1998 and 2001 and between 2006 and 2009 that give the foraging location of penguins while they are rearing chicks under 20 and 30 days old (Boersma & Rebstock 2009, Boersma et al. 2015; Figure **2.1**). This area consisted of 637 4x4 km pixels (2,548 km^2 total). We excluded observations where fewer than 85% of pixels had CHL data during the 5-day window. We chose 85% because it was near a breakpoint in the number of observations that had at least n pixels with CHL values, with n ranging from 0 to 637 (as in Rebstock & Boersma 2018). Excluded observations were generally clustered in the winter months when penguins are migrating and absent from the colony. During the breeding season (September-April), we retained 94% of observations. For each retained observation, we averaged all pixels to give a single CHL value for the five-day period.

Statistical Approach

Chlorophyll phenology:

To establish a metric of CHL phenology within the study area, we identified the start date of the spring/summer CHL bloom associated with the local tidal mixing front each year. To define the start date, we used a threshold bloom initiation method, which identifies the first date within a time period that CHL rises above a pre-determined value (Siegel 2002, Brody et al. 2013). Following Brody et al. (2013), we used five percent above the climatological median of the CHL time series as our threshold. For each year, we determined the maximum (i.e., peak) CHL date during the breeding season, then moved backwards in time until CHL values were below the threshold for 14 consecutive days. We defined the bloom initiation as the first date after the 14 days that the CHL was above the threshold. We then assessed whether CHL phenology remained constant over time using a linear regression with CHL initiation date as the response variable and year as the predictor variable.

Trends in trophic mismatch:

We tested the prediction that temporal mismatch between egg-laying and CHL phenology increased over the 20-year period when both penguin and CHL data were available (1998 to 2017). First, we calculated the median and mean penguin clutch initiation dates for each year between 1998 and 2017 using 3,319 nests. We then calculated a colony mismatch index, subtracting the CHL initiation date from the median clutch initiation date in each year. We performed a linear regression with colony mismatch index as the response variable and year as the predictor variable.

Phenology and reproductive success:

To assess how breeding phenology and mismatch from optimal CHL conditions was related to individual fitness, we examined the reproductive output of 2,923 nests with banded, breeding females between 1998 and 2017. We built a generalized additive mixed model (GAMM) using the *mgcv* package in R (Wood 2017) with number of chicks that survived to fledging as a binomially distributed response variable scored out of 2 (i.e. the typical clutch size for Magellanic penguins and the maximum clutch size for our study sample). We included the interaction between clutch initiation date and individual mismatch as a fixed effect and applied a smoother as the data followed a non-linear pattern. We calculated the individual mismatch index by subtracting the date of CHL initiation from the date the first egg was laid in the nest. We added female parent ID and breeding season as random effects. We then examined the model output to identify the overall optimal clutch initiation dates between 1998 and 2017. Last, to assess the extent to which penguin laying dates have occurred during this optimal breeding period over the course of the study, we built a linear mixed effects model using the *lme4* package in R (Bates et al. 2015). As the response variable, we calculated the number of days before or after the optimum window that each bird initiated its clutch. We included breeding season as a continuous predictor variable and female parent ID as a random-intercept term. We performed all analyses using R version 4.0.3 (R Core Team 2020).

2.3 RESULTS

Testing for a mismatch between penguin and resource phenology:

Between 1998 and 2017, bloom initiation dates near Punta Tombo frequently occurred in September and October, but dates were variable and spanned August through December (mean = Oct 8th, SD = ± 24.7 days, n = 20 years; Figure **2.2**a). Date of bloom initiation showed no trend over time (ß = 0.71, 95% CI = -1.32 - 2.75, p = 0.47, n = 20 years). Median laying dates of penguins between 1998 and 2017 (excluding 2011 when we did not have a field season) occurred in October and were much less variable than bloom initiation dates (mean = Oct 14th, SD = ± 3.50, n = 19 years; Figure **2.2**a).

Though CHL bloom and penguin breeding phenology both typically begin in the austral spring, we found high variability in the days of mismatch among years (Figure **2.2**). Colony-level mismatch varied between 46 days before and 56 days after the bloom initiation. This variation was largely driven by the CHL bloom phenology which had a standard deviation that was 7.06 times higher than that of penguin laying dates (Figure **2.2**a). We found no directional change in mismatch over time (ß = -0.49, 95% CI = -2.57 - 1.58, p = 0.62, n = 19 years; Figure **2.2**b).

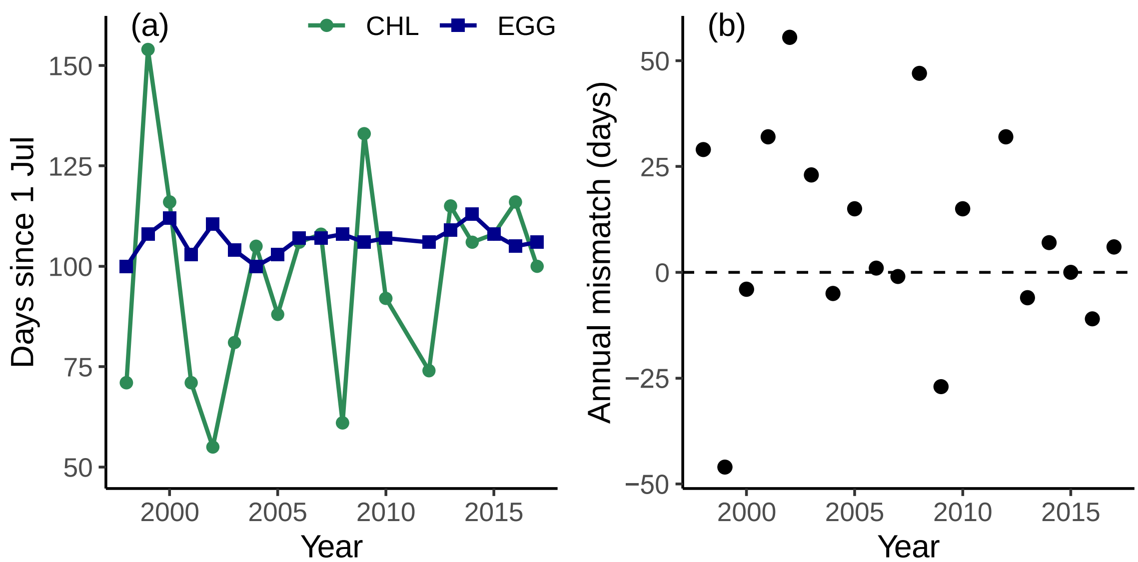

Figure 2.2: (a) Time series of CHL initiation dates (green circles) and median lay dates (blue squares) show that CHL phenology is more variable than penguin phenology at Punta Tombo (n = 19 years). (b) Days between colony laying and bloom initiation dates (i.e., mismatch) showed no significant trend over time (n = 19 years).

Yearly breeding phenology did not track inter-annual variation in CHL phenology; median laying dates did not correlate with the bloom initiation date of the concurrent (ß = 0.03, 95% CI = -0.04 - 0.10, p = 0.38, n = 19 years) or the previous year (ß = 0.03, 95% CI = -0.03 - 0.10, p = 0.28, n = 18 years). Laying dates, however, did align with the 20-year average timing of CHL initiation. Between 1998 and 2017 (excluding 2011), clutch initiation dates occurred 8 days (SD = ± 25) after bloom initiation on average, suggesting that rather than track local CHL phenology on an intra-seasonal scale, penguins bred at the long-term average of CHL timing (Figure **2.3**).

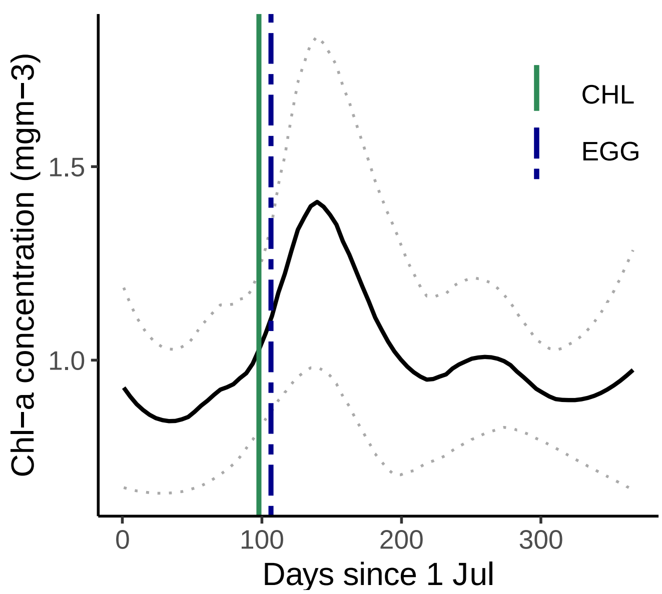

Figure 2.3: 20-year composite of smoothed daily chlorophyll-a concentration values from 1 Jul through 30 June (black line, ± 1 SD illustrated with the dotted curves). The 20-year average CHL initiation date (green, vertical line) occurred 8 days before the 19-year average egg laying date (blue, vertical line).

Effect of trophic mismatch and breeding phenology on reproductive success:

In support of the prediction that phenology drives fitness at Punta Tombo, we found that individual mismatch and clutch initiation date affected reproductive success (GAMM: deviance explained = 38%, edf = 13.10, p < 0.0001, n = 2,923 nests, Figure **2.4**a). Reproductive success was overall highest as absolute mismatch decreased and when birds laid eggs early within the breeding season; reproductive success peaked *ca.*10 days after CHL bloom initiation (Figure **2.4**b) and when clutch initiation occurred on or before October 4th (Figure **2.4**c). In years when the CHL bloom occurred substantially before penguin laying dates, the earliest breeding penguins had higher reproductive success. In the year with the latest CHL bloom (1999), penguins that bred later had higher reproductive success.

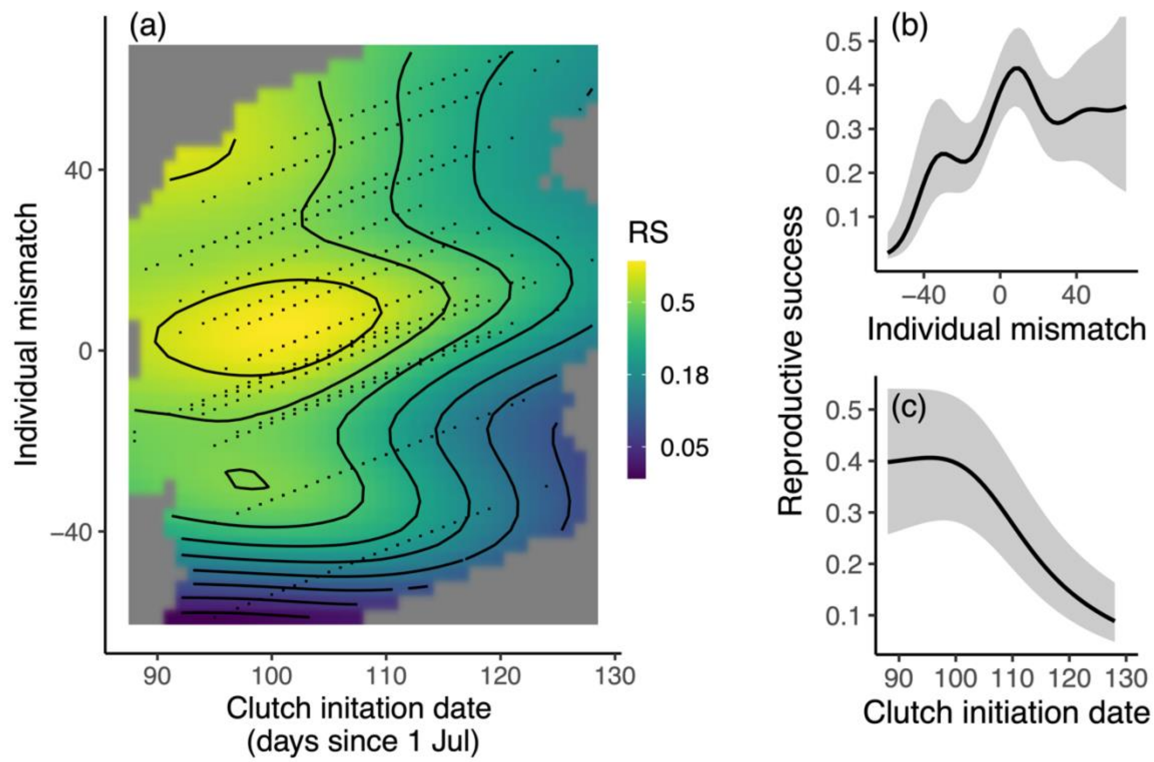

Figure 2.4: Model surface showing the likelihood of fledging chicks across clutch initiation dates and individual mismatch (days between clutch initiation and CHL initiation date) values (n = 2,923 nests). A negative mismatch value indicates the clutch was initiated before the CHL bloom. RS gives the reproductive success, i.e., the number of chicks predicted to fledge from the nest. The black points represent individual nests. (b) Predicted RS values from the full model across individual mismatch values and (c) clutch initiation dates.

Across all years, reproductive success was highest for birds that bred on or before October 4th. We found that birds laid eggs further from the optimal lay date over time (ß = 0.23, 95% CI = 0.19 - 0.26, n = 3319 nests; Figure **2.5**). Thus, though mismatch with yearly CHL conditions did not appear to increase over the course of the study (Figure **2.2**b), mismatch with the long-term CHL average did (Figure **2.5**).

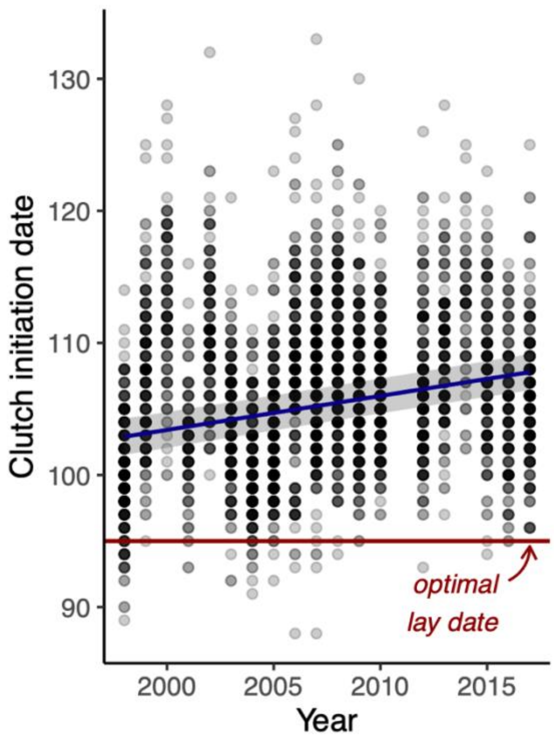

Figure 2.5: Relationship between individual lay dates and breeding season. Over time, lay dates moved further away from the optimal laying window on or before 4 October (n = 3,319 nests). The 95% confidence interval is represented by gray ribbon.

2.4 Discussion

To identify the mechanisms and extent to which animals will be affected by climate change, it is necessary to understand 1) how animals time life events to coincide with favorable environmental conditions, and 2) how constrained they are in tracking these optimal conditions. We found that for Magellanic penguins at Punta Tombo, the optimal date to lay eggs was closely aligned with the long-term average date of the spring CHL bloom initiation. Birds that initiated their clutch outside of this optimal window fledged fewer chicks. The timing of the CHL bloom, however, was over seven times more variable than that of egg laying, such that the phenological shift toward later breeding has not resulted in a directional increase in mismatch with yearly CHL timing. Nonetheless, the ongoing shift toward later breeding has meant that some individuals are less aligned the long-term CHL average, which reduces their reproductive success, and may have implications for the population as climate change progresses.

Effect of lay date and mismatch on reproductive success

Individual reproductive success was highest when eggs were laid closer to the initiation of the CHL bloom, peaking *ca.* 10 days after bloom initiation (Figure **2.4**b). This provides evidence that match-mismatch dynamics may drive reproductive success of individuals in this population. Starvation is the primary cause of chick death at Punta Tombo, with an average of 39% of chicks starving each year (Boersma and Rebstock 2014). For chicks to survive, there must be food within *ca.*100 km of the colony at the time of hatching, 38 to 42 days after egg laying (Boersma and Rebstock 2009, Boersma et al. 2013). Between 1998 and 2017, bloom initiation occurred, on average, in the first week of October. CHL peaked, on average, in mid-November when most chicks hatch. By timing egg laying with the onset of chlorophyll, adults likely ensure that by the time their eggs hatch, fish are abundant close to the colony.

We found that absolute laying dates also correlated with reproductive success, with later breeding individuals fledging fewer chicks than early individuals. This trend was reversed in one year (1999), when the CHL bloom initiation occurred over 40 days after penguins began laying eggs. In this year, later breeding individuals fledged more chicks that early individuals. Overall, reproductive success was highest when clutch initiation occurred on or before October 4th (Figure **2.4**c). Additional, but not mutually exclusive, explanations for the lower reproductive success of late breeders include late-returning adults obtaining lower quality nests (Stokes and Boersma 1998), being less efficient foragers, or beginning the breeding season in poor body condition (Rebstock and Boersma 2018). Additionally, chicks that remain in the nest late in the season may have higher exposure to summer heat waves on land (Boersma and Rebstock 2014, Holt and Boersma 2022).

Match-mismatch dynamics in a variable environment

Chlorophyll bloom phenology was over seven times more variable than that of egg laying, demonstrating that, even in a temperate environment with broadly predictable seasonality, the magnitude of fluctuations within seasons and among years can be high (Lof et al. 2012). Mismatch between breeding and CHL phenology ranged widely, with median laying dates occurring 46 days before to 56 days after bloom initiation. Rather than matching local CHL phenology each year, the Punta Tombo population appeared to initiate breeding closer to the climatological average of front timing; mean mismatch across all years was 8 days after bloom initiation, and the predicted optimal date for clutch initiation was October 4th, just four days earlier than the mean CHL bloom initiation.

Migratory animals are particularly susceptible to trophic mismatch because drivers of phenology in their non-breeding range can be dissociated from drivers in their breeding range (Both and Visser 2001, Both et al. 2010, Kristensen et al. 2015). For this population of Magellanic penguins, their inability to perceive local conditions before arriving in their breeding range, coupled with high inter-annual environmental variability, may have contributed to a life-history strategy where arrival to the colony aligns with the long-term average timing of favorable oceanographic conditions. Other migratory animals use long-term averages of resource availability to direct their seasonal movements, and in some cases, memory may be a stronger driver than perception of local environmental conditions (Mueller and Fagan 2008, Bracis and Mueller 2017, Abrahms et al. 2019). Though "playing the average" can result in low reproductive success when the environment deviates substantially from average, it may maximize fitness over a lifetime, particularly for a long-lived species that has many opportunities to breed (Lof et al. 2012)—Magellanic penguins begin breeding as early as four years old and can breed each year until they are over 30 (Boersma et al. 2013).

Over the course of the study, breeding occurred later at Punta Tombo while CHL initiation dates remained constant, on average. However, the scale of variability in CHL timing overwhelmed the changes observed in penguin breeding phenology, and we did not find evidence for increasing mismatch between penguin breeding and spring CHL blooms. A longer time series may be necessary for the signal of climate-driven changes in CHL phenology to emerge (Henson et al. 2018). Though we did not observe a trend in CHL phenology at Punta Tombo yet, substantial shifts will likely become apparent over the next century (e.g. phytoplankton phenology: Henson et al. 2018). Nonetheless, our results demonstrate that match between breeding and CHL bloom dates is important for reproductive success and that penguins are already experiencing increased mismatch from the average CHL conditions and their optimal breeding window. If changes in the timing of penguin migration and breeding continue, and as trends in CHL phenology become more apparent, the buffering capacity of aligning breeding with long-term CHL averages may be exceeded, and population dynamics are likely to be affected.

Conclusions

Climate change is rapidly altering the environments that animals experience. Understanding the mechanisms by which species shift their phenology in response to environmental variability and identifying the individual and population-level consequences of these shifts is an important component of predicting climate change outcomes. This study provides support for the potential of mismatch from long-term averages of resource phenology to decrease individual performance in long-lived, migratory animals. It also emphasizes the importance of considering the scale of environmental variability that animals experience, and their adaptations to cope with variability, when making predictions about phenological shifts as a driver of population dynamics through increasing mismatch. By assessing the outcomes of phenological shifts across life histories (e.g., migratory vs. resident, long- vs. short-lived) and in a range of environments (e.g., terrestrial vs. marine vs. freshwater), we can improve our predictions of climate change outcomes.

2.5 Acknowledgements

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Chapter 3.

SEXING GALÁPAGOS PENGUINS (*SPHENISCUS MENDICULUS*) BY MORPHOLOGICAL MEASUREMENTS

Citation: Cappello, C.D. and P.D. Boersma. 2018. Sexing Galápagos penguins (*Spheniscus mendiculus*) by morphological measurements. Endangered Species Research 35: 169-173 DOI: 10.3354/esr00879

Abstract

The ability to identify the sex of individuals is essential in studies of ecology, behavior, and conservation, but reliable methods for sexing species that exhibit low sexual dimorphism are often time consuming or invasive. Previous studies have evaluated the usefulness of morphological measurements as easy and minimally invasive means of sexing seabirds in the field. We used a discriminant function analysis (DFA) to determine the accuracy of sexing Galápagos penguins Spheniscus mendiculus using 6 morphological measurements: bill depth, bill length, head length, gape, flipper length, and foot length. Using these variables, we sexed 95% of study penguins correctly. Simplified functions, including bill depth and length, or bill depth only, also correctly classified the sex of 95% of study penguins. We also looked for sexual dimorphism in plumage, estimating the size of the white feather patch underneath the chin. Ninety-five percent of penguins with little to no white chin patch were female, while penguins with larger chin spots were both male and female. We show that Galápagos penguins, a rare and Endangered seabird, may be sexed accurately, even when data are limited to 1 morphological measurement.

Keywords: Sex determination; sexual dimorphism; morphology; Galápagos penguin; *Spheniscus mendiculus*; discriminant function

3.1 INTRODUCTION

Accurate and minimally invasive methods to determine the sex of individuals are important to studies of threatened populations (Clutton-Brock 1985, Zavalaga & Paredes 1997, Dechaume-Moncharmont et al. 2011). Knowledge of sex is critical to studies of breeding, behavior, ecology, population trends, and management. Sexing individuals of species that display low sexual dimorphism is difficult, however, and often necessitates invasive, time-consuming, and costly procedures, thus hindering studies important for conservation.

Many species of seabirds have low plumage and size dimorphism between sexes, making sexing individuals in the field difficult. Although molecular sexing techniques are reliable, they are costly and require permits for blood collection that are often challenging to obtain, especially when working with a rare or endangered species. Sexing birds by morphological measurements is a widespread field technique that is inexpensive, easy to implement, minimally invasive, and can be effective even for species with low sexual dimorphism (Dechaume-Moncharmont et al. 2011). For example, morphological measurements allow for sex classification in several penguin species, including Magellanic *Spheniscus magellanicus* (references in Vanstreels et al. 2011), Humboldt *S. humboldti* (Zavalaga & Paredes 1997, Wallace et al. 2008), African *S. demersus* (Pichegru et al. 2013), gentoo *Pygoscelis papua* and chinstrap *P. antarcticus* (Lee et al. 2015), rockhopper *Eudyptes chrysocome* (Poisbleau et al. 2010), royal *E. schlegeli* (Hull 1996), and little penguins *Eudyptula minor* (Arnould et al. 2004).

The Galápagos penguin *S. mendiculus* is the rarest penguin species and is listed as Endangered on the IUCN Red List of Threatened Species (Boersma et al. 2013). The population has 1500 to 4700 individuals and faces mounting threats such as the increasing frequency and intensity of El Niño, introduced predators such as rats and cats, fisheries, and habitat degradation (Boersma et al. 2013). Threats that limit food availability, such as El Niño and overfishing, may affect males and females differently if they forage at separate locations or depths or take different prey, as is the case in other penguins (Walker & Boersma 2003, Pichegru et al. 2013). Studies of Galápagos penguins will be more informative if the sex of individuals can be easily determined. Male and female Galápagos penguins look similar, but males are larger and have more distinct markings (Boersma 1977). These distinctions in size and plumage are subtle, however, and difficult to detect even when the birds are in hand. To assess morphology-based sex predictors, we collected morphological data for individuals whose sex was determined with genetic analysis. We then used a linear discriminant analysis to test the predictive ability of morphological measurements in sexing Galápagos penguins.

3.2 MATERIALS AND METHODS

Data collection

Known-sex samples:

We determined the sex of 61 (25 female, 36 male) adult Galápagos penguins through genetic analysis. We took blood samples from penguins of unknown age and breeding status captured on Fernandina, Isabela, Santiago, and Bartolomé Islands in Galápagos, Ecuador (0.95° S, 90.97° W) in 2010 and 2011. We collected blood through venipuncture of the interdigitary vein in the foot webbing and stored it in lysis buffer. Dr. Patricia Parker sexed individuals at the University of Missouri-St. Louis using a PCR-based approach (as described in Fridolfsson & Ellegren 1999).

Predictor variables:

During 8 research trips between 2010 and 2014, we used dial calipers (±0.1 mm) to measure bill length (length of exposed culmen), bill depth (measured at the nares), head length (occiput to tip of bill), and gape of the 61 penguins that we sexed genetically. We also measured flipper length (middle of elbow joint to tip) and foot length (back of heel to tip of middle toe) with a zero-stop ruler (±1 mm) (after Boersma 1974). We used the median measurement for each bird that we measured more than once as an adult, and the same person (P.D.B.) took all of the measurements. Because Galápagos penguins are difficult to capture, and non-invasive sexing techniques are preferable, we estimated the width of the patch of white feathers that grows under the chin (referred to as the chin spot). This can be estimated from several feet away and without capturing the individual. We assigned each individual to 1 of 4 categories: 0 (no chin spot), 1 (<0.5 cm across), 2 (0.5−1.5 cm), and 3 (>1.5 cm). For 41 individuals (16 females, 25 males), we also noted if the white chin was mottled with dark feathers.

Statistical procedures

We calculated mean and standard deviation for all continuous variables for each sex of our 61 known-sex penguins. To assess the overall size difference between sexes, we performed a 1-way analysis of variance for each variable using the *lm* function from the stats package in R. We then used morphological measurements from our known-sex samples to determine discriminant functions. We performed the discriminant analysis using the *lda* function from the MASS package in R (Venables & Ripley 2002). To assess the strength of the relationship between each variable and the canonical axis, we standardized the raw canonical coefficients to produce Pearson product-moment bivariate correlations (i.e., structure coefficients). To test the predictive ability of our models, we used a jackknife (leave-one-out) approach that predicted the sex of each individual based on the model fit when leaving that individual out of the dataset. We repeated this for each individual and calculated the proportion of individuals correctly sexed.

To determine our precision in measuring each morphological trait, we calculated the coefficient of variation for each trait of every adult Galápagos penguin that was measured 3 or more times between 1970 and 2017 (n = 7−21, depending on trait). We averaged these values to obtain 1 coefficient of variation per morphological variable. Because plumage may be more variable over time than bony structures, we fit a linear mixed effects model using all birds from our database with multiple chin spot measures (n = 68). We included chin spot as the response variable, time since first check and amount of breeding associated feather loss around the bill as fixed effects, and allowed random intercepts by individual ID.

3.3 Results

Males were significantly larger than females in all morphological variables in Galápagos penguins (Table **3.1**).

Table 3.1: Mean, standard deviation, range, and results of 1-way ANOVA for morphological measurements for known-sex male (n = 36) and female (n = 25) Galápagos penguins. Mean coefficient of variation (CV) and sample size (n) from repeated measurements of individuals are given for each trait. Significance is indicated by asterisks (***p < 0.001)

Variable (mm)	Females		Males		$F_{1,59}$	CV (n)
	Mean ± SD	Range	Mean ± SD	Range		
Bill depth	16.0 ± 0.7	14.8–17.6	18.7 ± 0.8	16.2–20.0	163.6***	2.22 (21)
Head length	115.8 ± 3.5	111.3–124.3	123.4 ± 3.1	117.1–128.4	82.7***	2.04 (7)
Bill length	54.3 ± 1.6	51.9–58.3	58.9 ± 2.3	51.4–62.1	73.1***	1.77 (21)
Flipper	120.3 ± 4.6	112.0–128.0	129.0 ± 3.9	120.0–140.0	62.3***	2.85 (17)
Foot	89.6 ± 4.3	75.0–96.0	97.0 ± 3.1	87.0–101.0	60.9***	2.31 (17)
Gape	20.4 ± 2.2	16.4–26.0	23.9 ± 2.1	20.7–29.4	39.0***	8.70 (16)

Using all continuous variables (we excluded chin spot from the discriminant analysis because data were categorical), we determined the following function:

$$D_1 = 0.042\ (\text{Bill length}) + 0.895\ (\text{Bill depth}) + 0.095\ (\text{Flipper})$$
$$+\ 0.019\ (\text{Foot}) + 0.038\ (\text{Head}) + 0.082\ (\text{Gape}) - 38.224$$

This function correctly classified the sex of 96.7% of study birds (97.2% of males, 96% of females; Wilk's lambda = 0.191, $p < 0.001$). One male and 1 female were misclassified. The distribution of discriminant scores is illustrated in Figure **3.1**a, and the canonical loadings for each variable are given in Table 3.2: Pearson product-moment bivariate correlations between each morphometric variable measured in Galápagos penguins and the canonical function. Bill depth, head length, and bill length had the largest loadings and best described the variance between males and females. Using the jackknife procedure, we correctly predicted the sex of 95.1% of study birds, misclassifying 1 male and 2 females.

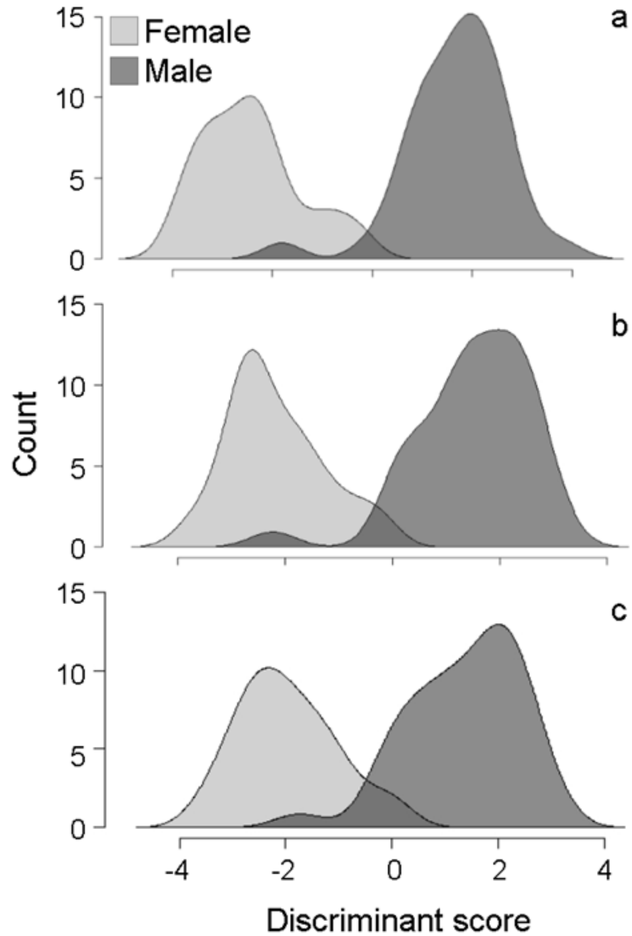

Figure 3.1: Distribution of discriminant scores for Galápagos penguins using (a) bill depth, bill length, head length, gape, flipper length, and foot length (D_1), (b) bill depth and bill length (D_2), and (c) bill depth only (D_3). The overlap between curves represents individuals misclassified by the functions before cross-validation. In (a), 1 male and 1 female were misclassified. In (b) and (c), 1 male and 2 females were misclassified

Because a discriminant function using only 1 or 2 variables may necessitate less handling time and reduce the stress on each individual, we derived 2 additional functions, one restricting the variables to bill length and bill depth, and one using bill depth only. We selected these variables because they best explained the variance in the previous function (Table 3.2: Pearson product-moment bivariate correlations between each morphometric variable measured in Galápagos penguins and the canonical function. Bill depth, head length, and bill length had the largest loadings and best described the variance between males and females). We selected bill length instead of head length because bill length is included within head length and was measured with higher precision than head length (Table 3.1: Mean, standard deviation, range, and results of 1-way ANOVA for morphological measurements for known-sex male (n = 36) and female (n = 25) Galápagos penguins. Mean coefficient of variation (CV) and sample size (n) from repeated measurements of individuals are given for each trait. Significance is indicated by asterisks (***$p < 0.001$)). Using bill depth and length, we derived the following function:

$$D_2 = 0.210 \text{ (Bill length)} + 1.021 \text{ (Bill depth)} - 29.950$$

This second function also classified 96.7% of study birds correctly, although it had a higher Wilk's lambda than the first function (Wilk's lambda = 0.229, $p < 0.001$; Figure **3.1**b). Our jackknifed accuracy was 95.1%. Reducing the equation to include bill depth only, we produced the following function:

$$D_3 = 1.254 \text{ (Bill depth)} - 22.06$$

D_3 correctly classified 95.1% of birds before and after jackknifing ($p < 0.001$; Figure **3.1**c). Using this third function, we calculated the discriminating threshold between male and female bill depth. We set D_3 to −0.49 (the intersection between male and female discriminant scores) and solved for bill depth, finding 17.2 mm to be the threshold between male and female bill depth, above which a penguin would be classified as male, and below which a penguin would be classified as female.

Bill length had the lowest coefficient of variation, followed by head length, bill depth, foot, flipper, and gape (Table 3.1: Mean, standard deviation, range, and results of 1-way ANOVA for morphological measurements for known-sex male (n = 36) and female (n = 25) Galápagos penguins. Mean coefficient of variation (CV) and sample size (n) from repeated measurements of individuals are given for each trait. Significance is indicated by asterisks (***$p < 0.001$)). We found substantial overlap between male and female chin spot size. Forty-three percent of penguins with a chin spot of category 2 were female, while 57% were male. Thirty-seven percent of penguins with a chin spot of category 3 were female, and 63% were male. There was less overlap in the little-to-no chin spot categories (0 and 1), with 95% of the group being female. We found that chin spot size did not differ over time (estimate −0.00003, profile confidence interval −0.002 to 0.001) but decreased with feather loss associated with breeding (−0.01; −0.16 to −0.04). Mottling in the chin spot did not provide additional clarity (44% of females and 60% of males had mottled chins).

Table 3.2: Pearson product-moment bivariate correlations between each morphometric variable measured in Galápagos penguins and the canonical function. Bill depth, head length, and bill length had the largest loadings and best described the variance between males and females

Variable	Structure correlations
Bill depth	0.95
Head length	0.85
Bill length	0.83
Flipper	0.80
Foot	0.79
Gape	0.70

3.4 DISCUSSION

Knowing the sex of animals is critical for many studies of their ecology and behavior. For a rare and Endangered species like the Galápagos penguin, finding effective means of sexing individuals while reducing stress is of value. We show that Galápagos penguins are sufficiently sexually dimorphic that they can be sexed accurately with just a few morphological measurements. Bill depth, bill length, and head length (which includes bill length as part of the measurement) were the strongest morphological indicators of sex. Bill measurements were the best predictors of sex for all other Spheniscus penguins (Wallace et al. 2008, Vanstreels et al. 2011, Pichegru et al. 2013), several other penguin species (Hull 1996, Lee et al. 2015), and seabird families (Grecian et al. 2003, Ferrer et al. 2016, Bourgeois et al. 2017). In reducing our discriminant function to bill depth only, we correctly sexed >95% of study penguins. This accuracy is comparable to the values reported in similar studies (91% in Arnould et al. 2004 and Lee et al. 2015; 93 and 97% in Hull 1996; 96% in Poisbleau et al. 2010). Chin spot size was potentially useful in identifying individuals with no or small chin spots as female, but was otherwise unreliable at separating the sexes and became smaller as breeding birds shed feathers around their bill. The ability to sex these penguins using only one measurement means less time in hand and less stress for each individual bird.

Bony structures like the bill were easier to measure precisely than the flipper, foot, or chin, which can vary depending on state of plumage or wear of toenail. Structures that lie under loose skin, like the occiput (bony point at the back of the skull used to measure head length), are more difficult to find than the exposed structures of the bill and may lead to more variation in measurement.

Sexual size dimorphism in Spheniscus penguins is likely a result of breeding behavior and niche segregation (Ainley & Emison 1972, Boersma 1977, Walker & Boersma 2003). Male Spheniscus penguins vie for nests and mates through physical competitions, and larger males have an advantage (Renison et al. 2002). Females fight less frequently and with less intensity (Renison et al. 2003). Resource partitioning between sexes in sexually dimorphic species has been suggested for a number of bird species (Selander 1966, Ainley & Emison 1972, Boersma 1977, Walker & Boersma 2003). Though male and female Galápagos penguins forage in the same horizontal range (Steinfurth et al. 2008), the sexual dimorphism in bill size could result in males eating larger prey than females. Males may also dive deeper than females, as in African penguins (Pichegru et al. 2013).

By establishing techniques for sexing individuals that are quick, minimally invasive, and accurate, we can better understand threats to endangered populations. Morphometric measurements, particularly those of bill depth and length, are accurate indicators of Galápagos penguin sex and are relatively easy to measure, making them useful tools for researchers.

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Chapter 4.

FIRST ESTIMATES OF MALE AND FEMALE SURVIVAL FOR THE RARE AND ENDANGERED GALÁPAGOS PENGUIN

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Abstract

Estimates of survival offer insights into species demography and global-change responses and can therefore support the conservation of threatened species. The Galápagos penguin (*Spheniscus mendiculus*) is a rare and endangered seabird, and its survival has not been rigorously estimated despite its conservation status. We built a mark-recapture model to estimate survival of males and female Galápagos penguins, using data from 484 marked adults that were captured during twice-yearly visits to Galápagos between 2010 and 2022. Because breeding status and location cannot be easily observed but are likely to influence detectability, we estimated detection probabilities for two separate classes that we assumed represented 1) a highly detectable class of individuals that bred within the study area, and 2) a less detectable class representing transient individuals that were captured when passing through the study area. We estimated apparent semiannual survival across all years to be 0.84 (95% CI = 0.78-0.92) for males and 0.85 (95% CI = 0.77-0.93) for females. Recapture probabilities were low, with median estimates of 0.18 during the hot season and 0.23 during cold season for the class with higher detectability and 0.02 in both seasons for the class with weaker detectability. Posterior estimates for survival overlapped substantially for male and female penguins. Survival was lowest between 2015 and 2016, coinciding with an El Niño, during which penguins did not breed and adults were observed to be in poor body condition. Overall, survival was lower than expected for Galápagos penguins. We discuss the biological reasons for these low survival probabilities as well as methodological limitations that might bias survival estimates. In all, our results highlight the potential and challenges of using mark-recapture models in deriving survival estimates for this rare and endangered seabird.

Keywords: Galápagos penguin; *Spheniscus mendiculus*; mark-recapture; Cormack-Jolly-Seber; individual heterogeneity; low detection

4.1 Introduction

Human activities have led to widespread declines in wildlife and loss of biodiversity (Ceballos et al. 2015). To mitigate climate-change and other anthropogenic impacts on threatened species, conservation planners frequently use models of population dynamics to evaluate and predict how wildlife will respond under varying management scenarios and environmental conditions (Brook et al. 2000). Population models are also used in classifying species based on their risk of extinction (e.g. the IUCN Red List of Threatened Species), which can be influential in decision making when allocating finite conservation resources (Rueda-Cediel et al. 2018). To better understand population dynamics, estimates of vital rates such as survival, fecundity, and recruitment are crucial (Lebreton et al. 1992) and rely on demographic data collected in the field.

Adult survival is often a key contributor to population dynamics, particularly among long-lived species such as seabirds (Sæther and Bakke 2000). Mark-recapture studies are a common approach to estimating survival that involve individual animals being captured, marked, released, and then recaptured (or resighted) during later occasions. Specific modeling frameworks are then applied to these data to estimate demographic rates. However, when species are rare, elusive, or live in remote locations, data collection is a challenge and detection of individuals can be very low, leading to inaccurate and imprecise survival estimates (Bröder et al. 2020). Modeling frameworks that can estimate survival while accounting for imperfect detection are therefore necessary in many wildlife studies.

The Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965) is a commonly used model formulation in ecology that jointly estimates survival and detection probabilities and can be extended to incorporate environmental and individual covariates such as sex, age, breeding status, and more (Lebreton et al. 1992). Cormack-Jolly-Seber (CJS) models rely on assumptions that are frequently violated in the wild (Pradel et al. 2005), however, including that individuals are equally detectable. When this assumption is violated, survival estimates may be biased low (Lok et al. 2019). The detectability of an individual can be driven by many factors, including its age, health, social status, and breeding status (Cubaynes et al. 2010). For example, an individual may alter its range during its breeding, non-breeding, and migratory stages. Depending on their breeding status, therefore, individuals may be more or less likely to overlap with survey routes and be available for detection. To overcome this obstacle in studies of birds, mark-recapture data are often collected during a breeding season, when many individuals will be breeding and have similar detectability (Pradel et al. 2005).

For populations that do not breed synchronously, constraining mark-recapture studies to a defined breeding period is not always possible. The Galápagos penguin (*Spheniscus mendiculus*), for example, is a marine predator endemic to the Galápagos Islands, Ecuador that has highly flexible and asynchronous breeding phenology (Boersma 1978). Adapted to the variable and unpredictable oceanographic conditions of Galápagos, these seabirds are opportunistic breeders and have been found with active nests in every month of the year (Boersma 1977, Boersma et al. 2013b). Without a set breeding season, it is difficult to plan data collection periods that maximize encounters with breeding individuals or individuals that are at a similar annual-cycle phase. Furthermore, Galápagos penguins do not breed in large or dense colonies like many other seabirds (Danchin and Wagner 1997), their breeding areas are remote, and their nests are difficult to locate because they are often inside tunnels and crevices in the lava (Boersma et al. 2013b). Thus, for reliable estimates of Galápagos penguin survival, careful consideration of their low and heterogenous detectability is essential.

Galápagos penguins are listed as Endangered on the IUCN Red List of Threatened Species, and thus, despite the challenges for data collection and modeling, studies of their survival are needed for designing and evaluating necessary conservation measures. The Galápagos penguin population is estimated to be about half of what it was in the 1970s (Vargas et al. 2005, Boersma et al. 2013b). This precipitous decline is likely due to mass-mortality events driven by the severe El Niños of 1982-1983 and 1997-1998, during which food was scarce for marine predators and breeding failure and adult mortality were high among seabirds (Dueñas et al. 2021). The frequency of severe El Niño events is expected to increase with climate change (Cai et al. 2014), and Galápagos penguins could face extinction from the additive impacts of strong El Niños and other ongoing pressures such as predation by introduced mammals and declines in prey availability (Vargas et al. 2007).

Here, we present a mark-recapture model to estimate survival rates of Galápagos penguins while accounting for imperfect detection and differences between male and female survival for the first time. We used 12 years of mark-recapture data, collected between 2010 and 2022, to estimate semiannual survival for adult penguins under varying El Niño conditions, predicting that survival would be lower at higher El Niño index values. We accounted for individual and temporal heterogeneity in detection probabilities to reduce bias in survival estimates. Recognizing that the rarity of the species and the variability its breeding phenology have hampered—and will likely continue to limit—precise estimates of Galápagos penguin survival, we present an analysis that aims to 1) better understand the data and quantitative tools necessary for precise estimates of survival rates for this species, and 2) lay a foundation for future models that can estimate population trends and project population dynamics under varying management and climate-change scenarios.

4.2 METHODS

Study system and species

Galápagos Islands:

The Galápagos Islands are a volcanic archipelago in the equatorial Pacific that supports high levels of biodiversity and endemism. The waters surrounding the archipelago are oligotrophic and iron limited (Martin et al. 1994), but topographic upwelling of the South Equatorial Countercurrent (i.e. Cromwell Current) and Humboldt Current delivers pulses of nitrate and iron into the photic zone along the islands (Martin et al. 1994). This upwelling is critical for driving phytoplankton blooms that sustain the diverse marine life of Galápagos, and is particularly strong on the western edge of the archipelago where the Cromwell Current flows into Fernandina and Isabela Islands (Jiménez 1981). The Galápagos archipelago experiences two seasons: a hot and rainy season from January to May, and a cold season (also referred to as the garua season) from June to December. Upwelling, though less predictable than in upwelling zones at higher latitudes (Villegas-Amtmann et al. 2017), is generally stronger during the cold season when breeding is more common among marine animals (Lack 1950).

The climate of Galápagos is affected by the climatic-oceanographic cycle known as El Niño—Southern Oscillation (ENSO). Abundant upwelling of nutrient-rich water occurs during the La Niña phase of ENSO. During the El Niño phase, upwelling and ocean mixing are disrupted, primary production slows, and food becomes scarce for marine life (Dueñas et al. 2021). During severe El Niño events in 1972-1973, 1982-1983 and 1997-1998, widespread reproductive failure and starvation occurred among Galápagos seabirds, marine mammals, and the endemic marine iguana (*Amblyrhynchus cristatus*) (Boersma 1978, Valle et al. 1987, Vargas et al. 2005).

Galápagos penguins:

The Galápagos penguin is endemic to the Galápagos Islands and breeds largely in the western archipelago, with the largest subpopulation being in the Canal Bolívar, along Fernandina and Isabela Islands (Boersma et al. 2013b; **Figure 4.1**). Smaller subpopulations persist at Floreana and Santiago/Bartolomé Islands (Figure **4.1**). Galápagos penguins are resident to Galápagos and do not migrate, foraging primarily on inshore, forage fish year-round. The population was last estimated to have between 1,500 and 4,700 individuals (Boersma et al. 2013b).

Galápagos penguins are less seasonal than other penguins and seabirds at higher latitudes and may breed and molt in any month of the year (Boersma et al. 2013b). Females lay two-egg clutches in protected, shaded crevices in the lava, producing clutches up to three times in a 12-month period (Boersma 1977). Male and female Galápagos penguins molt twice a year, typically before they breed (Boersma 1977).

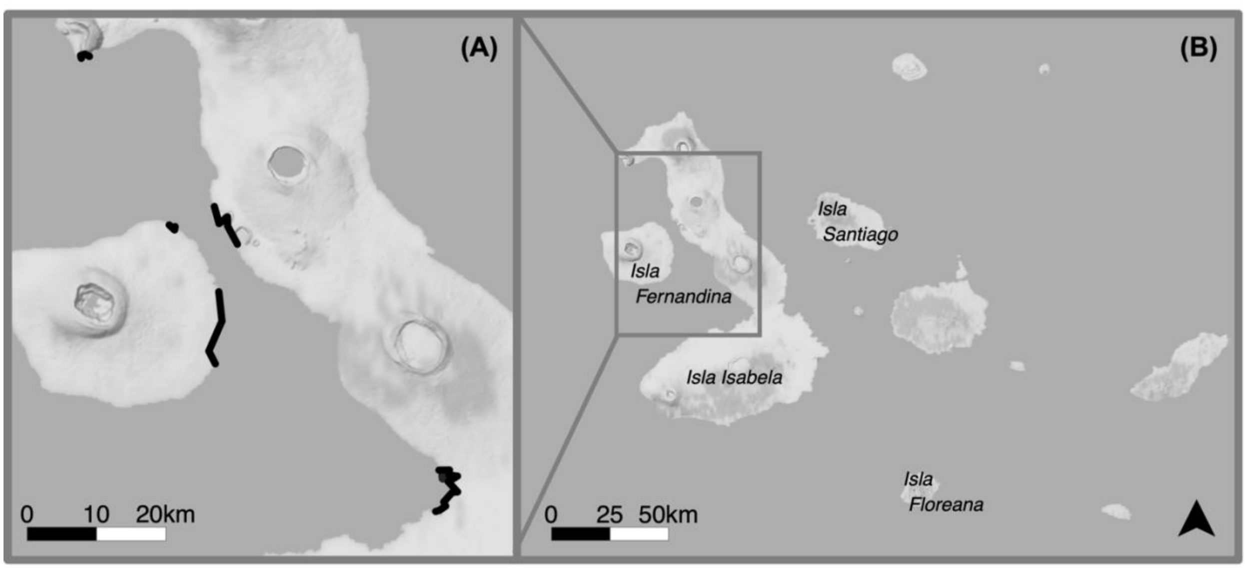

Figure 4.1: Map showing (A) the Canal Bolívar, separating the east coast of Fernandina Island and the west coast of Isabela Island in (B) Galápagos, Ecuador. Canal Bolívar study sites and survey routes are represented in Figure 1A by the black lines along the coast.

Data Collection

Field methods:

We visited the Galápagos archipelago one or two times each year between 2010 and 2022. Our aim was to visit once during the hot season (trips occurred in February or March), and once during the cold season (trips occurred in July or August, though one occurred in September). During each visit, we chartered a boat for 10 to 14 days and visited penguin breeding areas primarily along the coasts of Isabela, Fernandina, and Santiago/Bartolomé Islands (Figure **4.1**A). During visits to each site, we surveyed the shore from a small boat with an outboard motor, slowly cruising along the coast looking for penguins standing near the shore (Isabela and Fernandina survey routes shown in Figure **4.1**B). When we saw a penguin, and if it was accessible, we attempted to catch it using a ~1m metal hook, a large net, or our hands. We also searched for penguins in nests, which were either known from earlier occasions, found when a penguin ran into one, or identified from large amounts of guano observed on the surrounding lava, suggesting a nest was nearby. We weighed and measured captured penguins as described in Boersma (1974). If we found a penguin in a nest with eggs or chicks, we recorded it as breeding, but most individuals were captured outside of nests and their breeding status was unknown. We determined the sex of each bird based on the vertical depth (cm) of its bill, which can identify the sex of Galápagos penguins with 95% accuracy (Cappello and Boersma 2018).

We examined individuals for existing identification tags. If they were unmarked, we applied a small, stainless-steel tag (referred to as a web tag (WT)) to the webbing between the outer and middle toe of the left foot (as in Boersma and Rebstock 2010). If the outer web of the left foot was injured or missing, we applied the WT to the outer web of the right foot or the inner web of the left foot. We tagged every unmarked individual that we captured between 2010 and 2022. Two other research teams also applied WTs (using a separate numbering scheme) between 2000 and 2022.

These research teams additionally applied a second type of tag to some penguins: a radio-frequency identification tag (RFID) implanted below the surface of the skin on an individual's left tarsus. We read existing RFID tags using a BioMark handheld PIT tag reader. For the mark-recapture model, we considered birds that were tagged by the other research teams to have entered our study on the occasion that our team first captured it.

Ocean Niño Index:

As a measure of El Niño strength, we downloaded Oceanic Niño Index (ONI) values between 2010 and 2022 from the NOAA Climate Prediction Center using the *rsoi* package in R (Albers 2020). The ONI is a monthly index, giving the 3-month running mean of sea surface temperature anomalies in the Eastern Equatorial Pacific (Niño 3.4 region, 5ºN-5ºS, 120º-170ºW)(National Oceanic and Atmospheric Administration 2022). We averaged ONI values across the five months preceding each research trip to capture the ENSO conditions between sampling occasions. We then centered and standardized the averaged ONI values.

Statistical Approach

Data preparation:

We created capture histories for each tagged individual, assigning it a 1 for each sampling occasion (i.e., research trip) when it was captured alive and a 0 for occasions when it was not captured. A 0 could therefore mean that the individual was dead or was alive but undetected. We had uneven intervals between some sampling occasions because of skipped research trips due to the COVID-19 pandemic (cold season of 2020 and hot season of 2021) and a tsunami in Galápagos during the 2011 hot season. We accounted for missed sampling occasions by adding dummy columns to the capture-history matrix where all individuals were assigned a 0 (Sanz-Aguilar et al.

2019). When constructing subsequent models, we fixed the detection probability for these columns to zero (Sanz-Aguilar et al. 2019). Because we did not visit Floreana and Santiago/Bartolomé Islands during every trip and sample sizes were low, we focused our analysis on the Canal Bolívar population (n = 484 tagged individuals). The number of adult penguins captured in the Canal Bolívar during each trip ranged from 12 to 64 (median = 27).

General model and goodness of fit:

We fit a hierarchical, state-space extension of the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965) under a Bayesian framework to estimate apparent survival and detectability of Galápagos penguins. In the model, the state process (z) represented the probability that individual i was alive at time t. An individual survived the interval between t-1 and t with probability ϕ such that

$$z_{i,t} | z_{i,t-1} \sim \text{Bernoulli}\left(z_{i,t-1} \times \phi\right)$$

Here, ϕ represents the apparent survival probability rather than true survival because the model does not distinguish between mortality and permanent emigration. The observed capture histories (y) for individual i at time t were a Bernoulli draw parameterized on the true state ($z_{i,t}$) and the detection probability (p).

$$y_{i,t} | z_{i,t} \sim \text{Bernoulli}\left(z_{i,t} \times p\right)$$

No tests of goodness-of-fit test (GOF) is currently available for CJS models with temporal or individual covariates (Gimenez et al. 2018). As an approximation, we aggregated capture histories by frequency and examined GOF for a time-dependent CJS model without covariates (as in Tucker et al. 2019, Messerman et al. 2020). We performed the GOF test using the *R2ucare* package in R (Gimenez et al. 2017). We did not find evidence for heterogeneity among individuals in the length of time between captures (test 3.Sm: $\chi^2 = 2.20$, $p = 1.00$), nor did we find evidence of trap dependence among previously captured individuals (test 2.CT: $\chi^2 = 21.05$, $p = 0.18$; test 2.CL: χ^2 12.86, $p = 0.75$). However, test 3.SR indicated the presence of transients or floaters in the population ($\chi^2 = 49.20$, $p = 0.00$). We expected this result for our dataset due to the high number of individuals that we captured only once (Figure **4.2**). We hypothesized that some captured individuals breed within the study area while other individuals are captured while passing through the study area and are less likely to be encountered on a second occasion. These individuals would therefore have lower detection probabilities. Heterogeneity in detection probabilities due to transience or other unobserved factors can bias survival estimates low and lead to confidence intervals that are too narrow (Abadi et al. 2013). Bias is highest in cases where the majority of individuals are only captured once (i.e. right-skewed) or in scenarios where there are distinct detection probabilities among two or more groups (Abadi et al. 2013).

Removing bias due to heterogeneity in detection is possible in state-space models by including finite mixtures of hidden classes of individuals with distinct detection probabilities (Lok et al. 2019). In our dataset, we hypothesized that individuals had distinct detection probabilities based on their breeding location and status. When penguins are breeding, they forage close to their nest, with one tracking study showing birds remaining an average of 5.3 km from their nests while rearing chicks (Steinfurth et al. 2008). Penguins swim father when they are not breeding, with individuals observed up to 63.5 kilometers from their nesting site (Steinfurth et al. 2008). Because the penguins breed asynchronously and have been found breeding in every month of the year (Boersma et al. 2013b), we expect to catch a mix of breeding and non-breeding birds during each trip. However, since most penguins are captured on shore rather than in a nest, breeding status remains unknown for the majority of birds. Thus, we do not know if the activity center of a captured individual is centered within or far from the study area and, ultimately, if it likely to be encountered again. To account for this unobserved heterogeneity, we proceeded with a two-class mixture model, allowing for differing detection probabilities between classes, considering the classes to represent "highly detectable" and "weakly detectable" individuals (Pradel 2009, Cubaynes et al. 2010). In this approach, the latent variable π represented the probability that an individual belonged to the weakly detectable class, while 1 - π was the probability that an individual belonged to the highly detectable class.

Covariates:

We modeled survival probability as a function of sex and the Oceanic Niño Index (ONI). We predicted that survival would be lower for females than males, although we also anticipated overlap between the sexes. We predicted that when ONI values were higher, i.e., when El Niño conditions were stronger, survival would be lower. To account for unexplained variation among research trips, we included a residual term for capture occasion (ϵ_t) that was normally distributed with a mean set to 0.

From our personal observations, penguins are harder to find and capture during the hot season. This could be because they are less likely to be breeding and are thus not sitting in nest sites that we know to search. Furthermore, food is less abundant during the hot season, and penguins likely spend more time in the water foraging and less time on land where they are available for capture. For these reasons, we modeled detection as a function of season (i.e., hot and cold). The full models for survival and detection, respectively, were

$$logit(\phi_{i,t}) = \beta_0 + \beta_1 sex_i + \beta_2 oni_t + \epsilon_t$$

$$logit(p_{class,t}) = \alpha_0^{class} + \alpha_1 season_t$$

where p_{class} refers to the two detection classes (i.e., higher vs. lower detection probabilities).

Model implementation:

We conducted analyses in R version 4.1.2 (R Core Team 2020). We implemented the Bayesian model in NIMBLE (de Valpine et al. 2017, NIMBLE Development Team 2022) and specified non-informative priors for all parameters. We ran three Markov chains each with 400,000 iterations, a burn-in of 200,000, and we retained one out of every 200 iterations to reduce file size. This gave a posterior sample size of 1,000 for inference. We considered the model to have converged when the Gelman-Rubin statistic was < 1.1 (Gelman and Rubin 1992) and when visual inspection of trace plots showed satisfactory mixing of the chains. In the results, we present the medians of parameter estimates and 95% credible intervals (CI 95%).

Accounting for tag loss:

An assumption of CJS models is that tags are not lost or misread. While we assumed that we did not misread tags, we have observed that the web tags (WT) occasionally break and fall off the foot webbing. To quantify tag loss, we examined a subset of individuals that were double tagged with a WT and RFID (n = 87 individuals). We estimated WT retention rates using a parametric survival analysis with right-censoring of individuals that still had WTs at their last sighting (as described in Skalski and Whitlock 2020). In the model, we included all double-tagged individuals that had a known-age WT (i.e., our research team applied the WT) and that were captured more than once (n = 42 individuals). We fitted the survival model with an exponential distribution using the *flexsurv* package in R (Jackson 2016). We then used the estimated tag retention rate to adjust the survival probabilities from the mark-recapture model, using the equation $\hat{\varphi}_{adj} = \frac{\hat{\varphi}}{\hat{\theta}}$, where $\hat{\theta}$ represented the 6-month estimated tag retention rate (Arnason and Mills 1981, Brusa et al. 2020). Because 0 double-tagged individuals lost their RFID, we only adjusted survival for the portion of individuals that received a WT only. Because this is a preliminary analysis of tag retention, we report both adjusted and unadjusted survival rates in the results.

4.3 RESULTS

We captured 484 (276 male, 208 female) individual penguins in the Canal Bolívar a total of 654 times between September 2010 and February 2022. Of the 484 individuals, 400 were seen during one research trip only, 60 were seen during two trips, and 24 were seen during 3 or more trips (Figure **4.2**). The individual that we saw the most was captured during 9 research trips spanning 5 years.

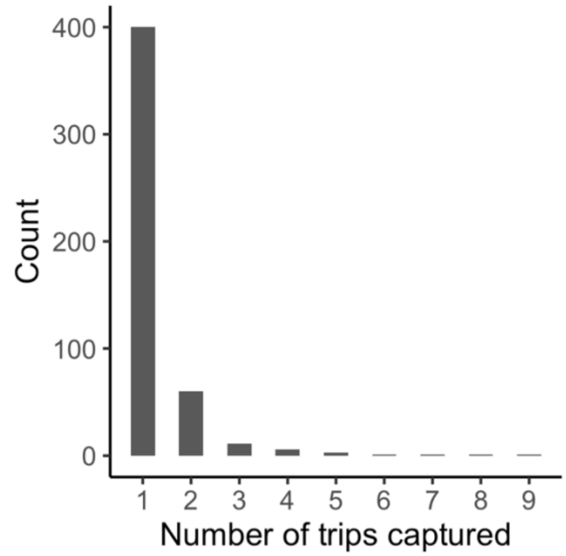

Figure 4.2: Histogram showing the number of individual Galápagos penguins that were captured during one or more research trips.

Estimated semiannual apparent survival was similar for males and females (Figure **4.3**), with median survival estimates of 0.84 (95% CI = 0.78 - 0.92) for males and 0.85 (95% CI = 0.77 - 0.93) for females at average ONI and ϵ_t values (Figure **4.3**B). Accordingly, we found no effect of sex on survival (Figure **4.3**C). Survival between trips ranged from 0.64 (95% CI = 0.39 - 0.90) to 0.91 (95% CI = 0.76 - 0.99) for males and 0.65 (95% CI = 0.40 - 0.90) to 0.91 (95% CI = 0.76 - 0.99) for females (Figure **4.3**A). Because sampling occasions occurred twice per year, annual survival rates from the model approximate to 0.71 (i.e., 0.84 × 0.84) for males and 0.72 (i.e., 0.85 × 0.85) for females.

Oceanic Niño Index (ONI) was not a significant predictor of survival in our model (Figure **4.3**C). However, though the posterior estimates of the ONI coefficient crossed zero, they were centered on negative values, suggesting that survival could be lower during an El Niño and/or higher during a La Niña. The trips with the lowest estimated survival were February and July 2016 (Figure **4.3**A), which captured survival over the 2015-2016 El Niño.

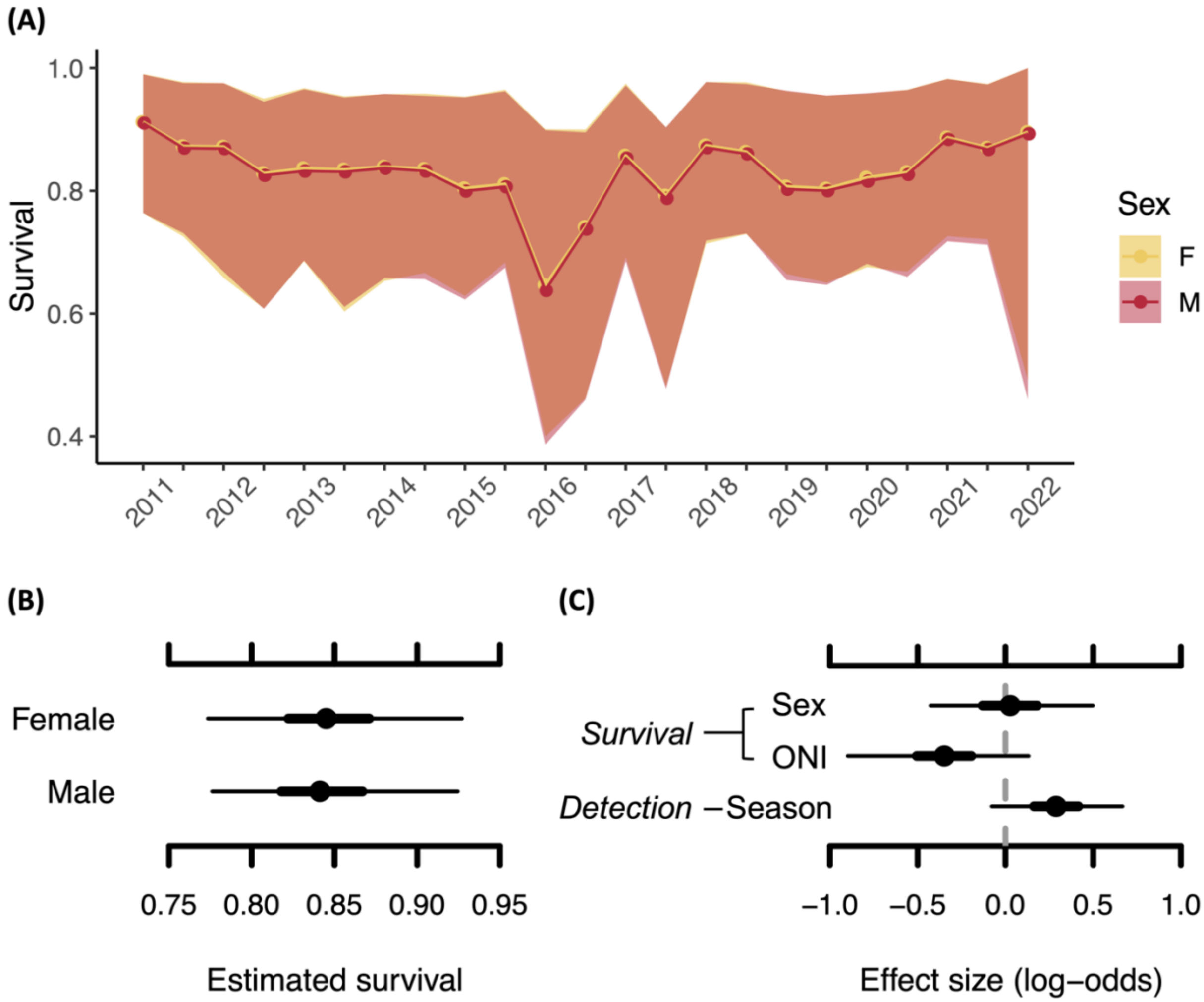

Figure 4.3: (A) Median apparent survival estimates and 95% credible intervals for male and female Galápagos penguins during each research trip. Two data points are presented for each year, the first representing the hot season, and the second representing the cold season. (B) Survival estimates of male and female penguins across all years at average values of ONI and ϵ_t. (C) Effect of covariates on survival (Sex, ONI) and detection (Season). In B and C, the black dot represents the median posterior estimate, the bold line gives the middle 50% of estimates, and the thin line gives the 95% credible interval.

Zero of the 87 double-marked individual lost their RFID over the course of the study, while 7 lost their WT. The parametric survival analysis estimated a tag retention rate of 0.96 between 6-month time steps (est = 0.007 loss per month, SE = 0.003, 95% confidence interval: 0.003 - 0.015, n = 42). Using this retention rate, we provide adjusted estimates from the mark-recapture model in Table **4.1**.

Table 4.1: Posterior estimates of semiannual survival (at average ONI and ϵ_t values) from the mark-recapture model before and after adjusting for tag loss in web-tagged individuals.

	Before adjustment for tag loss	After adjustment for tag loss
Male survival	0.84 (95% CI = 0.78 - 0.92)	0.87 (95% CI = 0.8 - 0.95)
Female survival	0.85 (95% CI = 0.77 - 0.93)	0.87 (95% CI = 0.8 - 0.96)

We did not find season to be a significant predictor of detection, though posterior estimates were generally centered on positive values, indicating higher detection during the cold season (Figure **4.3**C, Figure **4.4**). The two detection classes had non-overlapping values, with the "weaker detectability" group having a median detection probability of 0.015 (95% CI = 0.008 - 0.029) during the hot season and 0.021 (95% CI = 0.011 - 0.038) during the cold season (Figure **4.4**). The "higher detectability" group also had a low detection probability with a median posterior estimate of 0.184 (95% CI = 0.135 - 0.245) during the hot season and 0.232 (95% CI = 0.175 - 0.301) during the cold season (Figure **4.4**). The model estimated that 62% (95% CI = 47-72%) of individuals fell within the "weaker detectability" class, while the remaining 38% fell within the "higher detectability" class.

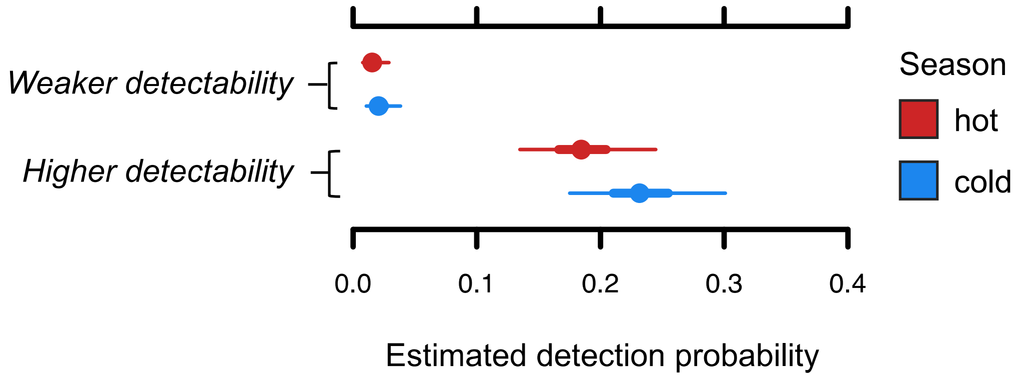

Figure 4.4: Detection probabilities for "weakly" and "highly" detectable individuals between 2010 and 2022. The black dots represent the median posterior estimates, the bold lines give the middle 50% of estimates, and the thin lines give the 95% credible interval.

4.4 Discussion

In this first study to estimate apparent survival of male and female Galápagos penguins, we found that survival probabilities varied little between sexes and were overall lower than expected. Survival appeared to be negatively correlated with the Oceanic Niño Index, although the credible interval for this parameter crossed zero. Detection probabilities were low overall, with non-overlapping estimates between the "highly" and "weakly" detectable classes. Below, we discuss these findings, as well as the value of our mark-recapture model in capturing critical demographic information for this endangered species.

Apparent survival

Median posterior estimates of semiannual survival, when adjusting for tag loss, were 0.87 for males and females at average ONI and ϵ_t values. This is lower compared to other penguins for which survival has been estimated, although we note that our credible intervals are wide (0.8-0.95 semiannually and ~0.64-0.91 annually for males; 0.8-0.96 semiannually and ~0.64-0.92 annually for females; **Table 4.1**). Annual survival rates reported for other penguins include 0.87-0.91 for little *Eudyptula minor* (Dann et al. 2014), 0.75-0.89 for gentoo *Papua gentoo* (Williams 1995), 0.82-0.86 for northern rockhopper *Eudyptes moseleyi* (Guinard et al.1998), 0.89 for Fiordland *Eudyptes pachyrhynchus* (Otley et al. 2017), 0.89 for macaroni *Eudyptes chrysolophus* (Horswill et al. 2014), ≥0.8 for royal *Eudyptes schlegeli* (Crossin et a. 2013), and 0.91 for emperor penguins *Aptenodytes forsteri* (Abadi et al. 2017). Lower survival rates are reported in a closely related species, the African penguin *Spheniscus demersus*, which has been in decline since the 1950s or earlier (Crawford et al. 2013). Apparent survival rates were below 0.7 each year at the colony on Robben Island between 2004 and 2012 and below 0.6 in 8 out of 10 years at Dassen Island between 2001 and 2012 (Sherley et al. 2014). Low survival rates are also reported in models when adult ages are known and estimated separately. In a population of Magellanic penguins (*Spheniscus magellanicus*), breeders and pre-breeders had high annual survival (>0.88), but average survival rates for adults over 19 years of age were between 0.7 and 0.78 (Gownaris and Boersma 2019).

Survival estimates for Galápagos penguins were also low relative to survival rates of species from other seabird families. Sæther and Bakke (2000) reviewed adult survival of 19 seabird species and reported a range of 0.77-0.95 (mean: 0.89 ± 0.05 SD). Horswill and Robinson (2015) conducted a review of adult survival rates among 32 marine birds and found a range of 0.73-0.94 (mean = 0.85 ± 0.06 SD).

Although the low apparent survival probabilities in Galápagos penguins compared to other penguins raise concerns for population decline in this species, the estimated survival rates may be low for reasons unrelated to global change and human impacts, as well as due to methodological limitations. Galápagos penguins differ from other penguin species in their life-history traits in ways that might lower survival rates, even in stable populations. For example, Galápagos penguins have smaller body size than all penguins except the little penguin (references in Garcia-Borboroglu and Boersma 2013), and body size is often positively correlated with survival (Lindstedt and Calder 1976, Sæther 1989). Additionally, life-history theory and comparative studies indicate that survival is negatively correlated with clutch size and yearly reproductive output in birds (Williams 1966, Sæther 1988). Galápagos penguins produce more eggs per year and likely have higher reproductive output than other penguins and many other seabird species (Boersma 1977). For example, emperor penguins lay one egg per year, king penguins lay one egg every 14 months, and *Eudyptes* and *Pygoscelis* penguins typically lay two eggs per year (references in Garcia-Borboroglu and Boersma 2013). Female Galápagos penguins regularly lay two eggs twice a year (Steinfurth 2007) and were observed laying three clutches in a year during breeding studies in the 1970s and 2000s (Boersma 1977, Steinfurth 2007). Furthermore, Galápagos penguins are one of only two penguin species known to provision their chicks after they fledge (the other species being the gentoo penguin; Polito and Trivelpiece 2008), which may help increase juvenile survival relative to what is expected for closely related species (Boersma et al. 2017). High levels of reproductive output or recruitment could compensate for lower adult survival in this species.

The mark-recapture study and modeling approach we employed also has limitations that may result in underestimates of survival rates. First, juvenile birds frequently have lower survival rates than adults due to lack of foraging skill, naivety around predators, and costs of long-distance dispersal (Riotte-Lambert and Weimerskirch 2013). Juvenile Galápagos penguins are distinguishable from adults by their plumage, but they molt into adult plumage as early as six months old (Boersma 1977). Other penguin species molt later (e.g. 15 (range 12-23) months for African penguins (Crawford et al. 2013), one year for Magellanic penguins (Boersma et al. 2013a), and one year for little penguins (Dann 2013)). Moreover, Galápagos penguins remain close to breeding areas year-round, and young penguins were not separated geographically from breeding birds during surveys, as is the case with other species (Weimerskirch 2001). Therefore, our study sample may include very young birds with low survival rates that we could not distinguish from older, more experienced adults, lowering the overall estimates of survival. Additionally, among 87 birds in our dataset that had both an RFID and a WT, 7 lost their WT over the course of the study. Although we provide a preliminary estimate of tag retention rates, a more comprehensive study of tag loss that could be incorporated into future mark-recapture models would likely improve model accuracy.

In summary, while these survival rates appear low for Galápagos penguins, true survival rates of adults when excluding young birds is likely higher. Furthermore, based on their natural history, Galápagos penguins may not be expected to have adult survival that is as high as other closely related species. Nonetheless, models that can determine population trends are important for evaluating whether these survival estimates indicate population decline.

Weak effects of sex and El Niño—Southern Oscillation on survival

We found substantial overlap between male and female survival and no effect of sex in our model. Nevertheless, identifying survival rates of sexes separately is an important component of population monitoring (Gownaris and Boersma 2019). Males and females differ in their behavior and physiology, which can result in sex-specific vital rates that affect population dynamics (Gownaris and Boersma 2019). In a large colony of Magellanic penguins (*Spheniscus magellanicus*), for example, higher mortality in females led to a highly skewed sex ratio, lowering the colony's effective size and contributing to population decline (Gownaris and Boersma 2019).

One hypothesis for higher male survival is that they are larger than females and can therefore eat larger prey, and travel farther and dive deeper in pursuit of prey. Male Galápagos penguins are larger than females (albeit with much overlap; Boersma 1977, Cappello and Boersma

2018), so we predicted that male survival would be at least marginally higher than female survival. Credible intervals around male and female survival in our model were wide, however, and the effect of sex was small. Few Galápagos penguins have been tracked at sea, but Steinfurth et al. (2008) tracked 23 Galápagos penguins during chick rearing and found no difference between the sexes in their distance traveled, distance from shore, or length of foraging trip. All penguins spent most of the time foraging at the surface of the water, though the mean depth limit for 90% of diving activity was 8.5m for males and 4m for females (Steinfurth et al. 2008). Although this study was limited to the chick rearing period, it indicates that males and females do not exploit different foraging locations or drastically different depths, suggesting that they have similar encounter rates with prey and with potential sources of mortality like pollution and fishing gear.

We expected that survival would be lower when the Oceanic Niño Index (ONI) was higher. While model estimates were centered on negative values (i.e., survival appeared to be negatively correlated with ONI), the 95% credible interval for this effect overlapped zero. The negative effects of El Niño on marine life were initially described in Peru, where strong El Niños decimated shorebirds and fish populations along the Peruvian Coast (Cai et al. 2014). The effects of El Niños have since been documented worldwide (Boersma 1978, Cai et al. 2014). In Galápagos, the El Niños of 1982-1983 and 1997-1998 were severe and led to mortality of seabirds, marine mammals, and marine iguanas (Dueñas et al. 2021). As the frequency of severe El Niño events is expected to increase with climate change (Cai et al. 2014), understanding the relationship between El Niño / La Niña events and penguin vital rates such as survival, recruitment, and reproduction is critical. Ocean indices indicated a severe El Niño in 2015-2016, with the max ONI value being 2.6 in November and December 2015. Max ONI values during the 1982-1983 and 1997-1998 Niños were 2.2 and 2.4, respectively (National Oceanic and Atmospheric Administration 2022). However, conditions in Galápagos in 2015-2016 were not generally considered to have been as harsh as expected based on the ONI (Riegl et al. 2019). We did observe during this time that penguins were in poor body condition, and none were breeding (Cappello, Merlen, and Boersma unpublished data). Additionally, we saw very few juveniles, suggesting that breeding had not occurred or been successful prior to our research trips. Under increasingly severe resource limitation, other measures of population vitality, like body condition of individuals, reproduction, and juvenile survival are often affected before adult mortality increases in long-lived species (Griesser et al. 2017). Therefore, though we see evidence of reduced survival in 2015-2016, it was likely less pronounced than during the El Niños of 1982-1983 and 1997-1998. Furthermore, the ENSO conditions at other times during this study may not have been not severe enough to drive a significant correlation between ONI and survival.

Future directions and management implications

One aim of this study was to increase understanding of the data and quantitative tools necessary for precise estimates of Galápagos penguin survival rates. We found that detection probability estimates were low in our model, which can lead to biased or imprecise results (Bröder et al. 2020). We expect that these estimates can be improved with additional data. For example, there may be ways to increase detection in future field efforts by expanding the size of the field crew or the length of each sampling occasion. Additionally, and perhaps more feasibly, this study system could benefit from the use of integrated population models (IPMs) that combine independent datasets (e.g. mark-recapture, census, nest productivity) into a single analysis with a joint likelihood (Besbeas et al. 2002). By sharing information across subcomponent models to estimate key parameters such as survival, productivity, abundance, and population growth, IPMs can produce more accurate and precise parameter values (Schaub and Abadi 2011). This is one avenue for improving estimates in scenarios where data are sparse and detection rates are low (Zipkin and Saunders 2018). The Galápagos penguin system appears to be a good candidate for such efforts.

We aimed to build a survival model that provides a useful foundation for evaluating population responses to—and predicting population dynamics under—various climate and management scenarios. Climate scenarios that should be considered include varying frequency and intensity of El Niño and La Niña events. Galápagos National Park also has several options for management of Galápagos penguins that could be explored. First, removal of introduced predators such as rats and cats from penguin breeding areas would likely increase survival of chicks, juveniles, and adults. Second, expansion and strict enforcement of no-take conservation areas, particularly in the western archipelago, could help protect prey availability for penguins. Third, the creation of nesting habitat, either through artificial nests or islets, could provide additional opportunities for penguins to breed successfully. By identifying population trends and how key demographic rates contribute to population dynamics, governmental and non-governmental organizations can better prioritize the use of finite resources to optimize Galápagos penguin conservation. Ultimately, more data and further analyses are needed to obtain more precise estimates of survival and to identify population trends in this endemic, charismatic species.

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