



# Population estimates of shorebirds on the Atlantic Coast of southern South America generated from large-scale, simultaneous, volunteer-led surveys

## Estimaciones de población de aves playeras en la Costa Atlántica del sur de Sudamérica mediante censos simultáneos a gran escala, realizados por voluntarios

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**ABSTRACT.** Population abundance and trend estimates are crucial to science, management, and conservation. Shorebirds, which are abundant in many coastal habitats and play important roles in coastal ecosystems, are facing some of the most dramatic population declines of any group of birds globally. However, accurate and up-to-date population estimates are lacking for most shorebird species. We thus conducted large-scale, simultaneous, and community scientist-led surveys of the Atlantic Coast of southern South America, stretching from central Brazil to Tierra del Fuego, to gather counts of shorebirds stratified by habitat that we combined with remote sensing analyses and two-step hurdle models that accounted for presence and abundance. Our objectives were to estimate shorebird densities by habitat, identify high-concentration areas, understand the environmental factors affecting their distributions, and provide population estimates for both Nearctic and Neotropical species. We counted a total of 37,207 shorebirds of 17 species and, from those counts, estimated that nearly 1.1 million shorebirds use the region's coastline. We found that the northern portion of the region was important for sandy beach specialists, while southern portions supported higher abundances of species that rely on intertidal mudflat and rocky habitats. We also found that shorebirds occurred in the highest densities in wetland habitats and that fewer shorebirds occupied areas that were further away from estuaries. Although not directly comparable, our results suggest the population sizes of the Nearctic species whose nonbreeding ranges are predominantly in southern South America may have declined substantially since previous estimates. At the same time, our study represents the first empirically derived population estimates for Neotropical breeding shorebird species and indicates that they are far more abundant than previously thought. Taken together, our results highlight the power of community scientists to carry out structured protocols at continental scales and generate critical data for a group of at-risk species.

**RESUMEN.** Las estimaciones de abundancia y de tendencias poblacionales son cruciales para la ciencia, el manejo y la conservación de la biodiversidad. Las aves playeras, abundantes en diversos hábitats costeros y con un importante rol ecológico en estos ecosistemas, se enfrentan a una de las disminuciones poblacionales más dramáticas a nivel global dentro del grupo de las aves. Sin embargo, se carece de estimaciones poblacionales precisas y actualizadas para la mayoría de sus especies. Con este fin, realizamos censos simultáneos a gran escala, llevados a cabo por voluntarios comunitarios a lo largo de la costa atlántica del sur de Sudamérica, desde el centro de Brasil hasta Tierra del Fuego. El objetivo fue recopilar recuentos estratificados por hábitat de aves playeras, que, combinados con análisis de percepción remota y modelos estadísticos Hurdle de dos etapas, permitieran estimar la presencia y la abundancia. Los objetivos específicos fueron: (1) estimar las densidades de aves playeras por hábitat; (2) identificar áreas de alta concentración; (3) comprender los factores ambientales que influyen en su distribución; y (4) proporcionar estimaciones de población tanto para especies neárticas como neotropicales. Se registraron un total de 37,207 individuos pertenecientes a 17 especies de aves playeras. A partir de esos conteos, se estimó que aproximadamente 1,1 millones de aves playeras utilizan la costa de la región. Se determinó que la porción norte de la región es de particular importancia para las especies especialistas de playas arenosas, mientras que las porciones del sur albergan mayores abundancias de especies que dependen de planicies intermareales fangosas y hábitats rocosos. Se observaron mayores densidades de aves playeras en humedales y menores densidades en áreas más alejadas de los estuarios. Si bien no son directamente comparables, nuestros resultados sugieren que los tamaños de población de las especies neárticas cuyos rangos de invernada se encuentran predominantemente en el sur de Sudamérica podrían haber disminuido sustancialmente en comparación con estimaciones previas. Paralelamente, este estudio presenta las primeras estimaciones de población derivadas empíricamente para las especies de aves playeras de reproducción neotropical indicando que son considerablemente más abundantes de lo que se estimaba anteriormente. En conjunto, nuestros resultados resaltan el valor de la participación de voluntarios comunitarios en la implementación de protocolos estructurados a escalas continentales, generando datos críticos para la conservación de este grupo de especies en riesgo.

**Key Words:** *abundance; Charadriidae; citizen science; remote sensing; Scolopacidae; waders*

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## INTRODUCTION

Population size estimates form the basis for understanding many ecological and evolutionary processes (Magurran et al. 2010, Ripple and Breschta 2012). Regional population size estimates are also vital for management and conservation, as they provide baseline data that can serve to identify local exposure to threats, vulnerabilities, and habitat-use patterns (e.g., Duan et al. 2020), as well as be a reference point for evaluating the success of on-the-ground actions (Mace et al. 2008, Monzón and Friedenbergl 2018). When applied at large spatial scales, estimates can help identify species' distributional patterns and biodiversity hotspots, and even be incorporated into broader analyses of ecosystem function and environmental health (Şekercioğlu et al. 2004, Stuart-Smith et al. 2013). Nonetheless, robust population estimates remain difficult to generate and a lack of such estimates hinders our ability to forecast species' vulnerabilities to declines and extinctions (Fraser et al. 2022).

Coastal wetlands support high levels of biodiversity and are among the most productive ecosystems globally (Mitsch and Gosselink 2015). Simultaneously, coastal wetlands are one of the most threatened ecosystems on the planet (Schuerch et al. 2018, IPCC 2022). Wetland habitats such as saltmarshes, estuaries, and coastal lagoons are facing a multitude of threats, including pollution (Naidoo et al. 2015, Hitchcock and Mitrovic 2019), sea level rise (Schuerch et al. 2018, Fagherazzi et al. 2020), and urban development (Lee et al. 2006, Freeman et al. 2019). In fact, most of the world's megacities are located in coastal areas and they continue to attract more people to these regions (Seto 2011, Brown et al. 2013). Increasing urbanization, in turn, constitutes one of the main causes of habitat fragmentation and loss in coastal areas (Liu et al. 2016). Consequently, coastal dependent organisms have been heavily impacted, and monitoring their populations is critical to assessing their conservation status and the health of coastal ecosystems (Studds et al. 2017, Avila et al. 2018).

Among coastal species, birds are recognized as sentinels of ecosystem health because they are visible, have broad public appeal, occupy a variety of habitats and trophic levels, and tend to respond quickly to environmental changes (Smits and Fernie 2013). Coastal birds, and especially shorebirds in the order Charadriiformes, are also among the most threatened groups of species in the world (Simmons et al. 2015), with many North American breeding shorebird populations exhibiting accelerating declines that have exceeded 50% over the past few decades (Smith et al. 2023). The existence of these trend estimates, however, belies the fact that they still need to be combined with complementary data collected throughout species' annual cycles to understand how close to extinction shorebird populations may actually be (Andres et al. 2012).

The Atlantic Coast of southern South America supports the majority of the hemispheric and global populations of a number of Nearctic-breeding migratory shorebird species during the nonbreeding season (Andres et al. 2012). Population estimates from the region were generated for these species nearly four decades ago (Morrison and Ross 1989) and are in urgent need of updating. Such updates are best developed from data collected in southern South America because (i) many Nearctic species are sparsely distributed during the breeding season across remote parts of the Arctic (McCarty et al. 2020) and (ii) rapid turnover rates make estimates harder to generate at migratory stopover

sites (Wang et al. 2022). Importantly, many Neotropical species also breed and occupy the coasts of southern South America throughout the year (del Hoyo et al. 1996), but no empirically derived estimates exist for their populations (Wetlands International 2017). Generating robust site-specific population estimates for both Nearctic and Neotropical species in the region is thus critical to developing targeted conservation efforts.

The limited number of range-wide population estimates that exist for shorebirds, as well as other taxa, can be partially explained by the difficulties posed by coordinating large-scale efforts, especially in terms of financial and/or human resources (Stroud et al. 2006). However, recent methodological advances can now facilitate the collection and analysis of data at necessarily large scales. For example, the development of remote sensing technologies has improved ecological studies and conservation actions via the enhancement of analytical tools and the quality and resolution of images available across vast geographic regions (Hansen et al. 2013, Nagendra et al. 2013, Rajah et al. 2019). More importantly, the dramatic increase in community science projects that draw participants from the general public has allowed the collection of large datasets that can be used to investigate the distributions (Newson et al. 2016, Schubert et al. 2019), behavior (Robbins et al. 1986), and long-term population trends of birds (Horns et al. 2018, Gillings et al. 2019). Combined, such approaches now make feasible large-scale studies that can generate shorebird population estimates across their nonbreeding ranges.

In this context, we conducted the first community scientist-driven, simultaneous, comprehensive survey of shorebirds along the Atlantic Coast of southern South America in 2019. By using a combination of on-the-ground surveys and remote sensing analyses, our objectives were to (1) create habitat-specific density estimates for shorebirds; (2) identify areas with high concentrations of shorebirds; (3) determine the environmental factors influencing shorebird distributions; and (4) generate population estimates for both Nearctic and Neotropical species in the region. Given the documented declines in many shorebird populations (e.g., Smith et al. 2023), we hope that these results can be used to guide management actions and decisions while also providing baseline data for future estimates of population trends.

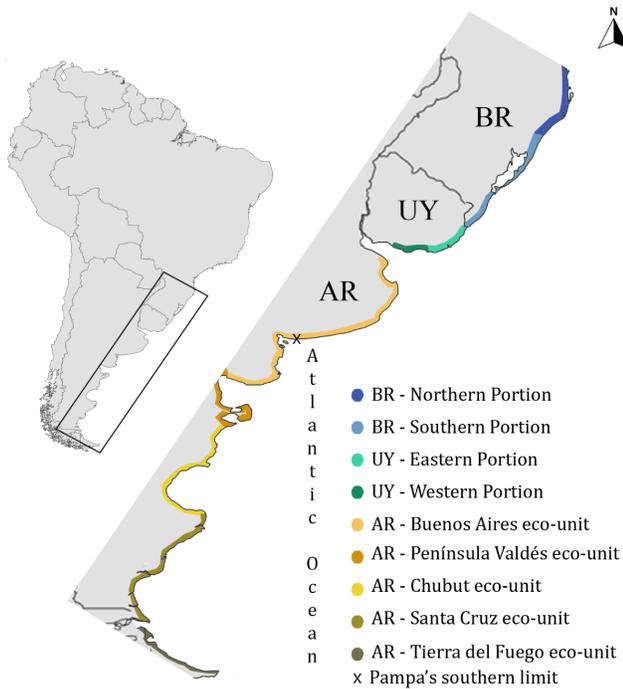
## METHODS

### Study area and habitats

Our study encompassed the southeastern portion of the South American Atlantic Coast, stretching from the southern Brazilian state of Santa Catarina (28°48'S) along the entire coasts of Uruguay and Argentina to the southern tip of the province of Tierra del Fuego (54°65'S), a total distance of 6575 km. Our surveys and estimates covered any habitats considered suitable for the shorebird species included in our study (see below) within 5 km of the coastline. We then divided the study area into nine major regions (two in Brazil, two in Uruguay, and five in Argentina) based on biogeographic boundaries (Spalding et al. 2007) and previous survey efforts (e.g., Morrison and Ross 1989; Fig. 1), which allowed some level of cross-study comparison with our population estimates.

Before our surveys began, we chose sites and habitats to survey by relying on previous information indicating their potential importance for migratory and resident shorebirds (Morrison and Ross 1989, Isacch and Martínez 2003, Bencke et al. 2006, Alfaro

**Fig. 1.** Map of southeastern South America where simultaneous shorebird surveys were conducted from 20 to 29 January 2019. Distinct colors indicate division of coastal regions used in the sampling design. Colored region width is illustrative and does not represent the 5 km buffer applied to the coast in the analyses. AR, Argentina; UY, Uruguay; and BR, Brazil.



and Clara 2007), searching the eBird database (Sullivan et al. 2009), and following the methodology developed by Senner and Angulo-Pratolongo (2014) and García-Walther et al. (2017). The habitats were divided in two broader types with different sampling methods (described below) as follows: *restingas* (broad rocky platforms extending to the lower intertidal zone; Morrison and Ross 1989), as well as rocky and sandy beaches were grouped as “beaches”; while intertidal mudflats, shallow water, and adjacent low vegetation height grasslands were grouped as “wetlands.” The latter two habitat types, shallow water and grasslands, only occurred in the Pampas Biome, which ranges from the Rio Grande do Sul state in Brazil to the southern tip of the Buenos Aires province in Argentina (Fig. 1).

#### Volunteer training

We hosted five workshops, one in Brazil, one in Uruguay, and three in Argentina, to guarantee that all participants received standardized training on shorebird identification, count methods, and data submission through the eBird website (<https://ebird.org/home>) before completing our surveys. During the workshops, we formed teams of observers based on the number of sites to be surveyed and the degree of experience of the participants, ensuring that all teams included at least one experienced observer. Each team then received georeferenced maps with pre-determined polygons and transects to be surveyed. Surveys were conducted by teams of at least two observers.

#### Shorebird surveys

To minimize the potential for birds to move among sites and avoid double-counting, we carried out all surveys within a country during a single 7-d window, while across all countries, we carried out the surveys within a single 9-d window. The survey design and effort were developed while taking into consideration the (i) number of volunteers and teams available, (ii) proximity and accessibility of sites, and (iii) previous knowledge of suitable shorebird habitat occurrence among sites. We were able to survey the majority of previously known areas with wetland habitats across all three countries. Within each of these areas, we surveyed at least one representative sample (i.e., a 4-ha polygon) of each of the three wetland types—shallow water wetlands, low vegetation height grasslands, and intertidal mudflats—that were present (Table A2.1). In addition to these known wetland areas, we randomly surveyed 247 sandy beach, 15 rocky beach, and 57 *restinga* transects that were selected before the surveys.

Our surveys were conducted following a standardized protocol that accounted for: survey day and hour; area covered (ha) or transect length (m); tidal conditions, when necessary (i.e., within  $\pm 3$  h of low tide); and number of observers. We also attempted to maximize detection by tailoring our survey methods to each habitat type. Thus, following Senner and Angulo-Pratolongo (2014), in grassland and shallow water sites, observers walked the borders of  $0.1 \times 0.4$ -km pre-determined polygons using binoculars to count all shorebirds and identify them to species level. For intertidal mudflats, observers walked a pre-defined transect bisecting the habitat and stopped every 0.4 km to perform unlimited time point counts during which they counted and identified every shorebird within a 0.2-km radius. The results from wetland habitats are presented as birds.ha<sup>-1</sup>. In *restingas* and along rocky and sandy beaches, observers walked pre-determined linear 0.5-km length transects counting and identifying all birds from the coastline to the habitat’s supralittoral limits. The results from beach habitats are presented as birds.km<sup>-1</sup>. Birds crossing transects or polygons in flight and birds identified to the genus level were not considered in our analyses.

#### Spatial analysis

Because we were unable to survey all of the shorebird habitat within each known wetland area, and because patches of shorebird habitat exist outside of previously known wetland areas, we obtained freely available Sentinel-2 satellite images (<http://glovis.usgs.gov>) to assess the extent of non-surveyed patches of habitats that could be classified as suitable and, therefore, potentially used by shorebirds across the entire study area (i.e., within 5 km of the coastline). Sentinel-2 satellites provide high-resolution ( $\sim 10$  m<sup>2</sup>) multispectral imagery with 13 bands in the visible, near infrared, and shortwave infrared portions of the light spectrum (Immordino et al. 2019). We opted for cloud-free images from the closest date to the survey period available (29 December 2018 to 22 February 2019). We analyzed each country separately and subset Argentina into two regions because of its large size (Fig. 1). Subsetting helped to increase the overall classification accuracy by reducing the number of land-cover types and spectral variation per region (Bhattarai and Giri 2011).

For the non-surveyed portions of beach habitats, we divided the entire coastline into 0.5-km length sections. Then, because no good remote sensing tools exist to differentiate among the habitats systematically, we visually classified each section as *restinga*, rocky

beach, sandy beach, or “unsuitable” (structures such as harbors/piers, factories, and cliffs). For the wetland habitats with polygon-based surveys, we generated multispectral images with spectral bands 8, 4, and 3, as near infrared is efficient at differentiating among vegetation types as well as detecting exposed soil/water (Stratoulis et al. 2015, Faria et al. 2021). In addition, we created polygons bordering all estuaries and cities (e.g., areas with > 10 ha of buildings and streets rather than simply areas within legal jurisdictional limits) along the coastline. We then used supervised classification models based on a maximum-likelihood algorithm to classify and distinguish among habitat types. This process involved translating the pixel values of a satellite image into distinct habitat categories (Horning et al. 2010) and allowed us to use our actual, on-the-ground, surveyed sites as training sites for the model.

We performed a first classification to detect waterbodies inside the 5-km buffer from the coastline. Then, we applied a 1-km buffer around these waterbodies—to restrict low vegetation height grasslands to this buffered area and avoid potential overestimation to habitats such as dry grasslands that are not used by shorebirds (see Faria et al. 2023)—and classified the remaining habitats to determine their extent. For each polygon/transect classified as suitable, we calculated the (i) central coordinates, (ii) distance to the nearest city, and (iii) distance to the nearest estuary. For polygons, we also calculated the size in hectares of each classified habitat. All GIS analyses were performed in ArcMap 10.8.

#### Population estimates

To develop shorebird population estimates for the study area that included both surveyed and unsurveyed patches of habitat, we had to account for the (potentially) separate factors influencing occupancy (i.e., the presence/absence of a species) and abundance (i.e., the sum of individuals from a given species within a given patch). To do this, we used “hurdle” generalized linear models, which involved two steps: an initial “binomial” step that can be used to evaluate the influence of predictor variables on a species’ presence within a survey area, and a second “continuous” step, a truncated count model to evaluate factors influencing a species’ abundance where it is present, assuming a Poisson distribution. This approach is useful in ecological studies where many sites may have zero count data (Potts and Elith 2006, Zuur et al. 2009). Models were fit separately for each country and survey design (i.e., transect or polygon-based surveys) in the R programming environment (v. 4.3.2; R Core Team 2020) using the “hurdle” function in the *pscl* package (Jackman 2015). In both stages of the model, we included species, habitat type, distance to nearest city, and distance to nearest estuary as predictor variables. Species was included as a variable to increase our overall sample size and, therefore, statistical power. Models for the polygon-based surveys (wetlands) also included habitat size (in ha) and region as predictor variables. Before we included them in the models, we standardized all numerical variables using the “rescale” function in the *lme4* package (Bates 2010). Model selection was based on a stepwise procedure using Akaike Information Criterion (AIC; Burnham and Anderson 2002), ensuring that the most parsimonious models were chosen based on their explanatory power and ecological relevance. Goodness of fit was evaluated using McFadden’s pseudo- $r^2$  (McFadden 1977).

Selected models were used to predict the abundance, and the 95% confidence intervals around that abundance (i.e., extrapolate), of each shorebird species in each of the non-surveyed patches (polygon

or transect) of coastal habitat classified as suitable by our remote sensing analyses using the “prediction” function in the *marginalEffects* package (Arel-Bundock et al. 2023). Finally, to generate site- and species-specific population estimates, we combined results from our on-the-ground surveys (i.e., species’ abundance in surveyed patches) with the predicted model values (i.e., the sum of species-specific predictions obtained from each model) from the beach and wetland areas that were not covered by our surveys. Surveys that (i) did not follow the protocol, or (ii) presented an exceptionally high number of individuals (i.e., > 10 standard deviations away from the mean value of a species’ abundance across all surveyed polygons) were included in our final estimates but not in the models (Table A2.1). Species detected in < 5 surveys were not considered in the study.

#### RESULTS

Between 20 and 29 January 2019, 189 volunteers conducted 452 surveys across the three countries. A total of 196 lists were collected in Brazil, followed by 180 in Argentina and 76 in Uruguay. We counted a total of 37,207 shorebirds from 17 species (11 Nearctic and 6 Neotropical) and 4 families (Charadriidae, Scolopacidae, Haematopodidae, and Recurvirostridae). Our models exhibited McFadden’s pseudo- $r^2$  values between 0.31 and 0.69 (Table A3.1), indicating that they were well fit (McFadden 1977). We therefore used our models to estimate from these counts that ~1.1 million Nearctic and Neotropical shorebirds used the 5-km wide Atlantic Coast of southern South America, from southern Brazil to Tierra del Fuego in Argentina, during the survey period (Table 1).

Most shorebirds were found in shallow water wetlands, low vegetation height grasslands, and intertidal mudflats (59.8% of individuals). Argentina supported 81.9% of all shorebirds, followed by southern Brazil (14.0%) and Uruguay (4.1%). Overall, the most abundant species were the Nearctic-breeding White-rumped Sandpiper (*Calidris fuscicollis*), with an estimated 335,500 individuals (95% CI: 118,041–595,151), and two Neotropical-breeding species, the Two-banded Plover (*Anarhynchus falklandicus*) with 181,275 individuals (95% CI: 62,496–301,070), and the Magellanic Oystercatcher (*Haematopus leucopodus*) with 165,357 individuals (95% CI: 43,711–297,015).

In general, the northern portion of the region was important for sandy beach specialists, such as Sanderling (*C. alba*) and American Oystercatcher (*H. palliatus*), while the southern portion supported higher abundances of intertidal mudflat species such as Hudsonian Godwits (*Limosa haemastica*) and Red Knots (*C. canutus*), as well as species that rely on rocky intertidal habitats, such as Magellanic Oystercatcher. Consequently, species exhibited distinct distributional patterns, varying from species that were predominantly restricted to the northern portion of the study area—Semipalmated Plover (*C. semipalmatus*), Buff-breasted Sandpiper (*C. subruficollis*), and Black-necked Stilt (*Himantopus mexicanus*)—to those restricted to the southern portion of the study area, Magellanic Oystercatcher and Red Knot, and, finally, a few widespread species, American Oystercatcher and White-rumped Sandpiper (Fig. 2).

Our models additionally indicated that increasing distances to estuaries had a negative effect on shorebird abundance, especially for beach habitats. However, we did not find a consistent negative

**Table 1.** Results of survey and population estimates of Nearctic and Neotropical shorebirds in southeastern South America in January 2019.

Species	Brazil				Count	Brazil				Count + Prediction	Total	
	Count	Beaches		U95		Count excluded	Wetlands		U95		L95	U95
<i>Phuvalis dominica</i>	204	1,714	799	2629	206	0	5056	1659	8603	7180	2868	11,642
<i>Phuvalis squatarola</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vanellus chilensis</i>	108	949	549	1,351	148	0	9764	3386	20,027	10,969	4191	21,634
<i>Charadrius semipalmatus</i>	61	778	0	1,580	669	0	7042	1933	12,366	8550	2663	14,676
<i>Anarhynchus falklandicus</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Haematopus palliatus</i>	573	5375	4291	6466	29	0	1431	132	4666	7408	5025	11,734
<i>Haematopus ater</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Haematopus leucopodus</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Himantopus melanurus</i>	914	8852	5382	12,325	516	0	27,894	6573	75,890	38,176	13,385	89,645
<i>Limosa haemastica</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calidris canutus</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calidris alba</i>	907	12,711	2220	23,202	176	8750	7853	210	32,567	30,397	12,263	65,502
<i>Calidris bairdii</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calidris fuscicollis</i>	1169	11,846	6550	17,144	522	0	26,572	7632	64,339	40,109	30,397	83,174
<i>Calidris subruficollis</i>	0	0	0	0	118	0	4,354	721	8156	4472	839	8274
<i>Tringa melanoleuca</i>	26	236	55	417	41	0	2515	468	7178	2818	590	7662
<i>Tringa flavipes</i>	6	61	0	159	78	0	4387	851	12,617	4532	935	12,860

Species	Uruguay				Count	Uruguay				Count + Prediction	Total	
	Count	Beaches		U95		Count excluded	Wetlands		U95		L95	U95
<i>Phuvalis dominica</i>	66	1161	306	2026	118	2780	1367	4196	4125	1857	6406	
<i>Phuvalis squatarola</i>	0	0	0	0	0	0	0	0	0	0	0	
<i>Vanellus chilensis</i>	51	795	408	1184	47	1714	595	2839	2607	1101	4121	
<i>Charadrius semipalmatus</i>	22	279	0	842	0	0	0	0	301	22	864	
<i>Anarhynchus falklandicus</i>	0	0	0	0	0	0	0	0	0	0	0	
<i>Haematopus palliatus</i>	116	1839	888	2,794	22	492	11	1073	2649	1037	4005	
<i>Haematopus ater</i>	0	0	0	0	0	0	0	0	0	0	0	
<i>Haematopus leucopodus</i>	0	0	0	0	0	0	0	0	0	0	0	
<i>Himantopus melanurus</i>	43	1109	23	2274	185	4265	1135	7415	5,602	1386	9917	
<i>Limosa haemastica</i>	0	0	0	0	94	1925	35	4336	2019	129	4430	
<i>Calidris canutus</i>	0	0	0	0	0	0	0	0	0	0	0	
<i>Calidris alba</i>	0	0	0	0	0	0	0	0	0	0	0	
<i>Calidris bairdii</i>	0	0	0	0	0	0	0	0	0	0	0	
<i>Calidris fuscicollis</i>	134	2251	105	4529	476	7897	1205	14,979	10,758	1920	20,118	
<i>Calidris subruficollis</i>	0	0	0	0	111	7559	0	19,167	7670	111	19,278	
<i>Tringa melanoleuca</i>	64	975	435	1518	18	477	88	886	1534	605	2486	
<i>Tringa flavipes</i>	106	11,775	653	2907	71	1791	741	2847	13,743	1571	5931	

Species	Argentina				Count	Argentina				Count + Prediction	Total	
	Count	Beaches		U95		Count Excluded	Wetlands		U95		L95	U95
<i>Phuvalis dominica</i>	59	5332	79	11,601	313	0	18,399	9189	27,632	24,103	9640	39,605
<i>Phuvalis squatarola</i>	0	0	0	0	50	0	3690	3028	4353	3740	556	7052
<i>Vanellus chilensis</i>	0	0	0	0	208	2	14,359	12,875	15,843	14,569	13,065	16,053
<i>Charadrius semipalmatus</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Anarhynchus falklandicus</i>	986	70,041	26,771	113,318	2820	295	107,133	31,624	183,651	181,275	62,496	301,070
<i>Haematopus palliatus</i>	295	24,171	13,465	34,876	559	193	33,696	12,773	54,735	58,914	27,285	90,658
<i>Haematopus ater</i>	169	9584	1163	18,403	20	0	872	0	2246	10,645	1352	20,838
<i>Haematopus leucopodus</i>	2121	116,879	38,025	195,789	774	995	44,588	1796	97,336	165,357	43,711	297,015
<i>Himantopus melanurus</i>	65	10,776	0	25,812	328	8	20,315	11,559	29,090	31,492	11,960	55,303
<i>Limosa haemastica</i>	347	24,591	538	52,937	876	91	28,352	7345	54,540	54,257	9197	108,791
<i>Calidris canutus</i>	99	6,171	0	16,108	19	0	259	0	717	6548	118	16,943
<i>Calidris alba</i>	400	22,555	1481	45,743	0	0	0	0	0	22,955	1881	46,143
<i>Calidris bairdii</i>	105	6976	1063	13,052	171	0	8274	361	17,711	15,256	1700	16,943
<i>Calidris fuscicollis</i>	1246	74,244	21,767	126,786	5117	1126	202,900	56,468	357,584	284,633	85,724	491,859
<i>Calidris subruficollis</i>	0	0	0	0	75	0	5566	787	10,512	5641	862	10,587
<i>Tringa melanoleuca</i>	29	2287	2263	2311	120	0	9381	8697	10,066	11,817	11,109	12,526
<i>Tringa flavipes</i>	11	1166	1154	1178	147	3	8782	8028	9535	10,109	9343	10,874

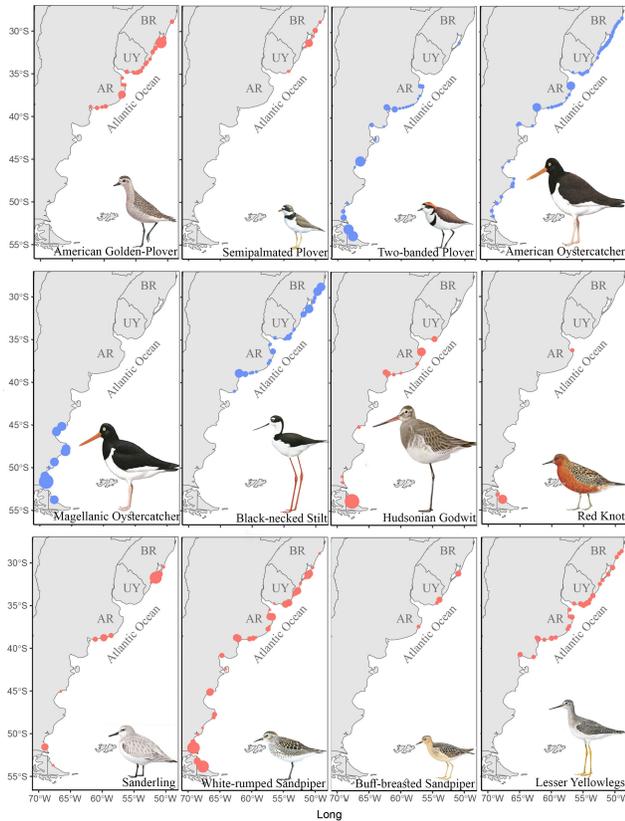
effect of proximity to cities on either shorebird presence or abundance (Fig. 3, Tables 2 and 3). Our species-specific results are presented in Appendix 1.

## DISCUSSION

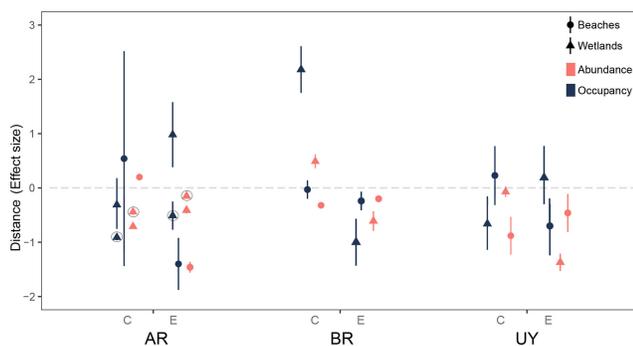
Shorebirds are one of the most threatened groups of birds on the planet, yet we lack robust population estimates for most species (Andres et al. 2012, Smith et al. 2023). Here, we present population

estimates for 17 Nearctic and Neotropical shorebird species from the Atlantic Coast of three countries in southern South America. Overall, the estimates generated in this study represent less than 20% of global population estimates proposed by Andres et al. (2012) for most Nearctic species, but are higher than previous estimates for Neotropical species (Wetlands International 2017). In addition, we found that both the presence and abundance of shorebirds in beach habitats were higher closer to estuaries. Taken

**Fig. 2.** Relative abundance and distribution of Neotropical (blue) and Nearctic (red) shorebirds counted during the simultaneous surveys conducted between 20 and 29 January 2019. The size of points is not directly comparable between maps. AR, Argentina; BR, Brazil; and UY, Uruguay.



**Fig. 3.** Predicted effects of distance to closest city (C) and closest estuary (E) on the presence and abundance of shorebirds counted in beaches and wetlands during simultaneous surveys conducted between 20 and 29 January 2019. The y-axis represents the estimated effect and standard deviation of variables in the three countries: AR, Argentina; BR, Brazil; and UY, Uruguay. Circled triangles represent wetlands from the Argentine region that includes the Pampas Biome.



together, these results complement information about recent Nearctic shorebird population declines, while underscoring the substantial knowledge gaps that exist about Neotropical species and highlighting the power of community scientists to carry out complex protocols across large spatial scales.

In general, we found that shorebirds used countries and habitats in similar ways to those detailed in previous studies. Along the Brazilian Coast, for instance, Neotropical species were widespread throughout the study area, while Nearctic species occurred mostly along the country's southern coast, with the highest concentrations of both groups found around Lagoa do Peixe. Furthermore, as with previous studies, the oceanic beaches from Lagoa do Peixe southward to the Uruguayan border were especially important for sandy beach specialists like Sanderlings (Vooren and Chiaradia 1990). In Uruguay, we corroborated previous studies, which had shown that Nearctic species were largely restricted to the country's eastern coast where there are a number of sizeable coastal lagoons, such as lagunas Rocha and Merín (Alfaro and Clara 2007, Aldabe et al. 2023). In Argentina, we found the highest shorebird concentrations in previously reported important shorebird areas, such as Bahía Samborombón (Martínez-Curci and Isacch 2017), Bahía Blanca (Blanco et al. 2006), the Estuario de Río Gallegos (Ferrari et al. 2002), and Tierra del Fuego (Morrison and Ross 1989, Baker et al. 2005).

Ours are not the first large-scale surveys of Nearctic shorebirds in the region. In 1982, Morrison and Ross (1989) carried out aerial surveys of the exact same coastline. Surprisingly, our estimates were generally higher than those obtained from their surveys. It is possible that this discrepancy is a methodological artifact, because (i) their survey methods resulted in lower detection probabilities and/or (ii) they categorized most individuals into size and not species-specific groups, making direct comparisons difficult. Even so, in the Brazilian region covered by both surveys, our estimates of small peeps (*Calidris* spp.) were 2.6× higher than their estimates (Morrison and Ross 1989). The same was true for our estimates from Uruguay (3.6× higher for small shorebirds) and, especially, Argentina (7.5× higher for small shorebirds). Some species are notoriously difficult to detect during aerial surveys, especially small grassland shorebirds, whose detectability decreases considerably at distances greater than a few tens of meters (e.g., Buff-breasted Sandpiper; Aldabe et al. 2019, Faria et al. 2023). Other studies using aerial surveys, however, have also found larger numbers of Nearctic shorebirds than Morrison and Ross (1989). For example, 9710 shorebirds were estimated from Bahía Samborombón, Argentina in 2014, a number 2.9× higher than that found by Morrison and Ross in 1982 (Martínez-Curci and Isacch 2017).

One species, Red Knot, however, exhibited notable declines in comparison to the counts from Morrison and Ross (1989). This population's decline has been well documented and resulted in their listing as a threatened species in the United States (USFWS 2021), with the *rufa* subspecies classified as an Endangered species in Canada (ECCC 2017). In South America, the *rufa* subspecies is considered Vulnerable in Brazil (MMA 2022), Endangered in Uruguay (Azpiroz et al. 2012), and Critically Endangered in Argentina (MAyDS and AA 2017). Despite covering many sites with historically large concentrations, including Bahía San Sebastian and Rio Grande on Tierra del Fuego, our results suggest that, along the Argentine Coast, the population has

**Table 2.** Effects of distance to nearest cities and estuaries on the abundance and occupancy of Nearctic and Neotropical shorebirds using beach habitats (*restingas*, sandy and rocky beaches) in southeastern South America, 2019. SE = standard errors. Bold values represent values of  $p < 0.05$ .

Beaches	Brazil			Argentina			Uruguay		
	Estimate	SE	<i>p</i> value	Estimate	SE	<i>p</i> value	Estimate	SE	<i>p</i> value
Estuaries									
Occupancy	-0.25	0.17	0.15	-1.41	0.48	<b>0.003</b>	-0.71	0.54	0.18
Abundance	-0.20	0.04	<b>&lt;0.001</b>	-1.46	0.1	<b>&lt;0.001</b>	-0.46	0.35	0.18
Cities									
Occupancy	-0.03	0.16	0.83	0.54	1.98	<b>0.006</b>	0.23	0.58	0.69
Abundance	-0.32	0.04	<b>&lt;0.001</b>	0.20	0.02	<b>&lt;0.001</b>	-0.88	0.35	<b>0.01</b>

experienced a nearly 75% decline since the early 1980s and now numbers ~6500 individuals. Even when considering the upper 95% confidence intervals of our estimates, the decline would be ~32%. These declines have been variously linked with climate change, a decline in food resources, and an increase in disturbance and habitat loss at migratory stopover sites, including sites within southeastern South America (González et al. 2006). Continued conservation efforts targeted at this species throughout its range are clearly critical.

In comparison with other, more recent, population estimates of Nearctic breeding shorebird populations, our results for the Nearctic species for which we covered the majority of their wintering ranges (e.g., White-rumped Sandpipers; Parmelee 2020) unfortunately mirror our results for Red Knots. In this case, our estimates were < 20% of those proposed by Andres et al. (2012) a decade ago, and < 40% when considering the upper bounds of our 95% confidence intervals. Although not directly comparable, because the estimates generated by Andres et al. (2012) are global, our results are worrying and may corroborate the accelerated declines suggested for most Nearctic species (Smith et al. 2023). This is especially so considering the scale of our study, as the southern coast of South America hosts a high proportion of numerous Nearctic shorebird populations during their nonbreeding season (e.g., Morrison and Ross 1989). That said, for most species, and even for those that spend the nonbreeding season exclusively in southern South America (e.g., Buff-breasted Sandpiper), we may have missed some important sites if they occurred more than 5 km away from the coast (Aldabe et al. 2023, Faria et al. 2023) or outside the geographic range of our study. Additionally, our sampling design did not allow for modeling the probability of detection, which could potentially increase estimates. In this sense, future surveys should attempt to estimate detection probabilities at a subset of sites to improve the estimation process (e.g., Bart and Earnst 2002, Brown et al. 2007).

In contrast to results for Nearctic species, our estimates for Neotropical breeding species, with the exception of Black-necked Stilt and Blackish Oystercatcher *H. ater*, were higher than previous estimates, even for species whose distributions extend outside of our study area (Wetlands International 2017). For example, the combination of our estimates for the coastal-dependent Magellanic Oystercatcher in Argentina, without considering the Pacific portion of the species' range, were 1.65× higher than previous estimates of the continental population of the species (Wetlands International 2017). This discrepancy likely stems from the fact that previous estimates were generated almost

entirely using the best guesses of experienced researchers, as no large-scale efforts had previously been made to generate reliable population size data on most Neotropical shorebirds (Wetlands International 2017).

Beyond our population estimates, our results indicate that shorebirds tended to occur closer to estuaries, especially in Brazil and Argentina. Previous studies have shown that beaches and intertidal mudflats adjacent to estuaries support higher densities of potential prey and are key shorebird habitats (Barter 2002, Canham et al. 2021). However, in habitats such as coastal grasslands, close proximity to estuaries can provide additional benefits. For example, grasslands adjacent to estuaries or large waterbodies can receive nutrient inputs enhancing potential prey biomass (Lenhart et al. 2015). It is important to note, however, that because species was considered a covariate in our models, we assumed that the relationships of all species with a given environmental factor, such as distance to the nearest estuary, was the same. Future studies should therefore aim to increase their effort and sample size or target specific species such that species-specific models can be employed. This would allow us to improve our understanding of the effects of proximity to estuaries, as well as other broadscale factors, on species' distributional patterns in the region.

Surprisingly, with the exception of wetlands in Brazil, we did not find evidence that the proximity of a given site to urban areas had a significant effect on either shorebird presence or abundance (Tables 2 and 3). We had predicted that a close proximity to cities would have a negative effect on both shorebird presence and abundance, especially for shorebirds using beach habitats, because several studies have previously indicated that proximity to humans affects shorebirds during the breeding (Liley and Sutherland 2007, Hevia et al. 2023), migratory (Pfister et al. 1992, Murchison et al. 2016), and nonbreeding seasons (LeDee et al. 2008, Palacios et al. 2022, Swift et al. 2023). However, most cities are located close to estuaries (Small and Nicholls 2003) and, thus, the reliance of shorebirds on estuarine habitats may be stronger than the pressure to avoid urban areas. Other factors may additionally influence shorebird habitat use, such as the distance between roosting and foraging sites (Rogers et al. 2006), predator densities (Goss-Custard et al. 1991, Whitfield 2003), and levels of disturbance from dogs and people that might be related to a city's size (Maguire et al. 2018). More focused research with a study designed specifically to investigate the influence of urban habitats on shorebirds is needed in South America to better answer this question.

**Table 3.** Effects of distance to nearest cities and estuaries on the abundance and occupancy of Nearctic and Neotropical shorebirds using coastal wetland habitats (mudflats, grasslands, and shallow waterbodies) in southeastern South America, 2019. SE = standard errors. Bold values represent values of  $p < 0.05$ .

Wetlands	Brazil			Argentina Region 1			Argentina Regions 2 to 5			Uruguay		
	Estimate	SE	<i>p</i> value	Estimate	SE	<i>p</i> value	Estimate	SE	<i>p</i> value	Estimate	SE	<i>p</i> value
Estuaries												
Occupancy	-1.15	0.45	<b>&lt;0.001</b>	-0.52	0.26	<b>0.04</b>	0.97	0.6	0.1	0.18	0.58	0.7
Abundance	-0.61	0.18	<b>&lt;0.001</b>	-0.15	0.04	<b>&lt;0.001</b>	-0.41	0.06	<b>&lt;0.001</b>	-1.37	0.16	<b>&lt;0.001</b>
Cities												
Occupancy	2.18	0.43	<b>&lt;0.001</b>	-0.91	0.03	<b>0.002</b>	-0.31	0.45	0.49	-0.66	0.48	0.16
Abundance	0.49	0.13	<b>&lt;0.001</b>	-0.44	0.06	<b>0.001</b>	-0.71	0.04	<b>&lt;0.001</b>	-0.07	0.1	0.5

It is also noteworthy that our estimates were made possible by the efforts of nearly 200 community scientists. The potential for community scientists to carry out large-scale surveys of shorebird populations is not new to either the region or the Western Hemisphere, as such efforts go back decades (Howe et al. 1989, López-Lanús and Blanco 2005). In our case, though, by relying on community scientists, we were able to both comprehensively cover every known wetland area in the region and survey all of those sites (largely) simultaneously, something that had never previously been attempted on the Atlantic Coast of southern South America, but complements similar efforts implemented on the continent's Pacific Coast over the preceding decade (Senner and Angulo-Pratolongo 2014, Garcia-Walther et al. 2017). Additionally, our focus on training community scientists allowed us to make use of habitat-specific survey protocols and pre-defined survey areas, generating density estimates that made possible our extrapolations to unsurveyed (and also previously unknown) patches of suitable habitat.

Ultimately, our large-scale, volunteer-based study generates updated and much-needed information about shorebirds along the Atlantic Coast of southern South America and should be considered in future revisions of population estimates for a range of Nearctic and Neotropical species occurring in our study area. Our results raise concerns, as our estimates represent a small fraction of the global shorebird population estimates previously generated by Andres et al. (2012) and likely, therefore, corroborate the population declines detailed by Smith et al. (2023). Nonetheless, our estimates for some Nearctic species were higher than those found in the region in 1982 (Morrison and Ross 1989), providing some hope that shorebirds can be resilient in face of environmental change and habitat loss. In combination with our findings about the influence of the proximity of estuaries and urban areas on shorebird distributions, we expect that our results can be used to support species assessments for country-wide red lists, guide management actions, identify areas for conservation action, and serve as a new baseline for future population monitoring and conservation-action evaluation.

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#### Data Availability:

*All the raw data used in this paper are deposited in Figshare: <https://doi.org/10.6084/m9.figshare.28104713>.*

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## APPENDIX 1

### *Neotropical shorebirds*

#### **American Oystercatcher *Haematopus palliatus***

This species was found in all three countries, occurring mainly in beaches but also in wetlands. The highest predicted proportion of the species population was found in Argentina (85.6%), followed by Brazil (10.7%). Mean densities in beach habitats ranged from 3.3 birds.km<sup>-1</sup> in Uruguay to 6.6 birds.km<sup>-1</sup> in Brazil and 7.9 birds.km<sup>-1</sup> in Argentina. The total population estimate was 68,791 birds (95% CI: 33,347 – 106,397).

#### **Magellanic Oystercatcher *Haematopus leucopodus***

In contrast to *H. palliatus*, this oystercatcher was found only in Argentina and occurred mostly on beaches (38.8 birds.km<sup>-1</sup>), but also wetlands (3.9 birds.ha<sup>-1</sup>). The Magellanic Oystercatcher was the most abundant species among the Haematopodidae in the study area, with an estimated of 165,357 individuals (95% CI: 43,711 – 297,015).

#### **Blackish Oystercatcher *Haematopus ater***

Similar to *H. leucopodus*, this species was found only in Argentina. However, unlike the other two *Haematopus* species, it occurred predominantly on beaches (91.6%). It was also the least abundant oystercatcher surveyed, with a mean density of 3.2 birds.km<sup>-1</sup> along Argentinian beaches. Its total population estimate was 10,645 individuals (95% CI: 1,352 – 20,838).

#### **White-necked Stilt *Himantopus melanurus***

The only Recurvirostridae shorebird included, this species occurred in all three countries. Unlike oystercatchers, the species was most abundant (~70% individuals) in wetlands in

comparison to beaches. Its total population estimate was 75,270 birds (95% CI: 26,731 – 154,865).

### **Southern Lapwing *Vanellus chilensis***

This species occurred in all habitats in all regions, except Argentine beaches, with the highest density found in Brazilian wetlands (1.6 birds.km<sup>-1</sup>). The total population estimate was 28,145 lapwings (95% CI: 18,377 –41,808).

### **Two-banded Plover *Charadrius falklandicus***

This species was included only in analyses of Argentine habitats, as just two individuals were found in Brazil. Argentine densities ranged from 9.3 birds.ha<sup>-1</sup> in wetlands to 23.1 birds.km<sup>-1</sup> in beaches. The total population estimate was 181,275 individuals (95% CI: 62,496 – 301,070).

### ***Nearctic shorebirds***

#### **American Golden-Plover *Pluvialis dominica***

This species was found in all three countries, both along beaches and in wetlands. The highest proportion of individuals was estimated to occur in Argentina (68%), but the highest densities occurred along the Uruguayan and Brazilian beaches (2.1 birds.km<sup>-1</sup>). The total population estimate was 35,408 birds (95% CI: 14,365 – 57,653).

#### **Black-bellied Plover *Pluvialis squatarola***

Contrary to *P. dominica*, this species occurred mainly in Argentina, with only 10 individuals observed in Brazil. Densities in Argentinian wetlands were estimated at 0.3 birds.ha<sup>-1</sup> and the total population estimate was 3,740 birds (95% CI: 556 – 7,052).

### **Semipalmated Plover *Charadrius semipalmatus***

This plover was restricted to the northern portion of the study area, absent from surveys in Argentina, and with 92.5% of its estimated abundance occurring in Brazil. The total population estimate was 8,851 individuals (95% CI: 2,685 – 15,540).

### **Greater Yellowlegs *Tringa melanoleuca***

This species occurred in all countries, both in beach and wetlands. The highest densities were found along Uruguayan beaches (1.8 birds.km<sup>-1</sup>), although the highest proportion of individuals was estimated from Argentina (73.1%). The total population estimate was 16,169 birds (95% CI: 12,304 – 22,674).

### **Lesser Yellowlegs *Tringa flavipes***

This species had similar occurrence patterns to Greater Yellowlegs and was present in both beaches and wetlands. As with *T. melanoleuca*, Uruguay was also the country with high density of individuals (20.3 birds birds.km<sup>-1</sup> beach habitats), and it was estimated that 48.4% of individuals occurred in this country. The total population estimate was 28,384 individuals (95% CI: 11,849 – 29,665).

### **Buff-breasted Sandpiper *Calidris subruficollis***

This species occurred only in wetlands. Uruguay hosted the highest proportion of individuals (43.2%), followed by Argentina (31.7%) and Brazil (25.1%). Densities were also higher in Uruguay (1.8 birds.ha<sup>-1</sup>, followed by Brazil (0.7 birds.ha<sup>-1</sup>) and Argentina (0.5 birds.ha<sup>-1</sup>). The population estimate was 17,783 individuals (95% CI: 1,812 – 38,139).

### **Baird's Sandpiper *Calidris bairdii***

This species was only detected in Argentina, with relatively similar proportions estimated from wetlands (54.4%) and beach habitats (45.5%). The population estimate was 15,526 individuals (95% CI: 1,700 – 31,039).

### **White-rumped Sandpiper *Calidris fuscicollis***

This was the most abundant shorebird in surveys and was present in all three countries, both in beach and wetlands. This also had the highest densities of any species in both beach (4.1 birds.km<sup>-1</sup> and 24.6 birds.km<sup>-1</sup>) and wetlands (2 birds.ha<sup>-1</sup> and 17.6 birds.ha<sup>-1</sup>) in Uruguay and Argentina, respectively. In Brazil, densities were 14.3 birds.km<sup>-1</sup> in beaches and 4.4 birds.ha<sup>-1</sup> in wetlands. The population estimate was 335,500 individuals (95% CI: 118,041 – 595,151).

### **Hudsonian Godwit *Limosa haemastica***

Godwits occurred mainly in Argentina (96.4%), but were also observed in wetlands in Uruguay. The species' density in these habitats was estimated at 2.5 birds.ha<sup>-1</sup> in Argentina and birds.ha<sup>-1</sup> in Uruguay. The highest density occurred along the Argentine beaches (8.13 birds.km<sup>-1</sup>). The total population estimate was 56,276 individuals (95% CI: 9,326 – 113,221).

### **Sanderling *Calidris alba***

This species was the most abundant shorebird in Brazil, mainly in beach habitats, where it was the densest species (15.0 birds.km<sup>-1</sup>). Absent from Uruguay, Sanderlings were also present along Argentine beaches, which hosted 43% of the estimated abundance of the

species in the southeastern South America. The total population estimate was 53,352 individuals (95% CI: 14,144 – 111,645).

**Red Knot *Calidris canutus***

This species was only detected during surveys in Argentina. However, contrary to *C. bairdii*, this species was mainly (95.7%) found in beach habitats, with a density of 2.0 birds.km<sup>-1</sup>. The population estimate was 6,548 individuals (95% CI: 118 – 16,943).

## APPENDIX 2

**Table A.2.1.** Country and habitat-specific measurements of survey efforts (i.e., surveyed areas) and extension of model predictions (i.e., area which models were extrapolated for) of shorebird simultaneous surveys conducted between 20 and 29 January 2019.

	<b>Country</b>	<b>Habitats</b>	<b>Survey Effort (<i>n</i> of surveys)</b>	<b>Prediction</b>
Beaches (km)	BR	Sandy	77.5 (155)	674
		Rocky	1.5 (3)	25.5
	UY	Sandy	19 (37)	387
		Rocky	6 (12)	149
	AR	Sandy	25.5 (55)	1,889.50
		Restinga	26 (57)	1002
Wetlands (ha)	BR	Grasslands	25.66 (26)	13,538.50
		Mudflats	27.3 (13)	540.2
		Shallow water	3.19 (7)	1,329.50
	UY	Grasslands	44.3 (10)	3,577.70
		Shallow water	60.3 (17)	507.9
	AR	Grasslands	80.8 (15)	15,733.20
		Mudflats	931.8 (43)	118,901.30
		Shallow water	100.6 (17)	9,744.40

### APPENDIX 3

**Table A.3.1.** Candidate model set for hurdle models of environmental influences on shorebirds abundance and occupancy. Degrees of freedom (*df*), log likelihood (*logLik*), and *AIC* are included, as also McFadden's (pseudo-r<sup>2</sup>) of selected models.

<b>Model</b>	<b><i>df</i></b>	<b><i>logLik</i></b>	<b><i>AIC</i></b>	<b>pseudo-r<sup>2</sup></b>
<b>Uruguay - Wetlands</b>				
Abund ~ h_type+Zdist_cit+Zdist_est+Sp	22	-662.3	1368.61	0.57
Abund ~ h_type+Zdist_cit+Sp	24	-660.5	1369.01	
Abund ~ h_type+Zdist_est+Sp	22	-667.7	1379.41	
Abund ~ Zdist_cit+Zdist_est+Sp	22	-705.2	1454.41	
<b>Uruguay - Beaches</b>				
Abund~h_type+Zdist_est+Zdist_cit+Sp	22	-582.3	1208.55	0.31
Abund ~ h_type + Zdist_cit + Sp	20	-584.1	1208.26	
Abund~h_type+Zdist_est+Sp	20	-585.5	1211.06	
Abund ~ Zdist_cit + Sp	18	-614.2	1264.36	
<b>Brazil - Beaches</b>				
Abund~h_type+Zdist_est+Zdist_cit+Sp	28	-3828	7712.42	0.41
Abund ~ h_type + Zdist_est + Sp	26	-3841	7734.69	
Abund ~ h_type + Zdist_cit + Sp	26	-3909	7869.07	
Abund~Zdist_est+Zdist_cit+Sp	24	-3978	8003.77	
<b>Brazil - Wetlands</b>				
Abund~h_type*Zarea_h+Zdist_est+Region+Zdist_cit+Sp	36	-1926	3923.17	0.44
Abund ~ h_type * Zarea_h + Zdist_est + Region + Sp	34	-1941	3949.78	
Abund ~ h_type * Zarea_h + Zdist_cit + Region + Sp	34	-1935	3938.57	
Abund ~ h_type * Zarea_h + Zdist_est + Region + Sp	34	-1950	3967.48	

<b>Model</b>	<b>df</b>	<b>logLik</b>	<b>AIC</b>	<b>pseudo-r<sup>2</sup></b>
Abund~h_type*Zarea_h+Zdist_est+Zdist_cit+Sp	34	-1941	3949.78	
Abund ~ h_type + Zdist_est + Zdist_cit + Sp	28	-2189	4433.23	
Abund ~ h_type + Zdist_est + Zdist_cit + Sp	24	-2280	4608.55	
<b>Argentina - Wetlands 1</b>				
Abund~h_type+Zdist_est+Zdist_cit+Sp	32	-3311	6686.84	0.45
Abund~h_type+Zdist_est+Sp	30	-3319	6698.78	
Abund~h_type+Zdist_cit+Sp	30	-3327	6713.19	
Abund~Zdist_est+Zdist_cit+Sp	28	-3367	6789.55	
<b>Argentina - Wetlands 2 a 5</b>				
Abund~Zdist_est+Zdist_cit+Region+Sp	30	-3515	7089.63	0.69
Abund ~ Zdist_cit + Region + Sp	26	-3622	7295.63	
Abund ~ Zdist_est + Region + Sp	26	-3738	7528.23	
Abund ~ Zdist_est + Zdist_cit + Sp	24	-5141	10329.96	
<b>Argentina - Beaches</b>				
Abund~h_type+Zdist_est+Zdist_cit+Region+Sp	40	-4732	9543.11	0.39
Abund~h_type+Zdist_cit+Region+Sp	38	-4836	9748.31	
Abund~h_type+Zdist_est+Region+Sp	38	-4836	9748.31	
Abund~h_type+Zdist_est+Zdist_cit+Sp	32	-4893	9850.96	