

Apparent annual survival of adult Whimbrels in the Pacific Americas Flyway

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For long-distance migratory species, understanding mortality, and inversely survival, across the annual cycle is crucial for identifying where bottlenecks to population growth occur so that effective conservation actions can be implemented. However, demographic information, including estimates of adult survival, are sparse or lacking for many Western Hemisphere shorebird populations. We therefore conducted a study to estimate the apparent annual survival of adult Whimbrels *Numenius phaeopus* on Chiloé Island, Chile, a major wintering area (austral summer) in the Pacific Americas Flyway. We studied Whimbrels at four bays on the eastern coastline of the island, where we cannon-netted, color-flagged and resighted Whimbrels during six periods between December and February, 2007–2012. Using resights of adult birds, we estimated apparent survival using Cormack-Jolly-Seber models. From the most plausible model, we estimated a constant apparent survival rate of 0.86 ± 0.01 (SE) for adult Whimbrels wintering on Chiloé Island from 2007 to 2012. Encounter rates varied with resighting effort and ranged from 0.59 ± 0.05 (SE) in years of low effort to 0.83 ± 0.02 in years of high effort. Our estimate of annual survival was higher than that reported for the Whimbrel population using the Atlantic Americas Flyway. Our estimate may serve as a gauge to evaluate the population health of Whimbrels in other flyways across the globe.

Keywords

Numenius phaeopus

adult survival

Chile

mark-resight

INTRODUCTION

High adult survival is considered an important component of population stability, particularly for long-lived, large-bodied shorebirds that exhibit delayed maturity and low fecundity (Piersma & Baker 2000, Sandercock 2003). A recent global assessment of one large-bodied shorebird group, godwits *Limosa* spp. and curlews *Numenius* spp., indicated that threats were intensifying throughout the annual cycle of these species, with 54% of the 13 species globally threatened or Near Threatened (Pearce-Higgins *et al.* 2017). In this assessment, negative effects on survival were most severe during the passage and stationary non-breeding periods and varied somewhat among the flyways where populations resided. In the Americas, perceived threats to godwits and curlews in the Atlantic and Central Flyways were greater than those in the Pacific Flyway (Pearce-Higgins *et al.* 2017). Only by understanding mortality, and inversely survival, across the entire flyway and annual cycle of a migratory population can conservation

actions be implemented that will have the greatest positive effect on the population (e.g. Piersma *et al.* 2015, Conklin *et al.* 2016).

Breeding Whimbrels *N. phaeopus* are distributed patchily across the sub-arctic region of the Northern Hemisphere (BirdLife International 2016) and include eight to nine recognizable populations (Pearce-Higgins *et al.* 2017). Two disjunct populations of Whimbrels occur in the Western Hemisphere (Andres *et al.* 2012), and both are less abundant than populations in northern Europe and Siberia (Wetlands International 2018). The more westerly population breeds in Alaska and western interior portions of Yukon Territory and migrates through the Pacific Americas Flyway. Although their nonbreeding distribution extends from northern Mexico as far south as southern Chile, substantial numbers of Whimbrels over-winter in the vicinity of Chiloé Island, Chile (Andres *et al.* 2009), as well as on shorelines and in estuaries in northern Chile and Perú (Senner & Angulo Pratolongo 2014,

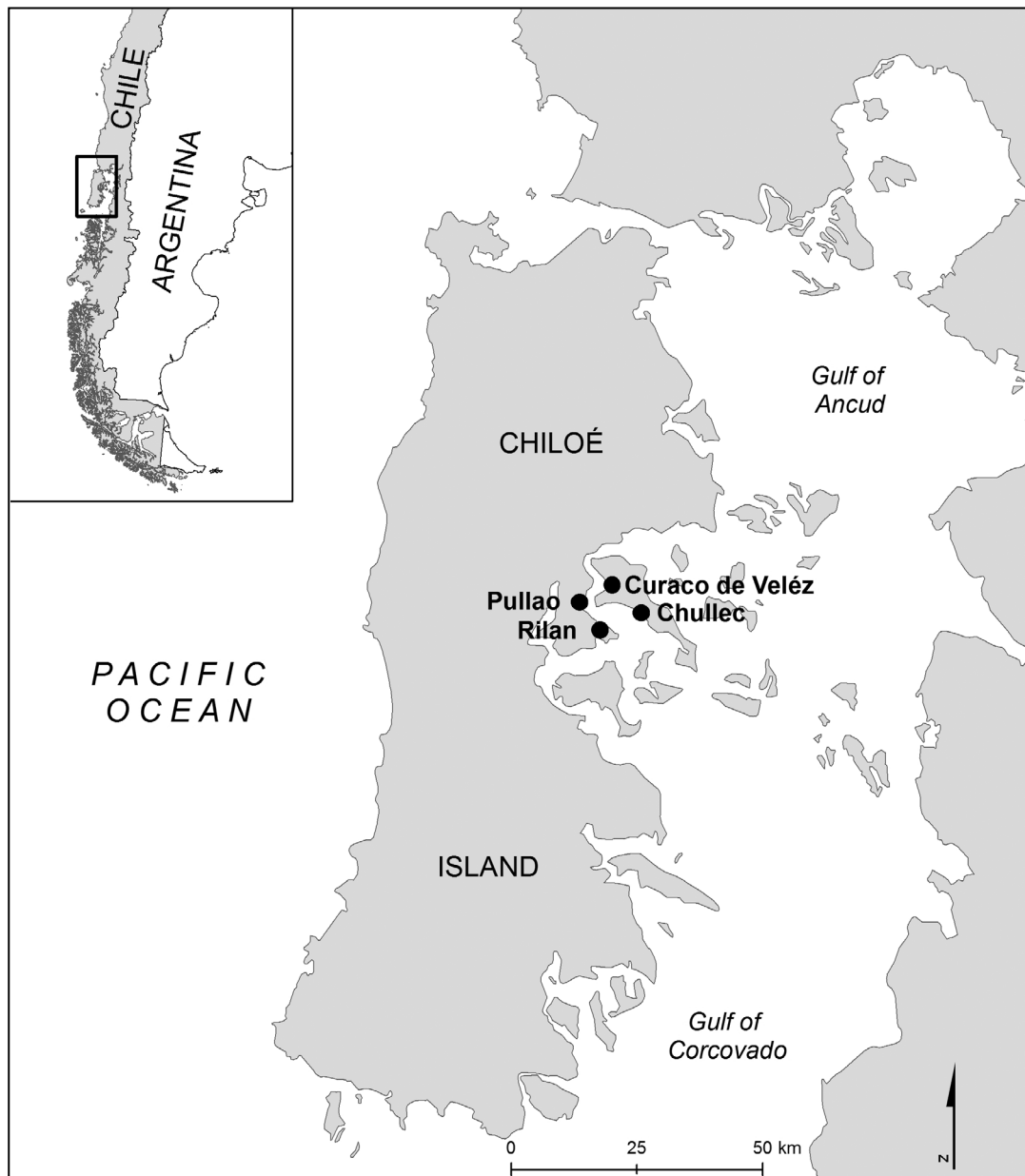


Fig. 1. Location of Whimbrel capture and resighting sites on Chiloé Island, Chile, 2007–2012.

García Walther *et al.* 2017). On Chiloé Island, Whimbrels aggregate in protected bays and estuaries and are scattered along gravel shorelines and sandy beaches (Andres *et al.* 2009). Whimbrels roost along shorelines during high tide but will also move onto grazed pastures and even structures associated with offshore aquaculture (Andres *et al.* 2007). During low tides, Whimbrels feed on crabs, polychaetes and bivalves (JAJ unpubl. data).

The second population of Whimbrels breeds in Canada in the northern Yukon and Northwest Territories and west and south of Hudson Bay, and migrates through the Atlantic and Central Americas Flyways. This population over-winters primarily on the northern coast of South America (Skeel & Mallory 1996, Wilke & Johnston-González 2010, Johnson *et al.* 2016; see http://www.wildlifetracking.org/index.shtml?project_id=369). Sizes of

the populations in the two flyways may differ, as do population trajectories (Watts & Truitt 2011, Andres *et al.* 2012). Within the Atlantic Americas Flyway, migration counts from aerial surveys on the coast of Virginia declined at a rate of 4% per year from 1994 to 2009 (Watts & Truitt 2011), and recent work has suggested low rates of adult survival (Perz 2014, B. Watts pers. comm.). One possible cause of the decline is harvest of adults on some Caribbean Islands and in northern South America (B. Watts pers. comm.). The Pacific Flyway population trend is uncertain, although recent monitoring on Chiloé Island indicates that this regional population is stable (Andres *et al.* 2009; JVR unpubl. data).

Both Western Hemisphere populations of Whimbrels were recently identified as shorebirds of high conservation concern (USSCPP 2016). Although estimates of adult

survival have recently become available for Atlantic Americas populations of Whimbrels (Perz 2014, B. Watts pers. comm.), information is still lacking for Pacific Americas Whimbrels. Following the recommendations of Sandercock & Jaramillo (2002) to focus studies of survival on wintering sites, we initiated a mark-resight study in 2007 to estimate apparent annual survival of adult Whimbrels wintering on Chiloé Island, Chile.

METHODS

Located in Chile's Las Lagos Region and within the Valdivian Temperate Rain Forest ecoregion (Fig. 1), the Chiloé Island archipelago (42°30'S, 73°45'W) has a wet-temperate climate that is strongly influenced by the Pacific Ocean. Annual precipitation exceeds 200 cm, with a mean annual temperature of 12°C (Errazuriz *et al.* 1998; Senda Darwin Biological Station, five-year record). The island is 190 km long and 55–65 km wide. The island's western coastline is steep, rocky and directly exposed to the Pacific Ocean, whereas the northern and eastern coastlines consist mainly of mixed sand and gravel beaches and numerous sheltered bays (Subiabre & Rojas 1994). Larger bays, which support the majority of the island's Whimbrels, provide mudflat and saltmarsh habitats that are used for feeding and roosting (Andres *et al.* 2009). Tidal range on the sheltered eastern side of Chiloé Island can exceed six meters. The northern and eastern coastlines also support the majority of the island's human population and industry, primarily aquaculture and agriculture (Errazuriz *et al.* 1998). Urbanization, aquaculture development and disturbance associated with human activities vary markedly among bays and shorelines in the region, and few sites are excluded from at least some low level of disturbance from humans, pets or livestock. We studied Whimbrels at four bays (Fig. 1): two on the eastern coastline of the island (Pullao and Rilan) and two on Quinchao Island (Curaco de Vélez and Chullec), a smaller island located just east of Chiloé Island in the Gulf of Ancud. We selected these sites because they were easily accessible, provided satisfactory capture sites and supported aggregations of >400 birds.

We studied Whimbrels between December and February, 2007–2012; capture visits lasted 2–5 days and resighting sessions 8–13 days (Table 1). We used a cannon net to capture individuals at high tide roosts. Following capture, we placed individuals in keeping cages, which we modified from Clark (1986) to accommodate large shorebirds, to reduce capture myopathy (Rogers *et al.* 2004) and immediately released any bird suspected of being in compromised health (e.g. not standing). We generally alternated capture locations among days, which minimized disturbance to the birds and the probability that they avoided sites because of our activities. Birds were individually marked with a red flag engraved with a unique two-character, alpha-numeric code (e.g. AA or 01; Clark *et al.* 2005) attached to the left tibia and a colored plastic ring (indicating the year of capture) above a numbered metal ring (of the U.S. Geological Service or Chilean Bird Ringing Office) attached to the right tibia. For each captured individual, we recorded biometric information and the extent of wing and body molt; we used wing feather molt to distinguish adults from sub-adults (Johnson *et al.* 2007). We released birds within three hours of capture.

Resighting of individually-marked birds occurred between December and February, a time during the nonbreeding season when Whimbrels on Chiloé Island are thought to be sedentary. Observers conducted the majority of resighting efforts at the four capture locations, although some additional effort was spent at other bays on the island's eastern coastline. Experienced observers searched for and recorded individually-marked Whimbrels during low to mid-tidal ranges when birds were distributed widely across intertidal feeding areas. Resighting effort was similar across years, except for 2008–2009 when it was limited to two observers and fewer resighting hours. Because Whimbrels were generally not wary while foraging, observers were able to closely approach birds (often within 30 m). We observed that some Whimbrels were able to remove their cohort color band, but we seldom observed individuals with a metal ring but without a flag and are confident that few flags were lost and that they were read correctly if present at our study sites.

Table 1. Dates, locations and number of Whimbrels captured and resighted on Chiloé Island, Chile, 2007–2012. Locations are shown in Fig. 1.

Season ^a	Capture dates ^b	Capture locations	<i>n</i>	Resighting dates ^b
2006–2007	2–7 Feb (5)	Curaco de Vélez; Pullao	93	–
2007–2008	25–28 Jan (3)	Chullec; Pullao	41	16 Jan–4 Feb (8)
2008–2009	12–15 Dec (3)	Chullec; Pullao	56	3–23 Dec 2 Feb (13)
2009–2010	17–24 Jan (4)	Chullec; Curaco de Vélez; Pullao; Rilan	88	8–24 Jan (12)
2010–2011	17–20 Jan (3)	Rilan; Pullao	31	5–16 Jan (10)
2011–2012	–	–	–	4–12 Jan (8)

^aEach season spanned December of the first year to February of the next.

^bDays of effort shown in parentheses.

We estimated apparent survival, which is a product of true survival and site fidelity, in Program MARK (Cooch & White 2017) using Cormack-Jolly-Seber models (Cormack 1964, Jolly 1965, Seber 1965). In all analyses, we excluded hatch-year and second-year individuals, because they likely do not migrate to breeding areas and likely have different survival rates than breeding adults (Marks & Redmond 1996, Skeel & Mallory 1996), and we did not address differences in survival between sexes in our sample. Because of sample size considerations, we did not generate site-specific survival estimates and treated the four bays, and additional observation areas, as a single site. We developed survival models that included combinations of apparent survival (ϕ) and/or encounter rates (p), which were allowed to vary among years or remain constant. Encounter rates are the product of the detection rate and site propensity (i.e. the probability that a bird returns to the capture area the next year without skipping a year). In general, our resighting periods were relatively short and met the assumption of a closed population. In the one case where resighting effort was

extended (2008–2009), all birds resighted in the latter period were also resighted in the previous December (see Table 1). To account for reduced resighting effort in 2008–2009, we included models in which encounter rates were allowed to vary based on effort (i.e., encounter rate differed between 2008–2009 as compared to all other years). We used Akaike's Information Criterion corrected for sample size (AICc) to rank candidate models, with individual models considered plausible when ΔAICc was < 2 (Burnham & Anderson 2002). We used a bootstrapping procedure with 1,000 simulations in Program MARK (Cooch & White 2017) to test for goodness-of-fit of the most general model (ϕ_p, p_t).

RESULTS

Of the Whimbrels captured and individually marked during our study, 309 after-hatching-year individuals were included in our analysis of survival (Table 1). Observers spent 51 days searching for marked Whimbrels across five annual resighting periods (Table 1) and recorded

Table 2. Cormack-Jolly-Seber models from Program MARK to estimate apparent survival (ϕ) and encounter rates (p) of adult Whimbrels wintering on Chiloé Island, Chile, 2007–2012.

Model structure ^a		Model statistics			
ϕ	p	K ^b	ΔAICc ^c	w_i ^d	Deviance
c	effort	3	0.00	0.75	88.75
c	t	6	2.60	0.20	85.26
t	effort	7	5.83	0.04	86.45
t	t	10	9.94	0.01	84.40
c	c	2	21.77	0.00	112.53
t	c	6	23.23	0.00	105.89

^amodel factors included: c = ϕ or p remained constant between years, t = ϕ or p showed annual variation, effort = p varied between years with low (2008–2009) and high (all other years) resighting effort.

^bnumber of parameters.

^cdifference between model's Akaike's Information Criterion corrected for sample size and the lowest AICc value.

^dAICc relative weight attributed to model.

Table 3. Parameter estimates from top-ranked Cormack-Jolly-Seber models estimating apparent survival (ϕ) and encounter rates (p), relative to resighting effort, of adult Whimbrels wintering on Chiloé Island, Chile, 2007–2012.

Parameter	Estimate	SE	95% CI
ϕ	0.86	0.01	0.83–0.88
p (low effort) ^a	0.59	0.05	0.49–0.68
p (high effort) ^b	0.83	0.02	0.79–0.87

^a2008–2009.

^b2008, 2010–2012.

555 resightings. Only 63 individuals (21%) were never resighted after their initial capture year. Additionally, only 30 individuals (10%) were observed at sites away from where they were captured, typically the nearest adjacent bay, and 18 of these individuals (60%) eventually returned to their original capture site. It is likely that disturbance related to our capture efforts caused some birds to emigrate temporarily. Following extensive surveys of all bays along Chiloé Island's eastern coastline, we did not observe Whimbrels marked during this study >15 km from their original capture locations, although it is feasible that some individuals may have wintered at sites away from Chiloé Island in years subsequent to capture.

Of the six candidate survival models, only the model with constant apparent survival and effort-influenced encounter rate was considered plausible ($\Delta AIC_c < 2$; Table 2). From this model, we estimated a constant apparent survival rate of 0.86 ± 0.01 (SE) for adult Whimbrels wintering on Chiloé Island from 2007 to 2012 (Table 3). Encounter rates varied with effort, ranging from 0.59 ± 0.05 in 2008–2009 to 0.83 ± 0.02 in all other years (Table 3). The bootstrapped goodness-of-fit test indicated that the model fit the data well ($\hat{c} = 1.63$).

DISCUSSION

Our estimate of apparent annual adult survival of 0.86 ± 0.01 (SE) is the first for Whimbrels occurring in the Pacific Americas. This estimate is similar to return rates of Whimbrels on the Shetland Islands, UK (0.89; Grant 1991) and to adult survival reported in other migratory North American-breeding curlews (0.85 in both Long-billed Curlews *N. americanus*, Redmond & Jenni 1986, and Bristle-thighed Curlews *N. tahitiensis*, Marks & Redmond 1996). However, our estimate exceeds the apparent adult survival estimate for Atlantic Americas Whimbrels throughout the annual cycle (0.54, annualized rate; B. Watts pers. comm.) and on the breeding grounds at Churchill, Manitoba, Canada (0.73, 95% CI = 0.60–0.83; Perz 2014). It should be noted that the study site at Churchill may have been too small to capture small-scale dispersal, which may have resulted in low-biased estimates (Perz 2014), and estimates from satellite-tagged birds may be low due to transmitter loss (B. Watts pers. comm.). On Chiloé Island, we also observed some dispersal away from capture sites ($\approx 4\%$), which may have added negative bias to our survival estimate.

Annual survival is considered the most important life-history trait for population dynamics of long-lived birds that have low reproductive rates (Stahl & Oli 2006). If survival does differ between the Atlantic and Pacific Americas Flyways, the difference might be attributed to differential harvest pressure. Within the Atlantic Americas Flyway, unregulated harvest at stopover sites on some Caribbean Islands and wintering areas along the northern coastlines of South America is thought to be a major source of mortality for Whimbrels in the flyway (B. Watts pers. comm.). Data from satellite-tagged birds showed that the greatest mortality occurred during migration

periods, particularly in the late post-breeding migration period, and it is thought that harvest pressure was the likely cause (B. Watts pers. comm.). In contrast, the western breeding population of Whimbrels is restricted to the Pacific Americas Flyway (L. Tibbitts pers. comm., JAJ unpubl. data), where shorebird harvest is likely minimal (Watts & Turrin 2016).

Habitat loss and degradation, largely from coastal development, are considered a major threat to Whimbrels at the global (Pearce-Higgins *et al.* 2017) and hemispheric scales (Wilke & Johnston-González 2010). If Whimbrels exhibit high site fidelity throughout the nonbreeding season, then loss of habitat at specific sites could reduce Whimbrel survival indirectly by causing changes in food resources needed for successful migration and reproduction (e.g. carry-over effects; Senner *et al.* 2015). In the Chiloé Island archipelago, the highest abundances of Whimbrels were found along the northern and eastern shorelines (Andres *et al.* 2009), which overlaps with the greatest extent of onshore and nearshore development. Although these developments often result in the loss and alteration of intertidal habitats used for foraging and roosting by Whimbrels, some types of development may be neutral or perhaps even beneficial to wintering Whimbrels. For example, Whimbrels are known to roost on the floats used by the aquaculture industry and in grazed agricultural fields (Andres *et al.* 2007). In addition, farming of algae in intertidal areas at many sheltered bays may increase crab densities (JAJ unpubl. data), a preferred food of Whimbrels. At present, these disturbances do not appear to be negatively affecting Whimbrels to the point of reducing their annual survival.

In addition to adult survival, Whimbrel nest survival may also differ between the Atlantic and Pacific Americas Flyway populations. Although studied at only a few local sites, nest survival was generally higher within the Pacific Americas Flyway (0.41, 95% CI = 0.26–55; 0.92, 0.55–0.99) at two sites in boreal Alaska (Harwood *et al.* 2016) relative to the Atlantic Americas Flyway (0.33, 0.25–0.42) at Churchill, Manitoba, Canada (Perz 2014). Thus, lower nest survival could also be contributing to population declines observed in Whimbrels in the Atlantic Americas Flyway.

Initiating a dual-flyway survival study of Whimbrels that used similar methods would enhance our ability to determine if differences between the flyways truly exist. The relatively high apparent annual survival of Whimbrels in the Pacific Americas Flyway could then serve as a gauge to evaluate the recovery of the Atlantic population. Information on survival rates of first- and second-year birds in both flyways would provide a comprehensive picture of the annual cycle of the Whimbrel in the Americas.

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