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



Medardo Cruz-López ^{a,b,*,1}, Luke J. Eberhart-Phillips ^{c,1}, Guillermo Fernández ^b, René Beamonte-Barrientos ^d, Tamás Székely ^e, Martín A. Serrano-Meneses ^{f,g}, Clemens Küpper ^{h,*}

^a Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Cd. México 04510, Mexico

^b Unidad Académica Mazatlán, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Apartado Postal 811, Mazatlán, Sinaloa C.P. 82040, Mexico

^c Department of Animal Behaviour, Bielefeld University, Morgenbreede 45, 33615 Bielefeld, Germany

^d Laboratorio de Ecofisiología, Centro Tlaxcala de Biología de la Conducta, Universidad Autónoma de Tlaxcala, México, Carretera Tlaxcala-Puebla km 1.5, 90070, Tlaxcala, Mexico

^e Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, UK

^f Laboratorio de Biología Evolutiva, Centro Tlaxcala de Biología de la Conducta, Universidad Autónoma de Tlaxcala, Carretera Tlaxcala-Puebla km. 1.5, 90070, Tlaxcala, Mexico

^g Departamento de Ciencias Químico-Biológicas, Universidad de las Américas-Puebla, San Andrés Cholula, 72810 Puebla, Mexico

^h Max Planck Institute for Ornithology, Eberhard-Gwinner-Strasse, 82319 Seewiesen, Germany.

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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

* Corresponding authors.

¹ These authors contributed equally.

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;

E-mail addresses: mcruz@ola.icmyl.unam.mx (M. Cruz-López), ckuepper@orn.mpg.de (C. Küpper).

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 (DeSucre-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-Isunza 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 (\pm 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

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