



The plight of a plover: Viability of an important snowy plover population with flexible brood care in Mexico



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ABSTRACT

Shorebird populations often rely on wetland habitats, for which they are considered important indicators of ecosystem health. Populations residing at low latitudes remain vastly understudied in comparison with populations from high latitudes. Here we use detailed behavioural and demographic observations during all life stages in combination with stage specific modelling to predict the population trajectory of a snowy plover (*Charadrius nivosus*) population at Bahía de Ceuta, Sinaloa, Mexico. In North America this shorebird is threatened, with many monitored populations declining. Our stochastic matrix model for the Ceuta population, which closely matched our field observations, suggests that the population is a sink with a 99.8% probability of going extinct within 25 years. Low apparent adult survival, which declined over time presumably because of poor reproductive success and/or permanent emigration in response to habitat degradation, had the largest impact on the population trajectory. We recommend urgent habitat management actions to address volatile water levels and hence increase reproductive success of this species at this important breeding site. Acknowledging the relative effects of flexible brood care on individual fitness and population dynamics presents an intriguing dilemma for conservation. We found that the flexible parental care system of snowy plovers affected chick survival: broods deserted by polyandrous females early after hatching had significantly lower survival than broods not deserted or those deserted late. Overall, deserting females raised fewer fledglings in this population than females that cared. Taken together, our study reveals unsustainable variation in local vital rate dynamics. To understand how this population contributes to regional source-sink dynamics, future research should evaluate the importance of immigration and emigration among neighbouring populations.

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1. Introduction

Wetlands cover approximately 6% of Earth's surface and harbour high levels of biodiversity (Junk et al., 2013). Recent estimates suggest that >50% of wetlands worldwide have been lost, which will detrimentally affect the diversity and persistence of wetland biota (Zedler and Kercher, 2005). For example, 40% of North American species that

show population declines depend on coastal habitats such as wetlands (NABCI, 2016). Most shorebirds (order Charadriiformes) rely heavily on wetland habitats for food, reproduction and survival meaning that their populations are important indicators of wetland health worldwide (Thomas et al., 2006). Habitat loss and degradation, predation, and invasive species competition are identified as key threats to shorebird populations (Cruz et al., 2013) with low chick and adult survival negatively impacting breeding populations (Koivula et al., 2008; Larson et al., 2002; Rickenbach et al., 2011).

Most information on shorebird population dynamics comes from breeding populations in temperate and arctic zones of the northern hemisphere (Bart et al., 2007; Laaksonen and Lehikoinen, 2013;

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Thomas et al., 2006; Lindström et al., 2015). By contrast, there are only a few studies from tropical and subtropical breeding populations, which are typically located in developing countries where monitoring is less well established. Wetlands in these regions often harbour the highest level of biodiversity (Sekercioglu et al., 2012). Moreover, human populations are projected to increase particularly in the coastal zones of developing countries (Neumann et al., 2015), which will further increase pressures on these wetlands and shorebird populations.

The snowy plover (*Charadrius nivosus*) is a near threatened shorebird native to the Americas (Küpper et al., 2009; BirdLife International-IUCN, 2016). It is one of the least abundant shorebirds in North America (estimated population size: 25,869) with many populations in decline and requiring intensive management (Thomas et al., 2012). Coastal snowy plover populations are especially at risk due to the threat of rising sea levels caused by climate change (Aiello-Lammens et al., 2011). Mexico harbours 9% of the entire North American snowy plover population (Thomas et al., 2012) and they occur in a variety of habitats from the Pacific coast to the Gulf of Mexico (DeSudre-Medrano et al., 2011; Galindo-Espinosa and Palacios, 2015; Mellink et al., 2009). The snowy plover has been listed as federally 'threatened' in Mexico since 2010 (SEMARNAT, 2010).

Snowy plovers exhibit a flexible mating system, dominated by female polyandry and uniparental male care (Warriner et al., 1986). Typically, females desert broods remate with a different male; sometimes even dispersing to other sites within the breeding season to search for new mates (Stenzel et al., 1994). Mating system and sex-biases can influence population growth dynamics via reproductive constraints on the limiting sex (Bessa-Gomes et al., 2004). A recent study suggests that this polyandrous mating system is driven in part by an adult sex ratio bias caused by male-biased survival (Eberhart-Phillips et al., 2017).

Since parental care improves offspring survival and reproductive success (Clutton-Brock, 1991), variation in parental care may have severe implications on population dynamics. For example, variation in parental care may affect offspring survival (Székely and Cuthill, 1999), a major vital rate that is important for population growth. Yet this variation is largely ignored when assessing population viability. Quantifying the costs that desertion has on chick survival provides an important first step to understand how individual behaviour modulates population dynamics.

A comprehensive survey conducted in 2007 concluded that one of most important snowy plover breeding populations in Mexico is located at Bahía de Ceuta (hereafter "Ceuta"), Sinaloa, a coastal wetland protected by the RAMSAR convention (Thomas et al., 2012). The snowy plovers at Ceuta are polyandrous (60% of females mate with more than one male per season, including first year breeders), and the population has a male-biased adult sex ratio estimated from surveys and population matrix modelling (mean ASR: 0.60–0.63, Carmona-Izunza et al., 2017; Eberhart-Phillips et al., 2017). Mean local tenure of snowy plovers is 2.7 years and the oldest individual recorded at Ceuta is at least 10 years old. Since annual monitoring efforts commenced in 2006, the population has shown dramatic fluctuations in population size probably caused by annual variation in environmental conditions and habitat changes. The main habitat change documented was the 150 m expansion of mangrove vegetation. This expansion increased sedimentation of the substrate, which in turn reduced the water storage capabilities of the salt flats and evaporation ponds where the plovers breed.

In this study, we aimed to quantify the viability of this population. Using seven years of detailed breeding surveys we (1) investigated temporal variation in the breeding population size and nesting activity, (2) identified factors explaining variation in survival during critical life stages, (3) evaluated the effect of parental desertion on offspring survival, (4) forecasted the threat of extinction, and (5) conducted sensitivity analyses that highlighted the most important vital rates contributing to past and future population changes.

2. Material and methods

2.1. Study area

We studied snowy plovers breeding at Ceuta, a subtropical lagoon (annual average temperature: 23.3 °C, annual average precipitation: 473 mm) surrounded by mangrove forests. Ceuta is located on the coastal plain of Sinaloa in northwest Mexico (23°54'N, 106°57'W, Fig. 1a). The plovers concentrate breeding mainly on salt flats that contain a number of abandoned evaporation ponds. This habitat (hereafter "flats") is characterised by open substrates with sparse vegetation. The breeding season starts when flood water recedes at the beginning of April and concludes usually by mid-July when rains and high tides flood the flats again. In drought years or at the end of the breeding season, plovers have been observed nesting and tending broods in a section of the lagoon northwest of the main study area where water bodies are accessible throughout the breeding season to snowy plover families (CK, MC-L, unpublished data). This area is separated from the flats by a stretch of mangrove forest (Fig. 1b).

2.2. Data collection

We monitored plovers daily between April and July from 2006 until 2012 using methodology described by Székely et al. (2008). We used a car and mobile hides to search for nests, identifying incubating plovers with binoculars or scopes. The coordinates of each nest (± 3 m) were recorded with a hand-held GPS device (Garmin, USA). For each nest, we estimated laying date and calculated hatching date by floating the eggs in lukewarm water assuming an incubation period of 25 days (Piersma and Wiersma, 1996). Clutches were revisited every 3–5 days and we documented causes of nest failure (i.e. depredated, flooded, abandoned, or unknown). After 20 days, we visited clutches daily to mark chicks before they left the nest.

Adults were captured using a funnel trap during the incubation period and marked with a metal ring and a unique colour combination of 3–4 darvic rings. Adult sex was established using plumage, molecular and/or behavioural characters (Vincze et al., 2017). We regularly resighted banded plovers to document individual movements and survival within and between years. Most chicks (90%) were captured in the immediate vicinity of the nest at hatching day, and 4% of chicks were captured and marked at opportunistic encounters with their parents. All captured chicks were marked with one metal and one colour ring, which allowed us to individually identify them based on their colour ring and the unique ring combination of their tending parents (Székely et al., 2008). We resighted broods approximately every other day to monitor daily survival over the course of the breeding season. Active broods were followed for a period of 25 days since hatch, after which we assumed fledging (earliest fledging occurred at 22 days, CK unpublished data). For each brood resighting we recorded the identity of the tending parent and the chicks present (Székely and Cuthill, 1999). We classified broods as deserted if one of the parents was not present in two consecutive encounters that were at least one day apart. We calculated the desertion date as the mean date between the last date that both parents were seen attending the brood and the first date that only one parent was tending the chicks. We searched the study area extensively to confirm that missing broods had not moved elsewhere and concluded that the last unfledged chicks had died if the tending parent(s) was seen alone and did not display any alarming behaviour when we approached it.

2.3. Statistical analyses

2.3.1. Population trends

We evaluated temporal trends using generalized linear models (GLMs). The annual number of nests, number of male and female

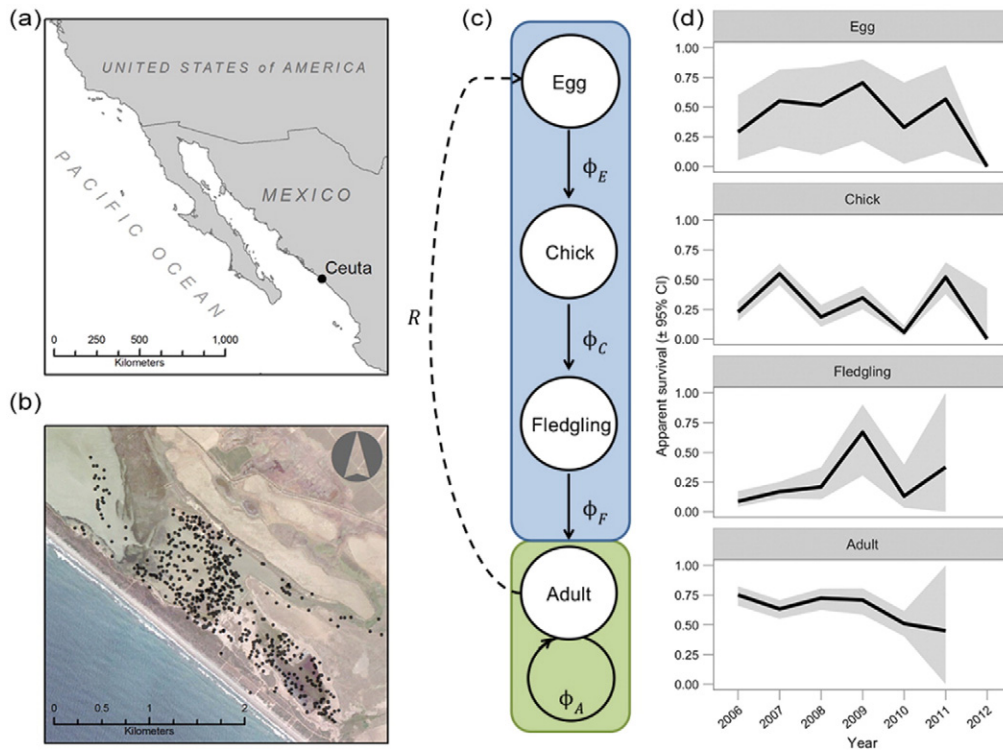


Fig. 1. (a) Location of Bahía de Ceuta, Mexico. (b) Snowy plover nests distribution at Ceuta from 2006 until 2012. (c) Life cycle used in the projection matrix model. Transition probabilities between life stages are egg survival (ϕ_E), chick survival (ϕ_C), fledgling survival (ϕ_F), adult survival (ϕ_A) and fecundity (R). Each coloured polygon represents one year, the projection interval of the model. (d) Annual variation in the apparent survival of eggs, chicks, fledglings, and adults between 2006 and 2012. Note that fledgling and adult survival is expressed as the survival from year t to year $t + 1$.

breeders captured were used as response variables using a quasi-Poisson distribution and log link function to account for overdispersion.

To assess within and between year trends in reproductive success, we used a generalized linear mixed model (GLMM) to describe annual variation in the number of fledglings per breeding male and female. The models were fitted with a Poisson distribution and a log link function. Only chicks with known fates (i.e. fledged or died) were used for this analysis. Standardised hatch date of brood per male and year were fitted as fixed effects. Since some males had more than one nest within a year, we added male ID as a random effect to account for the non-independence of siblings. The GLMM was constructed using the R package “lme4” (Bates et al., 2015).

We tested whether causes of nest failure changed over the time in the study site by employing log-likelihood ratio tests (G-test) with a Bonferroni correction (Blackmer et al., 2004). In a separate analysis we tested whether the cause of nest failures differed between early (2006 and 2007) and later years (2011 and 2012) of the study.

2.3.2. Vital rate estimation

We estimated five stage-specific vital rates describing important transitions in life history (Fig. 1c). These included egg survival (ϕ_E , probability that an egg will hatch), chick survival (ϕ_C , probability of a chick fledging), fledgling survival (ϕ_F , probability that a fledgling raised in year t will recruit into the adult population in year $t + 1$), adult survival (ϕ_A , annual survival and retention of adults in the population), and fecundity (R , annual average number of eggs attended by an adult male).

To quantify vital rates, we employed mark-recapture models, which account for temporal and stage-specific variation in encounter and survival probabilities, imperfect detection of marked individuals during surveys, and the inclusion of individuals with unknown fates. We conducted egg and chick survival analyses separately from their respective survival analyses of fledgling and adults because of differences in the temporal duration of encounter intervals (i.e. 25 days vs. one year, respectively; Fig. 1c). Chicks that were known to have died before fledging

were not included in the analyses of fledgling and adult survival. All survival models were constructed with the R package “RMark” (Laake and Rexstad, 2008), and subsequently analysed using maximum likelihood estimation in program MARK (White and Burnham, 1999).

Daily nest survival (DNS) was estimated based on variation in DNS as a function of year, nest initiation date, and nest age including all relevant two-way additive and interactive combinations (Table S1). The DNS parameter estimate of the top model was raised to the power of 25, the incubation time, to transform DNS to apparent hatching success.

We estimated daily chick survival (DCS) using Cormack-Jolly-Seber models with one-day encounter intervals modelled as a function of year, hatch date, and age. We first assessed the most appropriate structure of encounter probability (p) by fitting the three aforementioned variables and evaluating their ΔAIC_c support while holding DCS constant (Colwell et al., 2013). We then estimated variation in DCS as a function of all relevant two-way additive and interactive combinations of the three variables considered (Table S2). The DCS estimate of the top model was raised to 25, the brooding period, to transform DCS to apparent fledgling success. We estimated annual apparent survival of fledglings and adults using a similar approach but used one-year encounter intervals. We modelled apparent survival as a function of age (i.e., fledgling or adult) and year, with additive and interactive combinations included (Table S3).

2.3.3. Influence of parental care on chick survival

We used survival records of chicks to determine the influence of temporal and behavioural covariates on survival by employing Cox proportional hazards mixed regression models (CPHMs) implemented in the R package “coxme” (Therneau, 2009). By fitting brood ID as a random effect we accounted for non-independence of chick survival of the same family. Chick death was the terminal event. Chicks that reached the fledging age or families with unknown chick fates were censored (Küpfer et al., 2010). Our covariates of the initial model included desertion age (i.e. age of the oldest chick at which one of parents

abandoned the brood), standardised hatching date, and body mass of chicks at hatching. We removed nonsignificant terms during model simplification. In CPHMs, the statistic of interest is the hazards ratio $\exp(\beta)$, which provides a direct measure for the difference in death hazard between groups; when $\exp(\beta) < 1$, the hazard decreases, whereas it increases when $\exp(\beta) > 1$ (Rivers et al., 2012). For graphical presentation only, we split covariates of interest into two groups that describe the age of desertion (≤ 7 and > 7 days, respectively). We chose this cut-off based on observations that the first week is critical for chick survival since (i) 47% of chicks with known fate died during the first seven days and (ii) 77% of brood desertions occurred within one week after hatch (MC-L & CK, unpublished data).

2.3.4. Population viability

Population viability and extinction risk were assessed using projection matrix models (Caswell, 2001). Our population projection matrix model is described by the equation:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

where t is an annual time step, \mathbf{n} is a vector of the population distributed across life stages and the 2×2 matrix \mathbf{A} is expressed as:

$$\begin{pmatrix} 0 & R \\ \phi_E \times \phi_C \times \phi_F & \phi_A \end{pmatrix}$$

where transition probabilities (ϕ) between life stages are survival of eggs (ϕ_E), chicks (ϕ_C), fledglings (ϕ_F), and adults (ϕ_A). Fecundity (R) is annual average per capita number of eggs attended adult males. We implemented both deterministic and stochastic versions of the matrix model. The deterministic model used a matrix built from the seven-year averages of each vital rate whereas the stochastic model incorporated annual variation in vital rates by using year-specific matrices to maintain the covariation structure among vital rates.

To assess the validity of our model structure, we ran the stochastic simulation with a starting population structured the same as what was observed in 2006 (i.e., $N_E = 454$, $N_A = 204$) and projected 10,000 iterations over the 7-year period. We then compared the distribution of final population sizes from the simulation to the actual population size recorded in 2012 (Fig. S1a). We also visually inspected the distributions of the coefficient of annual variation (CV) and the final population sizes of all iterations in the simulation by comparing them with the observed coefficient of annual variation and final population size observed in the population over the 2006 to 2012 study period (Fig. S1b).

We evaluated population viability using three common metrics: 1) deterministic population growth, 2) stochastic extinction probability, and 3) a sensitivity analysis of population growth (λ) to changes in vital rates. We calculated deterministic population growth as the dominant eigen-vector of the deterministic matrix ($\hat{\mathbf{A}}_{2007-2012}$). Stochastic population extinction risk was estimated by projecting the current population into the future with a randomly drawn matrix for each annual time step. We ran 10,000 iterations of the stochastic simulation, with each annual matrix (i.e. $\hat{\mathbf{A}}_{2007}$, $\hat{\mathbf{A}}_{2008}$, ..., $\hat{\mathbf{A}}_{2012}$) being randomly drawn with an equal probability at each time step. We estimated extinction probability by determining the proportion of iterations that hit population size of two at 10, 25, 50, and 100 years after the last year of study. We calculated the deterministic sensitivities and elasticities of lambda to lower-level vital rates using partial derivatives. All statistical analyses and population viability models were conducted using the R version "Supposedly Educational" (R Core Team, 2016). All means are expressed with \pm one standard error (SE) or standard deviation (SD). We provide all computer code and documentation as a PDF file written in Rmarkdown (Supplementary Material Appendix A) together with all raw datasets needed to reproduce the analysis (Supplementary Material Appendix B).

3. Results

3.1. Population trends

A total of 231 females and 215 males were individually marked and 659 nests were monitored. The number of breeding females (GLM: $\beta = -0.178 \pm 0.046$ SE, $t_6 = -3.862$, $P = 0.011$), breeding males ($\beta = -0.165 \pm 0.042$ SE, $t_6 = -3.871$, $P = 0.011$) and nests ($\beta = -0.196 \pm 0.045$ SE, $t_6 = -4.341$, $P = 0.007$) declined over the study period reducing the population size from 204 in 2006 to 58 breeding adults in 2012. A decline was also detected by the deterministic matrix model ($\lambda = 0.859$). The stochastic matrix model predicted an average final population size of 52.12 ± 35.69 SD (Fig. S1a). The average coefficient of variation of all 10,000 iterations was 0.61 ± 0.31 SD, compared to an coefficient of variation of 0.42 observed between 2006 and 2012 (Fig. S1b).

3.2. Temporal patterns of reproductive success

The average number of fledglings per male (0.980 ± 0.073 SE) did not vary significantly over the study period (GLMM: $\beta = -0.017 \pm 0.041$ SE, $Z = -0.423$, $P = 0.673$). Nor did this vary annually for females ($\beta = 0.014 \pm 0.043$ SE, $Z = 0.327$, $P = 0.744$). Males breeding early in the season had significantly more fledglings than those breeding later in the season (1.153 ± 0.085 SE vs 0.471 ± 0.119 SE, respectively; $\beta = -0.457 \pm 0.105$ SE, $Z = -4.346$, $P < 0.001$). Likewise, females with early broods produced more fledglings ($\beta = -0.582 \pm 0.110$ SE, $Z = -5.288$, $P < 0.001$).

3.3. Nests fate and survival

Variation in DNS was best described by an interaction between temporal variation between and within years ($w_i = 0.92$, Table S1). DNS²⁵ varied over the study period with a maximum of 0.706 in 2009, a minimum of 0.00001 in 2012, and an average of 0.453 ± 0.08 SE (Fig. 1d). The fate of nests (i.e. successful vs. failure) changed over the study period (G-test: $G = 13.82$, $df = 6$, $P = 0.030$), with more successful nests in early years compared to latter years. The causes of nest failure also changed over time (G-test: $G = 68.31$, $df = 3$, $P < 0.001$) with predation being the most common cause of failure in early years and flooding being the most common cause of failure in late years.

3.4. Chick survival and brood desertion

Over the seven year study period, only five chicks known to have survived the first week evaded our capture efforts. In total we marked 895 chicks, with 310 (34.6%) chicks dying before fledging, 229 (25.6%) fledged, and the fate of 356 (39.8%) chicks were unknown. DCS was best described by an interaction between temporal variation between and within years (Table S2), this model received maximum support ($w_i = 1$). Average DCS²⁵ was 0.27 ± 0.08 SE (Fig. 1d), with desertion, hatch date, and year being strongly associated with chick survival. Desertion increased chick death hazard by 8% per day (Fig. 2, CPHM: $\beta = -0.076 \pm 0.014$ SE, $Z = -5.49$, $P < 0.001$). Females that deserted the first brood before the chicks reached an age of at least one week produced significantly fewer fledglings than females that stayed to care for this period (0.900 ± 0.075 SE vs 1.666 ± 0.172 SE, respectively; GLMM: $\beta = -0.728 \pm 0.169$ SE, $Z = -4.285$, $P < 0.001$). Chick survival also decreased over the breeding season ($\beta = 2.016 \pm 0.144$ SE, $Z = 13.99$, $P < 0.001$) and decreased 17% per year over the study period ($\beta = -0.175 \pm 0.040$ SE, $Z = -4.31$, $P < 0.001$). Body mass at hatching did not affect the survival of the chicks ($\beta = -0.211 \pm 0.138$ SE, $Z = -1.53$, $P = 0.130$).

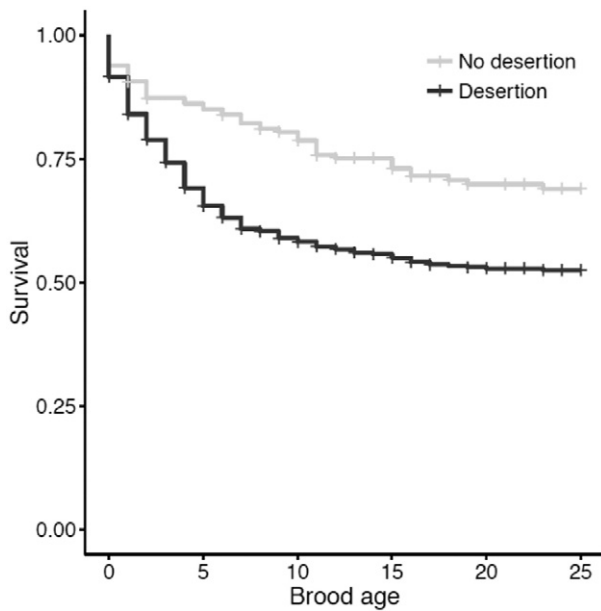


Fig. 2. Survival of snowy plover chicks from hatching to fledging in relation to desertion by one of the parents at Ceuta. Black line illustrate chick survival of broods where one parent deserted within seven days of hatching, whereas the grey line represents chick survival of broods where both parents cared for at least seven days.

3.5. Fledging and adult survival

Variation in annual survival was best described by life-stage (i.e. fledging or adult) and year ($w_i = 0.99$; Table S3). The maximum fledging survival was 0.52 between 2009 and 2010, the minimum was 0.09 between 2010 and 2011, and the average was 0.213 ± 0.066 SE (Fig. 1d). The maximum adult survival estimated was 0.753 between 2006 and 2007, the minimum was 0.275 between 2011 and 2012, and the average was 0.603 ± 0.073 SE (Fig. 1d).

3.6. Population viability

Our stochastic matrix projection model forecasts a rapid decline in the Ceuta breeding population in line with the observed dynamics in the population (Fig. 3a). According to our model, the population has a 47.5% probability of extinction within 10 years after 2012, 99.8% within 25 years, and a 100% chance of extinction in 50 years (Figs. 3b and S2). The sensitivity analysis revealed that population growth rate was most sensitive to perturbations in adult survival (Fig. 3c), whereas egg, chick, fledging, and fecundity all had equal elasticities (Fig. 3d and e).

4. Discussion

Our study reveals that subtropical resident shorebird populations may face similar problems as those at higher latitudes. Long-term monitoring of this population showed a strong decline by >70% between 2006 and 2012 and it is likely that the decline already started before our study. Based on the observed vital rates, this population is predicted to go extinct within 25 years if no conservation measures are undertaken. Similar declines of other snowy plover populations have been observed in the United States (Colwell et al., 2010; Page et al., 1991; Saalfeld et al., 2013). In Mexico, a study carried out in Baja California reported a decline of 42% between 1991 and 2008 (Galindo-Espinosa and Palacios, 2015). The growth rate was below replacement in our population but slightly higher than the other well-studied populations (Humboldt, California: $\lambda = 0.77$, Mullin et al., 2010). The Humboldt population has been maintained by strong immigration (Eberhart-Phillips and Colwell, 2014) and similarly, immigration at Ceuta slowed

down the decline with annual immigration rates of 15–77% for males, and 28–77% for females (CK & MC-L, unpublished data).

Apparent nesting success at Ceuta was higher than most other snowy plover populations without predator control for which comparable data are reported (0.20 to 0.32; Ellis et al., 2015; Galindo-Espinosa, 2015; Hardy and Colwell, 2012; Saalfeld et al., 2011) and comparable to those where lethal predator removal has been enforced (0.24–0.60; Lauten et al., 2014; Powell et al., 2002; Stern et al., 1990). A likely explanation for the observed high nest survival is the absence of avian nest predators at Ceuta (Stoddard et al., 2016), which are the major cause of nest failure in other populations (Colwell et al., 2011; Ellis et al., 2015; Powell et al., 2002). Causes of nest failure varied over the seven-year period, with predation contributing most failure in early years, and flooding being most significant in later years. Flooding and severe weather events have also been responsible for nest failures in other snowy plover populations (Ellis et al., 2015; Saalfeld et al., 2011; Sexson and Farley, 2012). At Ceuta and the surrounding region, range shifts in the natural vegetation are tightly linked to agri- and aqua-cultural development, which has affected water flow, tidal drainage, and spatio-temporal regimes of flooding and sedimentation (Alonso-Pérez et al., 2003) that have also affected the nesting behaviour of plovers. We observed that plovers moved to areas of the breeding site where water levels and therefore foraging opportunities are higher. However, in these areas the risk of nest flooding is also higher. For example, in 2012 when most plovers nested in this area, 35% of all nests were flooded during a single spring tide in early June. Thus, this newly colonised area may serve as an ecological trap for nesting plovers.

In contrast to the high nest survival, chick survival at Ceuta was low in comparison with most other plover populations (Catlin et al., 2013; Colwell et al., 2007; Stenzel et al., 2007). In plovers, chick mortality is often influenced by habitat type and quality, predation, and parental care (Colwell et al., 2007; Székely and Cuthill, 1999). Similar low chick survival is found for beach nesting plovers (Catlin et al., 2013; Colwell et al., 2007) whereas the main habitat at Ceuta is a mudflat. Chick mortality also frequently varies temporally (Székely et al., 2004; Verhulst and Nilsson, 2008). At Ceuta the number of fledglings per male did not change annually but decreased with time over the breeding season as reported from other bird populations (Verhulst and Nilsson, 2008). The seasonal decline has been explained with deterioration of environmental conditions and food availability over the breeding season. At Ceuta, deterioration is caused by the rapid evaporation of water, which reduces the availability of accessible wet foraging habitat for chicks. This effect may have been compounded by habitat changes induced by sedimentation (both natural and anthropogenic) and changes in the hydrological regime at Ceuta (Alonso-Pérez et al., 2003).

Chick survival increases with age, with the lowest probabilities of survival occurring during the first week after hatch (Colwell et al., 2007; Loegering and Fraser, 1995; Székely et al., 2004). This suggests that young chicks depend on parental care for thermoregulation, predator avoidance, and defence from aggressive conspecifics (Colwell et al., 2007; Kosztolányi et al., 2006). We found that desertion of one parent is related to chick survival, with biparental broods surviving better than uniparental broods when controlling for seasonal effects. However, brood desertion may also increase the overall productivity of the population since deserting females have the opportunity to produce more offspring than females restrained to care for their first brood. Snowy plovers rarely have clutches containing more than three eggs. Therefore, by deserting broods and pairing with a second or third male, females can more readily produce more offspring. Notably, females that deserted broods within the first seven days after hatch did not produce more fledglings locally than females that cared. It is possible that deserting females that left Ceuta and bred elsewhere were more successful. However, at least locally, desertion did not benefit individual reproductive success nor did it increase fledgling production at the population level and currently appears to be maladaptive. We suspect that seasonal variation in habitat quality could contribute to this result,

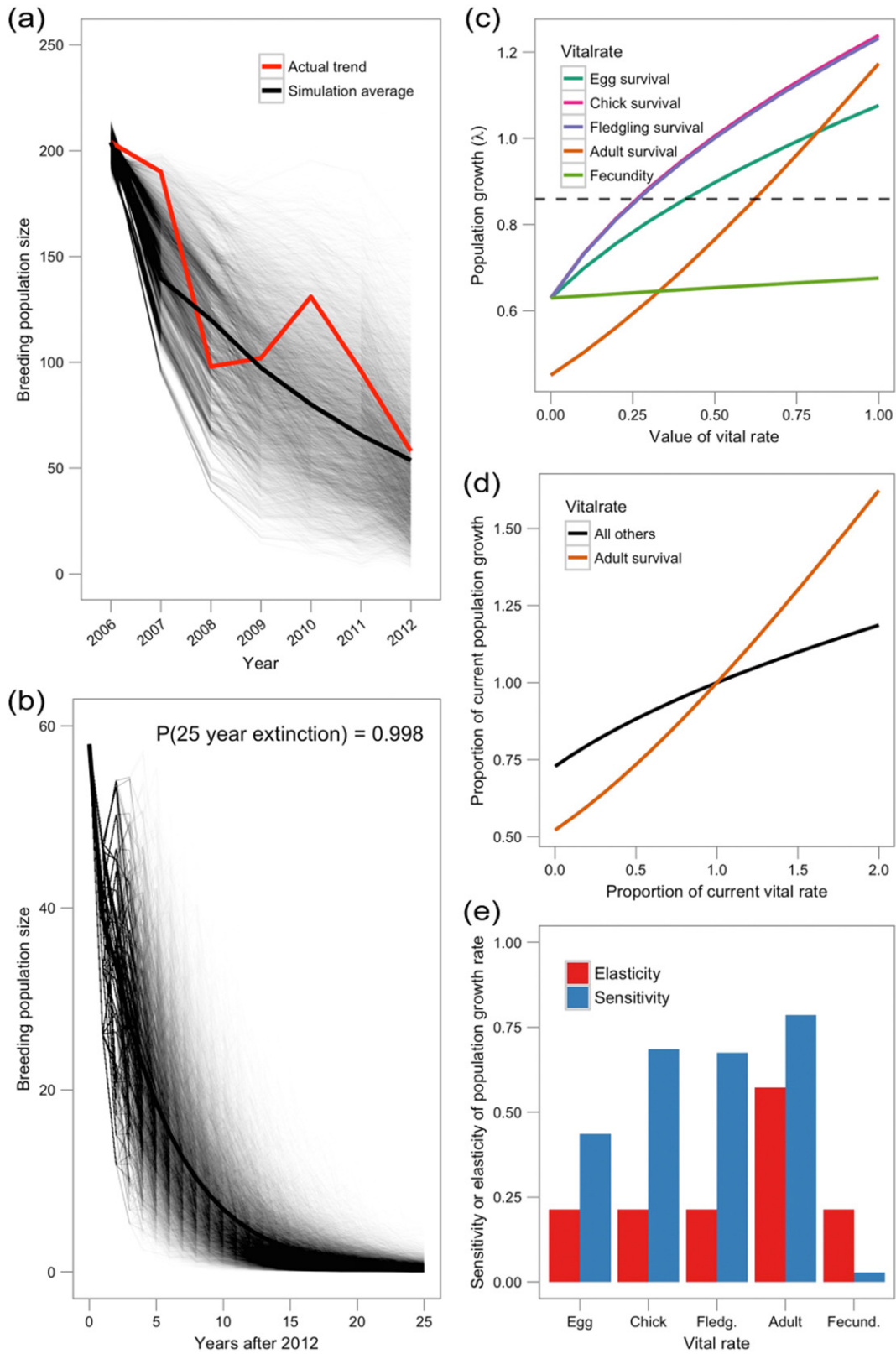


Fig. 3. (a) Validation model of the population trend of Ceuta snowy plovers between 2006 and 2012. Red line represents the real trend across the years and thick black line represents the simulation average. (b) Forecasted population size and extinction risk for 25 years after 2012. Black thin lines represent the 10,000 simulated trajectories and thick line represents the simulation average. (c) The effects of perturbing vital rates on population growth rate (λ). Horizontal dashed line indicates the deterministic population growth rate between 2006 and 2012 ($\lambda = 0.859$). (d) Influence of elasticities on vital rates. Fecundity and egg, chick, and fledgling survival all had the same trend line and thus were grouped into the “All others” category. (e) Comparison of stage-specific sensitivities and elasticities.

because biparental care is shown to increase brood survival especially when the environmental quality is low and/or competition for resources is high (Kosztolányi et al., 2006; Székely and Cuthill, 1999). It is unclear whether and how the flexible brood care system of snowy plovers contributes to population productivity and the species' conservation risk. Acknowledging the relative effects of flexible brood care on individual fitness and population dynamics presents an intriguing dilemma for the conservation and management of such species and requires further work.

Juvenile survival at Ceuta was lower than that reported from any other plover population in North America so far. Estimates across snowy plover populations of the Pacific coast ranged from 0.40 to 0.46 (Mullin et al., 2010; Stenzel et al., 2007; USFWS, 2007). Estimating juvenile survival is challenging given that fledged juveniles frequently disperse. For example, juveniles may move to other sites nearby, which are poorly monitored. Notably there have been no reported juvenile immigrants from Ceuta at a monitored population ~200 km South of Ceuta (Carlos Villar, personal communication). As reported in other shorebirds (Sandercock, 2003), we found that adult survival was higher than juvenile survival although it was decreasing over the years. Average apparent adult survival at Ceuta was lower than most rates reported from other snowy plover populations (Paton, 1994; Saalfeld et al., 2013) or other plover (Foppen et al., 2006; Sandercock et al., 2005,) with the exception of the Humboldt population, which had similar low apparent adult survival rates (Mullin et al., 2010).

The population viability analysis suggested that apparent adult survival is the limiting demographic parameter for population growth. Adult survival showed the highest elasticity, which implies that it has the greatest effect on population change (Larson et al., 2002; Sandercock, 2003). However, it is important to note that our estimate of apparent survival includes both true survival and permanent emigration. We did not observe any dead individuals nor were there any reports of environmental or epidemiological disturbances that could affect adult mortality. Hence the steady decline in apparent survival is likely the result of permanent emigration, perhaps in response to consistent low reproductive success or habitat degradation. Water availability during the spring arrival time to breeding area has been shown to influence regional fidelity rates in snowy plovers, with a decrease in site fidelity following low water levels (Saalfeld et al., 2013). In addition, plovers are long-lived site faithful animals but poor breeding success may provoke adults to abandon the breeding site and thus reduce their site fidelity between years (Haas, 1998; Porneluzi, 2003).

We have knowledge of neighbouring populations or suitable habitat for breeding plovers within a 200 km radius of Ceuta, however, only one of these locations has been regularly monitored. At this site, only a few marked emigrants from Ceuta have been resighted, and only once have we documented a marked immigrant originating elsewhere (MC-L & CK unpublished data). To fully grasp adult movement among these sites, a region-wide monitoring effort is needed. Snowy plovers have a flexible breeding biology that is characterised by long-distance breeding dispersal (Stenzel et al., 1994). This is particularly the case for polyandrous plover females, which can breed at multiple distant sites (Küpper et al., 2012). Moreover, every year we newly banded a large number of unmarked adults despite having marked nearly all hatchlings in the previous season. Taken together, this suggests that substantial adult movements occur regionally. Therefore, it is plausible that an improvement of the vital rates for eggs, chicks and especially juveniles at Ceuta will improve the retention of adults in the population and hence increase population growth.

Retaining adults in a population is a challenging task in avian conservation, since these individuals are highly mobile. One feasible approach could be to increase the per capita reproductive success of the Ceuta population by managing water levels at an optimal level for nest and chick survival. Local retention would also serve as social information to attract prospective immigrants to increase the size of the breeding

population and improve overall future reproductive success and hence population viability (Anthony and Blumstein, 2000; Blumstein, 2010).

In conclusion, our findings reveal that one of the most important breeding populations of snowy plovers in Mexico has low vital rates and is in severe decline. We suggest that habitat degradation is the principal reason for the decline. Urgent conservation management actions should first aim to improve chick and juvenile survival by addressing the fluctuating water levels at Ceuta. Abandoned evaporation ponds are ideal habitat for breeding plovers but require active management, which occasionally provides new conservation dilemmas. For example, the water channels feeding the ponds have been blocked by encroaching mangrove vegetation, a plant that is protected under Mexican law and illegal to remove. A possible solution would be to pump up ground water using a wind mill and flood the ponds during the breeding season—a restoration strategy that would not interfere with conservation and local agriculture. In time this could increase the retention of breeding adults, a life-stage identified in our models as being most important for population growth. Improving the situation for breeding snowy plovers will benefit other coastal wetland specialists and therefore generally increase ecosystem health.

Decisive actions are also needed at other levels since predictive models of human development forecast an ever-increasing pressure on coastal ecosystems (Neumann et al., 2015) and the pattern of declining breeding populations of snowy plovers suggest that suitable habitats in Mexico are becoming less and less, meaning that emigrating plovers face similar threats elsewhere in the region. Around Ceuta, we have witnessed large scale deforestation of federally protected mangrove forests combined with illegal beach development. We expect that these disturbances will put further pressure on the local snowy plover population, which are not yet captured by our current models. Taken together, we anticipate a genuine risk that the protected RAMSAR site of Sistema Lagunar Ceuta will quickly lose this iconic bird species. Given the vulnerability of snowy plovers to the consequences of climate change (Aiello-Lammens et al., 2011) the local extinction of the Ceuta population would severely hamper the intensive international efforts to recover the species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.biocon.2017.03.009>.

The following material can be downloaded from the GitHub repository found here: https://github.com/leberhartphillips/Ceuta_snowy_plover_PVA.

Appendix A. RMarkdown PDF file containing all computer code and documentation to reproduce all analyses presented in the paper.

Appendix B. Four datasets containing the raw data used in all analyses.

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