Shorebird Use of the Lower Colorado River Delta During Migration

Timothy D. Meehan[1], Alejandra Calvo-Fonseca[2], Osvel M. Hinojosa-Huerta[3], Jennifer Pitt[1], Eduardo Soto-Montoya[2], Jonathan Vargas[2], Stefanny Villagomez-Palma[2], and Chad J. Witko[1]

[1] National Audubon Society, New York, New York, USA

[2] Pronatura Noroeste, San Luis Rio Colorado, Sonora, México

[3] Cornell Lab of Ornithology, Ithaca, New York, USA

Abstract. The natural and anthropogenic wetlands of the Colorado River Delta are recognized as critical stopping and staging areas for migrating shorebirds. Given the importance of these wetlands and the uncertainty around their water sources, we conducted 9 paired, aerial and ground surveys between April 2021 and April 2023 to quantify migration season shorebird use across a study area of 486 km^2 that covered the lower Colorado River estuary and the Ciénega de Santa Clara. We estimated that an average of 272,515 individual shorebirds occupy the study area at any given time during the active migration season. Shorebirds were most abundant in mudflats and flooded playas of the Ciénega de Santa Clara, followed by wetlands of the lower estuary. Shorebird abundance was positively related to the proportion of a count site covered by mudflats and flooded with surface water, and was positively related to the proportion of a year that a count site was flooded with surface water. While 21 shorebird species were recorded during ground surveys, 8 species made up more than 90% of the total birds counted. Estimated average abundances for these species were: 103,132 Western Sandpiper; 31,763 Red-necked Phalarope; 30,067 Long-billed Dowitcher; 23,527 American Avocet; 20,196 Least Sandpiper; 19,197 Black-necked Stilt; 10,901 Snowy Plover; and 8,993 Long-billed Curlew. We speculate that the study area hosts at least 1% of the North American population for 11 shorebird species during migration. Results confirm the importance of these wetlands for migrating shorebirds and highlight the need for securing water sources given increasing human water demands and decreased water availability due to climate change.

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INTRODUCTION

Nearctic-breeding shorebirds migrate thousands of kilometers across the Western Hemisphere annually between breeding and non-breeding areas (Myers et al. 1987, Piersma and Lindström 2004). During migration, these birds concentrate in coastal and inland wetlands that function as networks of stopping and staging areas (Warnock 2010), where birds rest, refuel, gather information, wait out poor migration conditions, and participate in social interaction (Linscott and Senner 2021). These stopping and staging areas provide unique and valuable resources that help shorebirds meet various challenges of the migration season (Senner 1979, Morrison 1984), and these concentrations of birds often represent large fractions of global populations (Morrison 1984). Overcoming challenges during migration is critical for annual adult survival (Myers et al. 1987, Alerstam and Lindström 1990) and annual adult survival is a critical demographic parameter for maintaining stable populations (Morris and Doak 2002).

Wetlands in northwestern México support large numbers of Nearctic-breeding shorebirds during migration (Mellink et al. 1997, Gómez-Sapiens et al. 2013, Hinojosa-Huerta et al. 2013). Within northwestern México, the wetlands of the Colorado River Delta (CRD) have been recognized as Sites of Hemispheric Importance for migrating shorebirds (WHSRN 2024), Wetlands of International Importance in the Ramsar Convention (Ramsar 2024), and Globally Important Bird Areas for their avian abundance and diversity (BLI 2024). The wetlands of the CRD once covered more than a half-million hectares (Pitt et al. 2000). Over the last century, the CRD lost roughly 80% of its wetlands due to the construction of dams, diversions of water for human consumption, increases in agricultural activity throughout the entire Colorado River basin, and because no water was allocated for environmental purposes in the distribution of water rights (Pitt 2001, Zamora-Arroyo et al. 2005). The wetlands of the CRD are now mainly sustained by agricultural runoff, sporadic flood flows, underground flows, treated wastewater, and the tidal regime of the Upper Gulf of California (Glenn et al. 2001). More recently, these sources have been supplemented by environmental flows allocated for restoration by a coalition of environmental organizations and the governments of the United States and México, under binational agreements known as Minute 319 and Minute 323 (Pitt and Hinojosa-Huerta 2022).

As natural wetlands in the CRD have disappeared, shorebirds have begun to rely on anthropogenic wetlands with uncertain futures (Hinojosa-Huerta et al. 2004, Gómez-Sapiens et al. 2013). The largest of these anthropogenic wetlands, the Ciénega de Santa Clara, is located on the eastern edge of the CRD. The Ciénega is currently the most ecologically important wetland complex in northwestern México, extending over 16,000 ha and encompassing marsh, mudflat, and open water habitats (Glenn et al. 2001). Nearly 90% of the Ciénega's water supply originates as agricultural drainage water delivered through canals from the Wellton-Mohawk Valley in Yuma, Arizona (Glenn et al. 2001). The remaining water supply consists of agricultural drainage from nearby farms in Sonora (Glenn et al. 2001). Neither the United States nor México have protected the water supplies for the Ciénega, and they are at increased risk of development as the Colorado River experiences increased aridification due to climate change (Pitt et al. 2000).

While it is clear that the CRD is important to shorebirds, relatively few published studies report the relative importance of different wetlands within the CRD or the total number of birds using the CRD during migration. Regarding the relative importance of different wetlands, Gómez-Sapiens et al. (2013) found that migrating shorebird densities were especially high in the Santa Clara Slough, the anthropogenic wetlands of the Ciénega that are created by mixing of brackish water from Ciénega marshes to the north with seawater from the Gulf of California to the south (Fig. 1). Regarding the total number of birds using the CRD, one migration-season aerial survey conducted over the coastline, adjacent islands, and the Ciénega during March 1994 reported a raw total count of 74,266 individual shorebirds (Mellink et al. 1997). More recent aerial surveys conducted over the coastline, adjacent islands, and the Ciénega during April 2007, 2010, and 2011 reported raw totals of 129,575; 26,443; and 37,334 shorebirds, respectively (Gómez-Sapiens et al. 2014). While total bird numbers from previous studies are impressive, they are likely underestimates (Laursen et al. 2008). These raw counts do not account for omissions due to partial coverage of the survey area or poor detection of birds at flight speeds and altitudes. These reported counts also lack estimates of uncertainty.

A major reason for limited information on the relative importance of different wetlands and the total number of shorebirds in the CRD has been complicated sampling logistics. Much of the CRD is remote and inaccessible from the ground. While aerial surveys allow researchers to increase the area surveyed, they are expensive and are known to miss substantial numbers of shorebirds on the ground (Kingsford and Porter 2009). To improve our understanding of migrant shorebird use of the region, we formed an international partnership between Pronatura Noroeste (México), LightHawk Conservation Flying (USA), and the National Audubon Society (USA) to conduct the Colorado River Aerial Shorebird Survey (CRASS) project. The CRASS project combined ground surveys at accessible locations with concurrent aerial surveys over a larger study area to have maximum aerial coverage while providing a means to estimate the fraction of birds missed during aerial surveys (Pollock and Kendall 1987).

Here, we report results from the initial descriptive phase of the CRASS project. Our main objectives were to (1) describe the spatial distribution of shorebirds across the study area, (2) determine how spatial distribution was related to spatially varying habitat covariates, and (3) determine how shorebird abundance varied across years, seasons, and count methods. Objectives also included (4) estimating the average total abundance of shorebirds using the study area on a typical day during migration, (5) using species composition information from ground counts to divide estimated total abundances into abundances per species, and (6) comparing species abundances to estimates of continental population sizes.

METHODS

Survey Area

The study area for the CRASS project was chosen based on two important considerations. The first was the inclusion of the lower portion of the main channel of the Colorado River, where river water mixes with tidal water (Fig. 1). This was done to quantify how shorebirds use wetlands enhanced through ongoing habitat restoration and increased surface-water flows. The second was the inclusion of Ciénega de Santa Clara, especially the Santa Clara Slough (Fig. 1), where previous studies have demonstrated relatively high shorebird use compared to other parts of the CRD (Hinojosa-Huerta et al. 2004, Gómez-Sapiens et al. 2013). These considerations determined the flight lines for aerial surveys, and the study area was defined as the concave polygon that included all flight lines buffered by 1000 m (Fig. 1).

Survey Approach

Two types of shorebird surveys were conducted concurrently within the survey area: aerial surveys and ground surveys (Fig. 1). Aerial surveys allowed shorebird counts to be conducted over a large and remote study area (Kingsford and Porter 2009). Concurrent ground surveys were conducted at a subset of locations (Fig. 1) to correct the visibility bias of aerial surveys (Pollock and Kendall 1987) and to transform estimates of average total shorebird abundance into average species-specific abundances.

Aerial Surveys

Aerial surveys were conducted by a volunteer pilot from LightHawk Conservation Flying and an experienced shorebird field biologist from Pronatura Noroeste on 9 separate occasions from 2021–2023 (Fig. 1). Those 9 occasions occurred on (Fig. 1): 20 April, 3 May, 19 May, 29 September, and 11 October of 2021; 8 April, 24 April, and 17 May of 2022; and 12 April of 2023. Pilots attempted to follow the same flight line during each survey and to fly at elevations ranging from 30–60 m, with speeds ranging from 120–180 km h-1 (Morrison et al. 1992, Mellink et al. 1997, Page et al. 1997, Shuford et al. 1998). During aerial surveys, shorebird counts were made from the passenger seat on the aircraft's right side as the plane was oriented approximately 50 m from the edge of the sampling area. The single observer counted all birds seen within the strip transect, extending out to 300 m from the plane, giving a strip transect width of 250 m. When a group of birds were observed, the counter noted the location (geographic coordinates of the group centroid) and estimated the proportion of land within a 250 m radius of the location that was covered by mudflats or flooded with surface water. When time allowed, the observer also noted locations with zero birds, along with mudflat and flooded land proportions, which allowed us to gain insight into preferred habitats within the study area. Counting and identification of birds was done visually, without the regular use of binoculars, and with the help of a digital voice recorder.

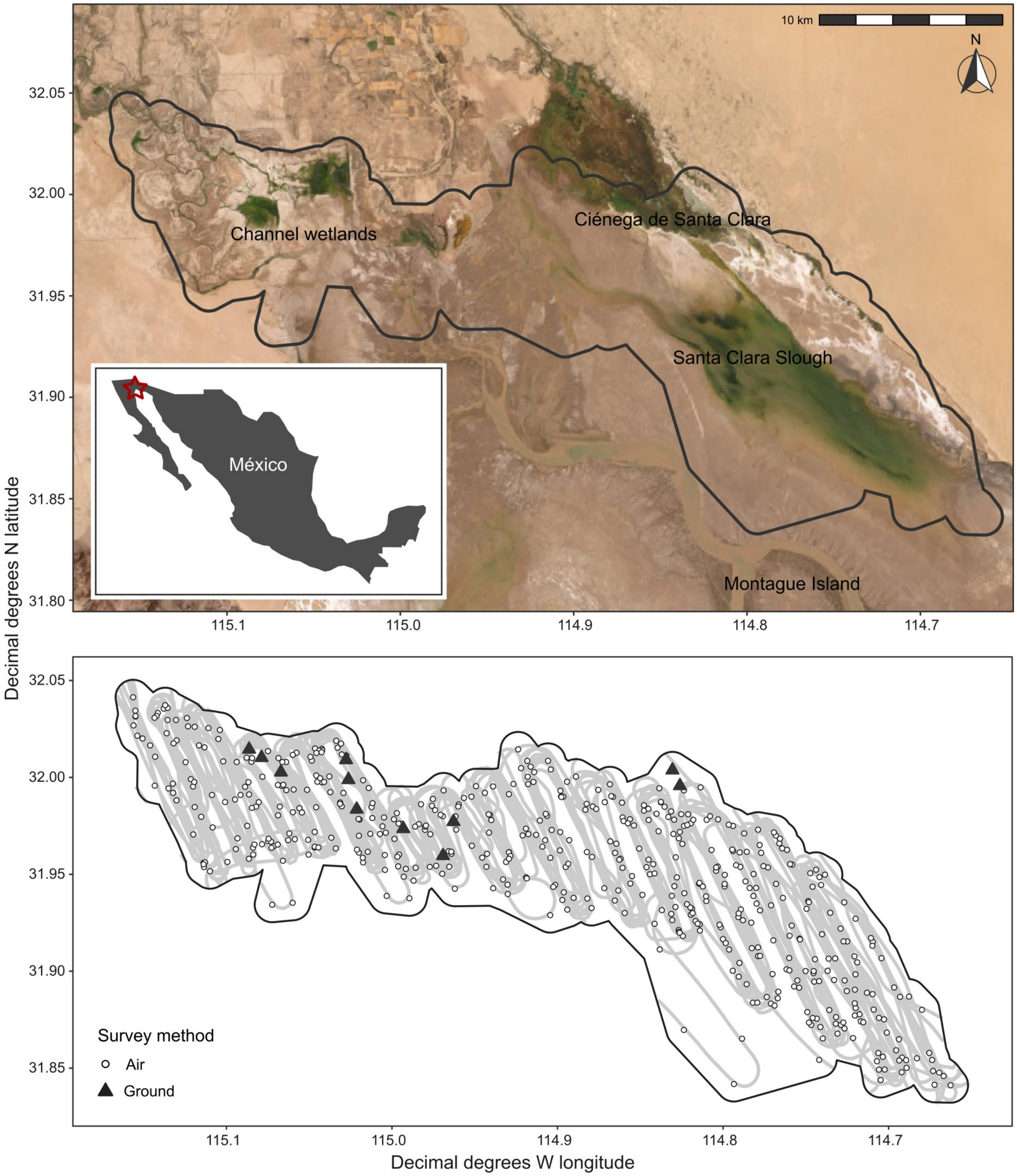

Fig. 1. Satellite image of the study area in northwestern México (note the red star on the inset map) along with locations of aerial and ground surveys (lower panel). Circles depict locations of shorebird counts (zero-count sites included) during aerial surveys and triangles illustrate locations of concurrent ground surveys.

Strip transect lengths and areas (total length × 250 m wide) were calculated per sampling date using flight waypoints and spatial analysis software. For a given date, the transect area was divided by the total study region area to obtain the ratio of the study region that was sampled by the strip transect, R_{sample}.

Ground Surveys

For each of the nine aerial sampling occasions, a concurrent ground survey was conducted over a subset of the study region (Fig. 1). We randomly selected ground sampling units from a larger list of potential sampling sites to capture variation in the parameters of interest (e.g., birds, mudflat area, flooded area). Note that this random sample of units was restricted to areas accessible by automobile via roads or by boat via the main river channel. A two-day prospecting visit was carried out prior to the first ground survey in which the area of interest was explored, and the main access points were identified (Reiter et al. 2020). In this way, eight sampling units were defined with a radius of approximately 500 m and a survey area, A_{ground}, of 78.5 ha. A ninth ground survey location, with dimensions of 300 m × 900 m and A_{ground} = 27 ha, was previously established for the Migratory Shorebirds Project (http://migratoryshorebirdproject.org/).

During ground surveys, two to four teams of multiple observers from Pronatura Noroeste counted simultaneously in the sampling units concurrent with aerial surveys. Observers took as much time as needed to count all birds within view during ground surveys. Our statistical analysis assumed that ground surveys had errors but that, on average, they were an unbiased representation of the true number of birds in a survey area. Counting and identification of the shorebirds in ground sampling units was carried out with the help of binoculars and spotting scopes. Surveys were preferably carried out during neap tides to reduce the probability that the birds were moving due to the tide.

After ground surveys, the ratio of the total sampling unit that was visible to ground surveyors (R_{ground}) and the proportions of the areas covered by mudflats or flooded with surface water were estimated and recorded. Before statistical analysis, ground counts were area-corrected to match the spatial coverage of concurrent aerial surveys. We calculated a coverage correction factor as A_{aerial} / (A_{ground} × R_{ground}), where A_{aerial} was the area of the 250 m strip transect that intersected with each ground survey unit.

Taxonomic Considerations

During aerial and ground surveys, birds were identified at the species level whenever possible. In situations where species could not be identified, individuals were assigned to taxonomic groups, often at the generic level, as follows (PRISM 2018). Small Plovers included Snowy Plover (*Anarhynchus nivosus*), Semipalmated Plover (*Charadrius semipalmatus*), and Wilson's Plover (*Anarhynchus wilsonia*). Yellowlegs included Greater Yellowlegs (*Tringa melanoleuca*) and Lesser Yellowlegs (*Tringa flavipes*). Peeps included Spotted Sandpiper (*Actitis macularius*), Least Sandpiper (*Calidris minutilla*), and Western Sandpiper (*Calidris mauri*). Dowitchers included Long-billed Dowitcher (*Limnodromus scolopaceus*) and Short-billed Dowitcher (*Limnodromus griseus*). Phalaropes included Red-necked Phalarope (*Phalaropus lobatus*) and Wilson's Phalarope (*Phalaropus tricolor*). If placement into these intermediate taxonomic groups was not possible, individuals were placed into the following groups based on body size (PRISM 2018). Small Shorebirds included Small Plovers, Peeps, and Phalaropes, as above, as well as Dunlin (*Calidris alpina*). Medium Shorebirds included Yellowlegs and Dowitchers, as above, as well as Killdeer (*Charadrius vociferus*), Black-necked Stilt (*Himantopus mexicanus*), and Stilt Sandpiper (*Calidris himantopus*). Large Shorebirds included Black-bellied Plover (*Pluvialis squatarola*), American Avocet (*Recurvirostra americana*), Willet (*Tringa semipalmata*), Whimbrel (*Numenius phaeopus*), Long-billed Curlew (*Numenius americanus*), and Marbled Godwit (*Limosa fedoa*). Anything not placed into the above groups was considered an Unidentified Shorebird.

Count Covariates

Two count covariates – proportion of a count site covered by mudflats (hereafter "mudflat proportion") and flooded by surface water (hereafter, "flooded proportion") – were collected during both aerial and ground surveys to gain insight into shorebirds' preferred habitats in the study area. In addition, a third covariate called "flooded duration" – the proportion of time that a count location was flooded with surface water – was extracted for all locations where counts (including zero counts) were collected. This duration estimate was extracted from the Surface Water Occurrence layer from the Global Surface Water Dataset (Pekel et al. 2016). Briefly, this dataset uses Landsat imagery from the past 32 years to estimate the proportion of that period where 30 m × 30 m pixels were covered by surface water. Flooded duration estimates were extracted from this raster map and averaged for a circular buffer with a 250 m radius around each count-location centroid.

Data Analysis

To address our different research objectives, we pooled aerial and ground count data, summed across all taxonomic and size groups per location and sampling date, and modeled total shorebird counts with a spatially structured mixed-effects model. The model assumed that observed counts came from a negative binomial distribution with an expected count, μ, and a dispersion parameter. The linear predictor for the natural log of an expected count was:

$$\log(\mu) = \alpha_{global} + \alpha_{spatial} + \alpha_{method} + \alpha_{date} + \alpha_{season} + \alpha_{year} + \beta_1(mudflats) + \beta_2(flooded) + \beta_3(duration),$$

where α_{global} was a global intercept, $\alpha_{spatial}$ was a spatially structured, zero-centered random intercept, α_{method} were zero-centered intercepts for different count methods, α_{date} were zero-centered intercepts for different sampling dates, α_{season} were zero-centered intercepts for different seasons, and α_{year} were zero-centered intercepts for different years. The parameters β_1, β_2, and β_3 were global log-linear effects of the proportion mudflats, proportion flooded, and flooded duration, respectively.

The spatially structured effect comprised a Matérn covariance function that specified how the spatial correlation of counts decayed with the distance between locations in space (Blangiardo and Cameletti 2015, Krainski et al. 2018). A single spatial field common to all sampling dates was used because initial exploratory analysis indicated that spatial patterns in shorebird abundances were similar over the entire study period (Fig. 2) and because we were interested in generalized spatial information about shorebird abundance and were not interested in survey-specific spatial variation. The count method intercepts were included to account for variation in counts due to visibility bias associated with aerial surveys, serving a similar purpose as the ground-count correction factor described by Pollock and Kendall (1987). Those authors defined a correction factor as the mean of ground counts divided by the mean of aerial counts. Here, the difference between ground and aerial survey intercepts comprised a multiplicative offset in the spatial field attributable to ground versus aerial counts. Estimation of a correction factor in the context of a Bayesian hierarchical model is somewhat comparable to methods described by Zimmerman et al. (2012). The date and year random effects were not of ecological interest, *per se*, but were added to the model to account for potential statistical correlations of abundances within sampling dates and years. We added a seasonal random effect because, after accounting for other temporal effects, we expected higher counts during the fall migration season due to annual reproduction. We note that 2023 was only sampled once during spring, and the fall season was only sampled during 2021, so year and season effects should be interpreted with caution. The global effects of mudflat proportion, flooded proportion, and flooded duration were added to help identify general habitat preferences of shorebirds while using the study area.

The model was analyzed in a Bayesian statistical framework and computed using the *inlabru* (Bachl et al. 2019) and *R-INLA* (Rue et al. 2017) packages for *R* statistical computing software (R Core Team 2024). Prior distributions for variance parameters for all α were penalized complexity priors with the upper limit on the standard deviation associated with an effect set to 1 and an exceedance probability of 0.01 (Simpson et al. 2017). The prior distribution for the range parameter of $\alpha_{spatial}$ was a penalized complexity prior with an upper limit on the range set to 10 km and the exceedance probability set to 0.50 (Fuglstad et al. 2019). Prior distributions for β were vague normal priors with mean of 0 and standard deviation of 10,000. The full linear predictor for the model, along with all observed covariate values, were used to obtain fitted values per survey location and survey date. We judged the correspondence between observed and fitted values based on the correlation between posterior median fitted values and observed counts.

To address our first research objective – visualizing the general spatial distribution of shorebirds across the study area – we used the model's linear predictor, without the zero-centered date, season, and year terms, to calculate expected counts for 1-km^2 grid cells across the study area (Fig. 2). Given the absence of date, season, and year terms, these predictions were spatially explicit abundance estimates that assumed generalized migration-season conditions across date, season, and year. For these predictions, we forced the method to ground-surveys to correct for visibility bias associated with aerial counts. Mudflat proportion, flooded proportion, and flooded duration values used in the linear predictor were max values from observations falling within each 1-km^2 grid cell. Max values were used for visualization purposes instead of mean values because water features were often small relative to grid cells and their effects would be less visible on the study area map.

We addressed research objectives two and three – determining how shorebird abundance was related to spatially varying habitat covariates, years, seasons, and count methods – by inspecting posterior distributions for α and β parameters

Table 1. Components of the spatially structured mixed-effects model.

Component	Estimate[1]
Fixed-effect estimates (on log-scale)	
Intercept	1.29 (-0.33–3.01)
Mudflat proportion	3.14 (2.28–4.02)
Flooded proportion	3.44 (2.59–4.30)
Flooded duration	2.38 (0.44–4.36)
Variation attributed to random effects (SD)	
Count method	0.73 (0.44–1.23)
Count date	1.06 (0.70–1.58)
Count season	0.24 (0.14–0.42)
Count year	0.16 (0.11–0.24)
Spatially structured intercept	1.72 (1.41–2.09)
Range of spatial intercept (km)	2.31 (1.66–3.37)
Observed versus posterior median predicted correlation (r)	0.73

1 Posterior median and 95% credible interval.

(Table 1, Fig. 3). We addressed objective four – estimating a typical number of shorebirds using the study area during a given day during migration – using the linear predictor from the model to obtain fitted values for all survey dates and locations with non-zero counts. Fitted values were based on observed covariate values and, as for the first objective, were calculated for the ground-survey method. These survey-method-corrected expected counts, $C_{corrected}$, were then summed for the entire transect on a given survey date, and that sum was divided by the appropriate sample ratio, R_{sample}, described above, giving a method-corrected total number of birds expected for the entire study area on a given sampling date, $N_{date} = (\sum C_{corrected}) / R_{sample}$. N_{date} values were then averaged across the nine sampling dates giving $\dot{N}$.

We addressed objective five – estimating average abundances per species – by multiplying $\dot{N}$ by the average proportions of total shorebirds represented by each species, $\dot{p}_{species}$, derived from ground counts, giving $\dot{n}_{species} = \dot{N} \times \dot{p}_{species}$. In order to propagate uncertainty from model parameters to derived statistics, calculations yielding $\dot{N}$ and $\dot{p}_{species}$ were conducted for each of 10,000 samples from posterior distributions of model parameters.

To accomplish objective six – comparing local species abundances to continental breeding population sizes – we compared estimates to species' total population sizes for birds breeding in Canada and the continental USA north of Mexico from Rosenberg et al. (2019). Through this comparison, we hoped to understand what proportion of the continental breeding population is using the study area on a given day during the active migration season. We acknowledge that results from this type of comparison are highly approximate given the uncertainty in abundance estimates, species proportions, and continental breeding population sizes. However, we maintain that such comparisons are valuable for informing conservation

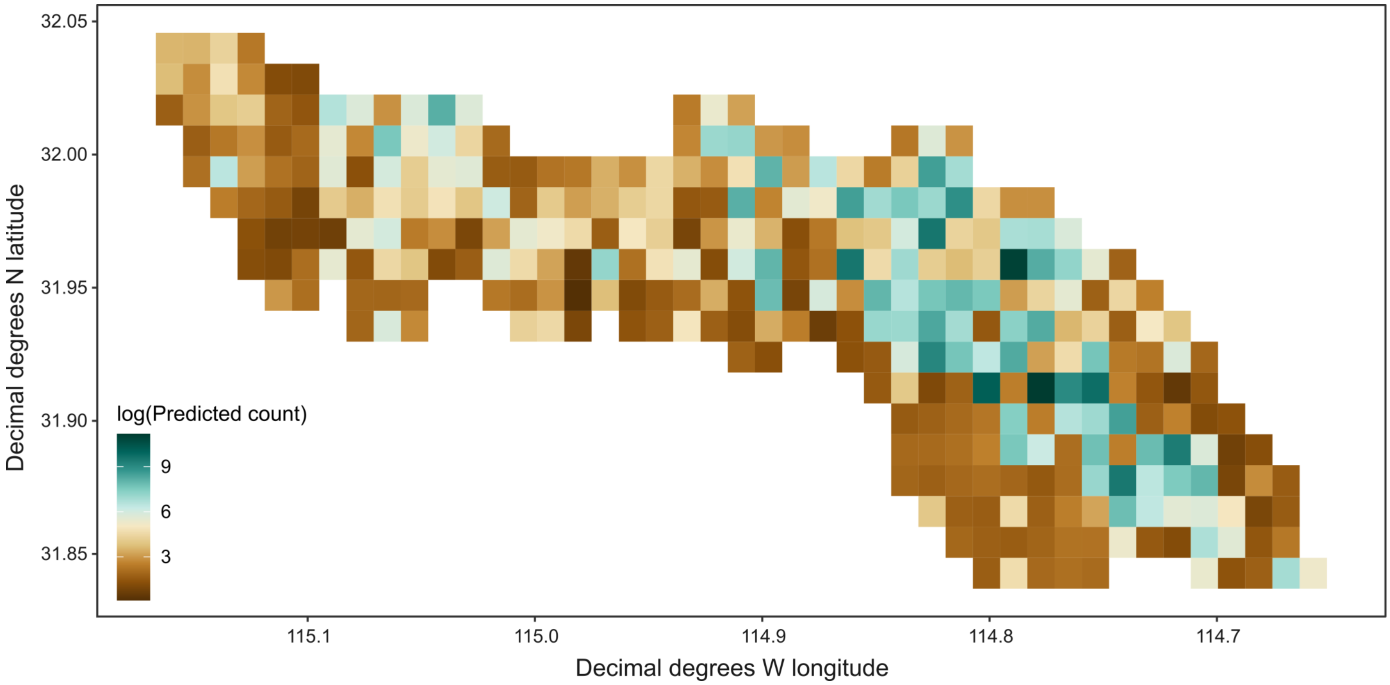

Fig. 2. Predictions from the spatially structured mixed-effects model illustrating areas of high and low shorebird average abundance. Note that the color gradient for the prediction surface is on the natural-log scale.

decisions, provided that the assumptions are also communicated.

RESULTS

During aerial surveys, planes were flown at speeds between 120–180 km hr^{-1} and at elevations ranging from 33–167 m. Thus, speeds were typical of those commonly used in aerial surveys. However, elevations were higher on average than those commonly used. Pilots generally were able to follow the same flight line during each of the 9 aerial surveys, although there was some unavoidable variability (Fig. 1). Aerial strip transects ranged in length from 195–351 km and averaged 303 km (Fig. 1). The areas sampled ranged from 48–85 km^2 and averaged 74 km^2. Given the total study region area of 486 km^2, the proportion of the study area sampled, R_{sample}, across the 9 aerial surveys ranged from 0.10–0.17 and averaged 0.15.

The spatially structured mixed-effects model fit the data reasonably well, with a correlation coefficient between observed and posterior median fitted values of $r = 0.73$. The spatial predictions from the model indicated that average total shorebird abundance was generally highest in two regions within the study area (Fig. 2). One small area of high average abundance occurred in the northwestern portion of the study area, where wetlands are formed by the main channels of the Colorado and Hardy rivers mixing with ocean water during high tides (Fig. 1, Fig. 2). A second, much larger area of high average abundance occurred in the eastern part of the study area, in the southern portion of the Ciénega de Santa Clara known as the Santa Clara Slough (Fig. 1, Fig. 2). This area is fed by brackish water exiting the marshes of the Ciénega and flowing over mudflats and playas.

Inspecting the posterior distributions for α and β parameters showed that total shorebird abundance increased considerably with the proportion of mudflat cover, the proportion of area flooded by surface water, and the duration of surface water flooding (Table 1, Fig. 3). Of the random effects in the model, most variation was attributed to the spatially structured intercept and sample date, with less associated with count method, and relatively little associated with season and year (Table 1, Fig. 3). The range parameter from the Matérn covariance function suggested that the spatial correlation among counts extended to approximately 2.31 km. The method effects indicated that aerial counts were approximately 16% percent of concurrent ground counts, which translates to a correction factor of approximately 6.25 (Fig. 3). The weak temporal effects suggested that abundance might be higher in fall than in spring and that there were no strong systematic differences across years (Table 1, Fig. 3). We reiterate that temporal effects should be interpreted with caution as 2023 was only sampled once during spring and the fall season was only sampled during 2021.

The estimated average number of shorebirds using the area on a given day during the height of migration was 272,515 individuals (95% credible interval = 83,052–982,874) across the 9 migration-season surveys (Table 2). A total of 21 shorebird species were positively identified through ground counts (Table 2). A single species – Western Sandpiper – accounted for nearly 40% of the total birds counted, and together with the next 7 most abundant species comprised more than 90% of the total birds counted (Table 2). In descending order of abundance, those 8 species were Western Sandpiper, Red-

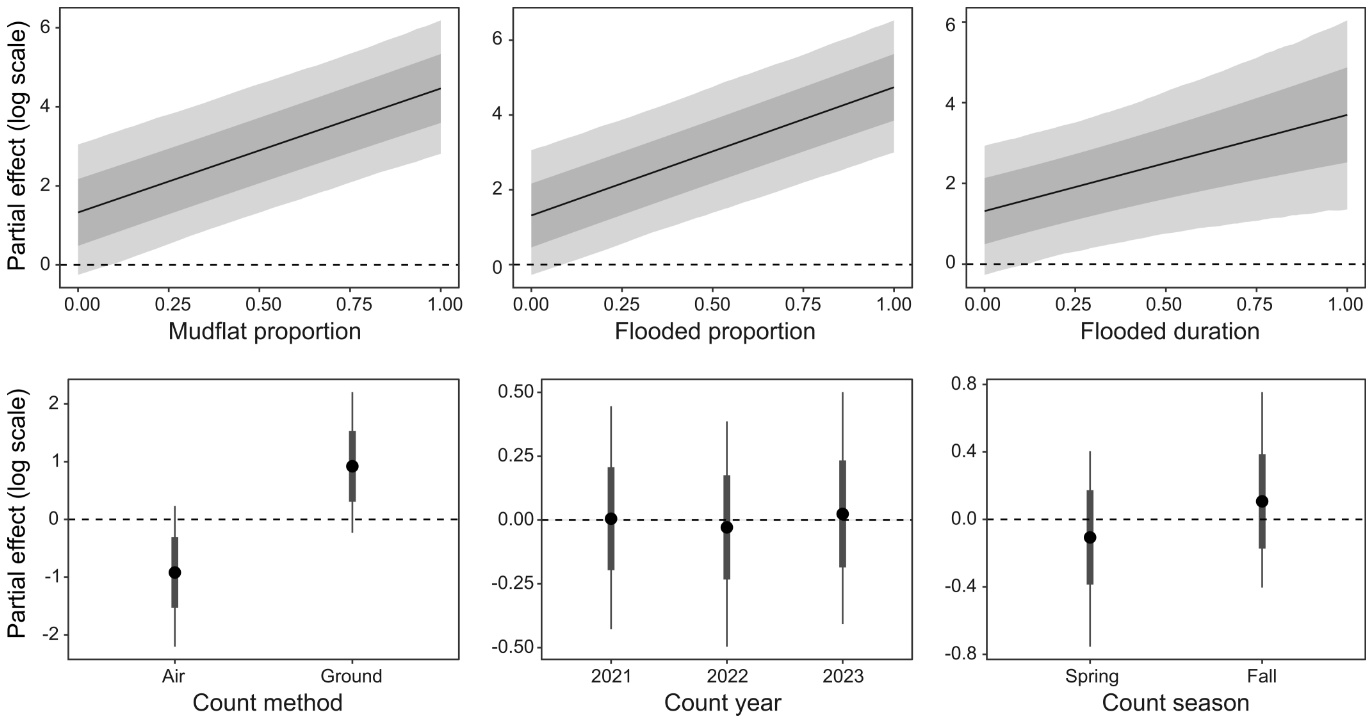

Fig. 3. **Partial effects of mudflat proportion, flooded proportion, flooded duration, count method, count year, and count season. In the top three panels, dark and light gray bands represent 50% and 95% credible intervals, respectively. In the bottom three panels, wide and narrow vertical lines represent 50% and 95% credible intervals, respectively. Partial effects were computed by setting values for all other model terms to zero, except for the top three panels where the global intercept and its uncertainty were also incorporated.**

necked Phalarope, Long-billed Dowitcher, American Avocet, Least Sandpiper, Black-necked Stilt, Snowy Plover, and Long-billed Curlew (Table 2).

When comparing species-specific average abundances (Table 2) to published total population sizes north of México (Rosenberg et al. 2019), we estimate that, during a typical day during Spring or Fall migration, the study area hosts roughly 3% of the Western Sandpipers that breed in northern North America. Analogous percentages for other species common in the study area were: 1% for Red-necked Phalarope, 6% for Long-billed Dowitcher, 5% for American Avocet, 3% for Least Sandpiper, 11% for Black-necked Stilt, and 6% for Long-billed Curlew. Other species with continental breeding proportions ≥ 1% included Whimbrel (4%), Greater Yellowlegs (2%), and Semipalmated Plover (1%).

DISCUSSION

On a typical day during the active migration season, the wetlands of the Colorado River Delta host roughly a quarter-million Nearctic-breeding shorebirds. Given periodic turnover of individuals, the total number of shorebirds that use the CRD during an entire migration season could be well over a half-million individuals, the criterion that certifies a Landscape of Hemispheric Importance (WHSRN 2024). The highest, previously reported migration-season one-day total count of 129,575 individual shorebirds (Gómez-Sapiens et al. 2014) was roughly half the current estimate despite covering a larger sampling area. The higher number reported in this study is partly due to our correcting for partial coverage of the survey area and visibility bias associated with counting birds at high flight speeds and altitudes. We intend to use this estimate of a quarter-million shorebirds as a benchmark for future studies that explore how shorebird numbers in the study area change with future changes in climate and land and water management in the Colorado River Basin.

When we explored spatial patterns of shorebird abundance in our study area, we found that the largest concentrations of individuals were located on mudflats and flooded areas of the Santa Clara Slough, a part of the Ciénega de Santa Clara that relies on agricultural wastewater from the United States for 90% of its water supply (Flessa et al. 2012). This finding supports other studies (Mellink et al. 1997, Gómez-Sapiens et al. 2013, Hinojosa-Huerta et al. 2013, Gómez-Sapiens et al. 2014) that demonstrated the importance of anthropogenic wetlands in the CRD, where a century of water development has reduced natural wetlands by 80% (Pitt et al. 2000). The Ciénega, in particular, is an anthropogenic system with a highly uncertain future due to the transboundary nature of its water supply. While there is precedent in a binational agreement from 2010, known as Minute 316, for the U.S. and Mexican sections of the International Boundary and Water Commission to ensure the Ciénega's water supply is not diminished, the two countries at present have not addressed the sustainability of the water supply or the Ciénega (Pitt and Hinojosa-Huerta 2022). Climate change is further diminishing an already over-

Table 2. Estimated average proportional and absolute shorebird abundances per species.

Species[1]	Size category	Proportional abundance[2]	Total abundance[3]
Western Sandpiper	Small	0.3784	103,132 (31,431–371,963)
Red-necked Phalarope	Small	0.1166	31,763 (9,680–114,559)
Long-billed Dowitcher	Medium	0.1103	30,067 (9,163–108,444)
American Avocet	Large	0.0863	23,527 (7,170–84,855)
Least Sandpiper	Small	0.0741	20,196 (6,155–72,842)
Black-necked Stilt	Medium	0.0704	19,197 (5,851–69,238)
Snowy Plover	Small	0.04	10,901 (3,322–39,315)
Long-billed Curlew	Large	0.033	8,993 (2,741–32,435)
Lesser Yellowlegs	Medium	0.0177	4,814 (1,467–17,364)
Killdeer	Medium	0.0131	3,573 (1,089–12,887)
Wilson's Plover	Small	0.0124	3,391 (1,034–12,231)
Whimbrel	Large	0.0122	3,331 (1,015–12,013)
Greater Yellowlegs	Medium	0.0121	3,300 (1,006–11,904)
Semipalmated Plover	Small	0.0072	1,968 (600–7,099)
Willet	Large	0.0069	1,877 (572–6,771)
Marbled Godwit	Large	0.003	818 (249–2,949)
Stilt Sandpiper	Medium	0.0029	787 (240–2,839)
Wilson's Phalarope	Small	0.0016	424 (129–1,529)
Black-bellied Plover	Large	0.0006	151 (46–546)
Dunlin	Small	0.0006	151 (46–546)
Spotted Sandpiper	Small	0.0003	91 (28–328)
Total shorebirds			272,515 (83,052–982,874)

[1] In order of study area abundance.

[2] Averaged over all ground counts.

[3] Averaged over all aerial counts, given as posterior median and 95% credible interval.

developed Colorado River, and states and water users in the Colorado River basin that experience water shortages have proposed development of the Ciénega's transboundary water supply, for example, through operation of the Yuma Desalting Plant (Davis 2024). This development could have important implications for the Santa Clara Slough and hundreds of thousands of migrating shorebirds that rely on this area.

When we parsed the average total number of shorebirds into average abundances per species using average species-specific ratios from ground surveys, we found that the percent of continental populations using the CRD at a given time during migration for 11 species was over the criterion of 1% that certifies a Landscape of Regional Importance (WHSRN 2024). These results further support the notion that wetlands of the CRD are critical resources for Nearctic-breeding shorebirds during migration. Interestingly, the percentages derived from the present study are not far from those estimated through very different methods. For example, we estimate that approximately 3% of Western Sandpipers that nest in the Canadian Arctic can be found in the study area on a given day during migration. A similar conclusion is given by an online web application hosted by the Cornell Lab or Ornithology (Fink et al. 2023), that produces weekly species distribution maps for hundreds of species using eBird data and calculates the percent of the modeled population that can be found within a user-defined polygon using methods similar to those of DeLuca et al. (2021). That web application estimates that up to 2.6% of modeled Western Sandpiper relative abundance can be found in our study area on a given week during migration. Web application estimates for other species in our study are also comparable to those produced in our study: suggesting that 6.2% of Long-billed Dowitcher, 2.2% of American Avocet, 1.1% of Least Sandpiper, and 4.8% of Long-billed Curlew modeled relative abundance can be found in the study area at some point during migration. Comparisons are not possible for other species in our study because their breeding ranges extend to large areas outside the continental USA and Canada.

Similar to numerous previous studies, we found that aerial counts were biased low compared to concurrent ground counts due to lower visibility of birds from fast-moving, high-flying airplanes. We were able to derive a parameter from our analytical model that is similar to the ground-survey correction factor proposed by Pollock and Kendall (1987). Our results suggested that aerial counts were 16% of ground counts, which equates to a visibility bias of (1.00 - 0.16) × -100 = -84% and an equivalent correction factor of 6.25. These visibility bias and correction factor values, and their uncertainty (Fig. 3), are comparable to those from other studies where different survey methods are contrasted in a hierarchical model context. For example, Zimmerman et al. (2012) estimated correction factors for helicopter versus fixed-wing aircraft surveys and reported factors up to 9 and credible intervals ranging over 10 units. Nevertheless, our visibility bias and correction factors, and their uncertainty, are large relative to most of those reported elsewhere in the literature. One reason for the relatively large values could be that most previous studies have focused mainly on waterfowl (Gilbert et al. 2021), a group of larger-bodied birds that are usually less cryptic than shorebirds. Indeed, studies that consider both waterfowl and shorebirds found larger negative count biases for shorebirds relative to waterfowl (Laursen et al. 2008). A second probable cause could be that the elevations of aerial surveys in this study averaged higher than those often used in aerial surveys of waterbirds (Morrison et al. 1992, Mellink et al. 1997, Page et al. 1997, Shuford et al. 1998).

The migrating shorebird abundance estimates from this study relied on a few important assumptions. First, our methods assumed that the relationships between ground counts and aerial counts, and shorebird counts and habitat covariates, were constant across the study area and sample dates. Second, our methods assumed that species occurred in similar proportions across the study area and sample dates. These assumptions should be considered when interpreting the spatial and temporal patterns in shorebird abundance reported here. Readers will also note that the shorebird abundance estimates reported here came with large uncertainty. For example, 95% credible intervals around abundance estimates ranged approximately one order of magnitude (Table 2). Some of the uncertainty in our estimates resulted from using Bayesian methods to propagate uncertainty in the method parameter through to subsequent abundance predictions. This approach contrasts with many previous studies that treat method correction factors as known constants. Figure 3 illustrates the uncertainty in the method effect, where the offset could possibly have been very small to very large. The large uncertainty in the method adjustment was likely driven by error in both aerial and ground counts and by a lack of perfect alignment of aerial and ground counts in time and space, despite our best efforts. The very approximate nature of abundance estimates from aerial surveys has been discussed for decades (Caughley 1974, Kingsford and Porter 2009), and the general consensus is that the approximate nature of aerial counts is an unavoidable and necessary tradeoff of counting animals over large and otherwise inaccessible areas.

Despite many methodological differences, our results have qualitative similarities to other studies conducted in the region during the migration season. For example, Mellink et al. (1997) surveyed coastal sites on the southern edge of the CRD; Fleischner and Gates (2009) surveyed coastal wetlands at Estero Santa Cruz, approximately 360 km southeast of the CRD; and Shuford et al. (2002) and Shuford. et al (2004) surveyed locations around the Salton Sea and adjacent Imperial Valley, approximately 120 km to the northwest of the CRD. In all five studies, 20 or more shorebird species were recorded during migration seasons. All five studies reported Western Sandpiper as the most abundant species during migration seasons. Finally, all five studies reported American Avocet, Long-billed Curlew, and dowitchers as other frequently encountered species. These similarities underscore the idea that the Colorado River Delta is part of an important network of sites that several species rely upon during a critical stage of their annual cycle.

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