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Monitoring winter shorebird populations in the Bay of Panama: 2013–2017

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The wetlands of the Bay of Panama are composed of mangroves, mudflats, marshes, and sandy or rocky beaches extending for over 200 km along the Pacific coast of Panama. This area is one of the most important sites for migratory shorebirds in the Western Hemisphere. As part of a wider shorebird monitoring project along the western flyway, the Panama Audubon Society has conducted an annual winter ground-based shorebird census from 2013 to 2017 over three sites which include 21.2 linear km of the wetlands most heavily used by shorebirds. Eight species, out of 23 recorded over the five years, comprised 99.5% of all shorebirds counted and their census numbers provide a baseline against which to measure any future changes in winter population or habitat usage. Four of these species had the highest linear density at the site closest to the city and which had experienced a significant increase in mangrove growth coincident with substantial urban growth over the previous two decades. Three smaller, but much more abundant, species preferred the coast farthest from the urban area with no mangroves. Recognition of the importance of the wetlands of the Bay of Panama for shorebirds is based in part on an aerial survey in January 1993 (Morrison *et al.* 1998). Our results show that the winter populations of several species are substantially higher than the 1993 survey, either because of a difference in methodology or an actual increase in their winter populations. Regardless of the underlying cause, our study shows that these wetlands have more shorebirds than previously thought.

Keywords

Whimbrel

Marbled Godwit

Willet

Black-bellied Plover

Short-billed Dowitcher

Western Sandpiper

Semipalmated Sandpiper

Semipalmated Plover

INTRODUCTION

The wetlands of the Bay of Panama are composed of mangroves, mudflats, marshes, and sandy or rocky beaches extending along the coast for over 200 km from Punta Chame to the border of Darien Province. The offshore sediments have a very low gradient, and with a tidal range of over 6 m, are exposed as mudflats between 2 and 5 km in width at the lowest tides. These wetlands are an important foraging area for many species of migratory shorebirds, some of which molt there during migration. A large part of the wetlands, 100 km of coastline, has been declared a Ramsar Wetland of International Importance (Ramsar 2003), and is part of the Western Hemisphere Shorebird Reserve Network (WHSRN) as a Site of Hemispheric Importance, now protected by Panama law (WHSRN 2018).

In a winter aerial survey in January 1993, Morrison *et al.* (1998) found 169,648 shorebirds on the 44 km of mudflats between Panama City and the Río Bayano (their sector 62), 67% of all shorebirds they counted in Panama. Watts (1998) found that a 100 km stretch of shoreline centered on Panama City hosted well over a million shorebirds during the fall migration in 1997 with nearly 80% of those, primarily Western Sandpipers *Calidris mauri*, on the 30 km of shoreline extending east from Panama City. Buehler *et al.* (2004) found numbers similar to Watts in aerial and ground surveys of shorebirds in September 2003. These surveys established the importance of the wetlands of the Bay of Panama for migratory shorebirds and form the basis for the accepted estimates of shorebird populations there.

Since these earlier aerial surveys, Panama City has grown, there have been substantial changes to the coastal habitat, and there is an ongoing threat of more changes. Consequently, monitoring current shorebird populations, as well as how they may have changed over the past two decades and how the urban environment affects them, is critical for directing conservation actions.

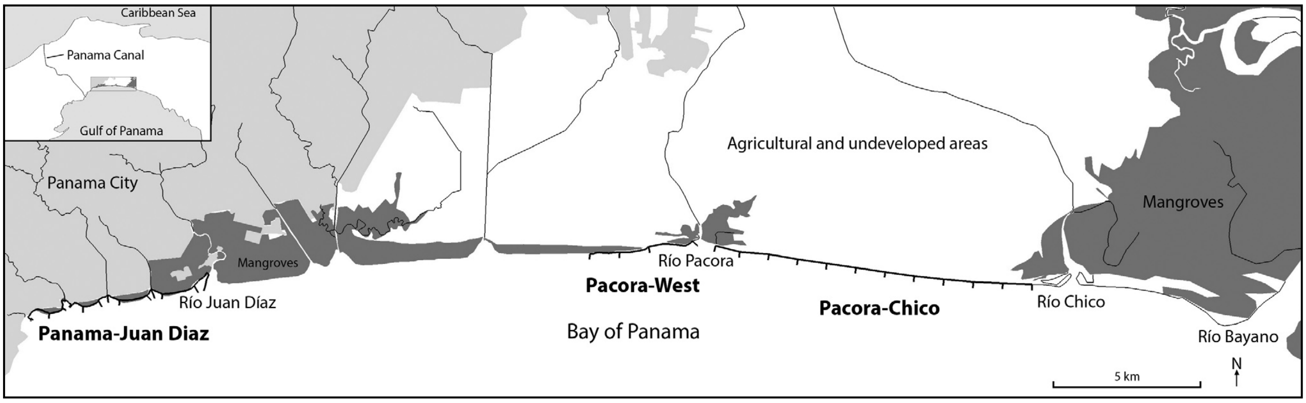

Fig. 1. Project sites: Panama-Juan Diaz, Pacora-West and Pacora-Chico. The tick marks show the individual subsites. For Panama-Juan Diaz they are Pan A to Pan L (Pan A at west end), for Pacora-West they are PW01 to PW03, and for Pacora-Chico PC01 to PC11, both starting with 01 at the east end. Mangrove, urban, and agricultural areas are based on Google Earth imagery from 2018.

Although fall migration populations in the Bay of Panama are larger and have received the most attention, the constantly changing numbers passing through as the migration proceeds makes it impossible to census the birds with just a single count, unlike a winter census with a relatively stable population for the season. A single winter census provides not only a good estimate of the local population but serves as an index of habitat quality for all seasons. For this reason we are now conducting an annual winter census of 21.2 km of shoreline extending east from Panama City. It encompasses the entire coastline between Panama City and the Río Bayano that is accessible by car with some walking. All of the survey area is within the 30 km stretch of coastline found to be critical for Western Sandpipers (Watts 1998) during fall migration.

Although our surveys are conducted at high tide, we consider the offshore area, 500 m to 4,000 m wide at low tide and inaccessible to ground-based observers, to be the actual survey area as we assume birds are pushed directly onshore from their low tide foraging areas. This is a reasonable assumption given the uniform appearance of the mudflats from aerial photos and, although it is undoubtedly violated to a greater or lesser degree by each species, this assumption provides a first order estimate of the location of the main foraging areas for the birds we count. It is likely a better estimate for the larger shorebirds for which we have observed less lateral movement as they first appear on a rising tide. Smaller shorebirds, especially Western and Semipalmated Sandpipers *C. pusilla* and Semipalmated Plovers *Charadrius semipalmatus*, can often be observed flying parallel to the coast in large flocks before joining others foraging in front of the advancing tide; their offshore foraging area may be substantially farther away from any one of our sites than that of larger birds.

Our survey program was designed to monitor the annual winter population of shorebirds at their high tide roosting area and thus, indirectly, the condition of the critical offshore mudflats. The high tide roosting areas are likely to be affected further by urban growth, particularly the site adjacent to Panama City. This paper reports on the results of the initial five years of our monitoring program and provides baseline data to evaluate current overwintering shorebird populations, and their relation to coastal habitat. We also examine changes to the shoreline over the past 30 years, evaluate habitat preferences for the more common species, and compare current populations with those recorded in earlier aerial surveys. This paper will contribute to analysis and monitoring of flyway-wide threats to shorebirds through our participation in the Migratory Shorebird Project, a winter shorebird census along the Western Flyway of the Pacific Americas led by Point Blue Conservation Science.

METHODS

We conducted an annual winter census at three main sites (Fig. 1) along the high neap tide coastline of the offshore feeding area, along either the seaward edge of mangroves growing onto a mudflat or along a distinct break between the mudflats and a steeper sandy beach. Two sites were surveyed from 2013 to 2017: Panama-Juan Diaz, adjacent to Panama City and including the Juan Diaz area (6.76 km), and Pacora-Chico between the Río Pacora and the Río Chico (10.86 km). Pacora-West just to the west of the Río Pacora (3.58 km) was added in 2014, so that we included all of the neap tide shoreline, a total of 21.2 km, that was accessible by car and foot between Panama City and the Río Bayano, about 40 km to the east (Table 1). The main sites were divided into 26 subsites that ranged in length from 0.21 to 1.58 km measured parallel to the shoreline.

The accessibility of the subsites varied depending on weather and other factors; so each year, some subsites could not be censused. The subsites were surveyed during neap tides in January and early February by one or two teams of 2–4 people each. The census began when the rising tide pushed the birds to within 300 m of the shore and was generally completed by high tide or shortly thereafter. At Panama-Juan Diaz and Pacora-West, the sites were censused while walking along the high neap tide waterline. A team could complete 1–3 subsites before high tide. At Pacora-Chico, all subsites except one were accessible by driving along the beach, and 10 km could be censused during each high neap tide. Two cars were used on the beach with a team in one to count small shorebirds while the other counted medium and large shorebirds. Our use of the terms small, medium and large as applied to shorebirds is shown in Table 2 and matches that used in earlier aerial surveys.

To reduce lateral movement into and out of the site and to provide longer observation times during the census, each survey was conducted during high neap tides when the water level was between 3.2 m and 4.2 m. During these tides, one to three hours were available when birds were within counting range of shore on both the rising and falling tide and when the mudflat above the high neap tide was dry enough to walk on. In contrast, during spring tides, as few as 15 minutes would have been available on a rising tide before the birds were pushed off of the mudflats and into the mangroves or onto the beach.

Eight species of small shorebirds were encountered during the surveys. The three most abundant small shorebirds (Western Sandpipers, Semipalmated Sandpipers, and Semipalmated Plovers) could not be easily separated when found in huge flocks and were recorded in the field as Small Shorebirds. When capitalized, the term Small Shorebirds refers to just these three species in this paper. Five other small shorebird species were relatively rare and often foraged or roosted separately from the three most common small shorebirds. Consequently, they could generally be counted separately, although some individuals, such as Wilson's Plovers *Charadrius wilsonia*, might have been overlooked if mixed in with the huge flocks of the three more common species.

The Small Shorebirds were often very active, flying back and forth parallel to the beach in large flocks as the tide rose. When a large flock was present at Pacora-Chico, we often had to count its birds separately from the other species, sometimes returning on a second day. We would wait until a large portion of the flock, sometimes as many as 200,000 birds, was roosting or feeding along the incoming tide line and then counted them quickly with 20x or 30x spotting scopes (Kowa or Swarovski) in groups of hundreds using a hand-held tally counter.

There were two exceptions to this counting procedure. In 2013, the great majority of the Small Shorebirds at Pacora-Chico were observed flying back and forth over the beach and we recorded only a rough estimate of 150,000 flying birds. In 2017 on a falling tide, we found a large portion of the Small Shorebirds present at Pacora-Chico roosting long enough for us to make a series of 51 overlapping telephoto photographs (Canon EOS 7D with 300 mm lens) from one location. We estimated this portion to be about two-thirds of those present at the site. The birds were counted by stitching the photos together using Photoshop (Adobe Systems, USA), superimposing a grid over the image of the flock, and estimating the proportion of each cell covered by birds for of one out of every six grid cells. We then multiplied the sum of those cells by six to obtain a total of 71,686 birds. Adjusting for the proportion of the flock represented in the photographs, we estimated the total flock to be 107,529 birds, and we used this number as our best estimate of the number of Small Shorebirds present at Pacora-Chico that year.

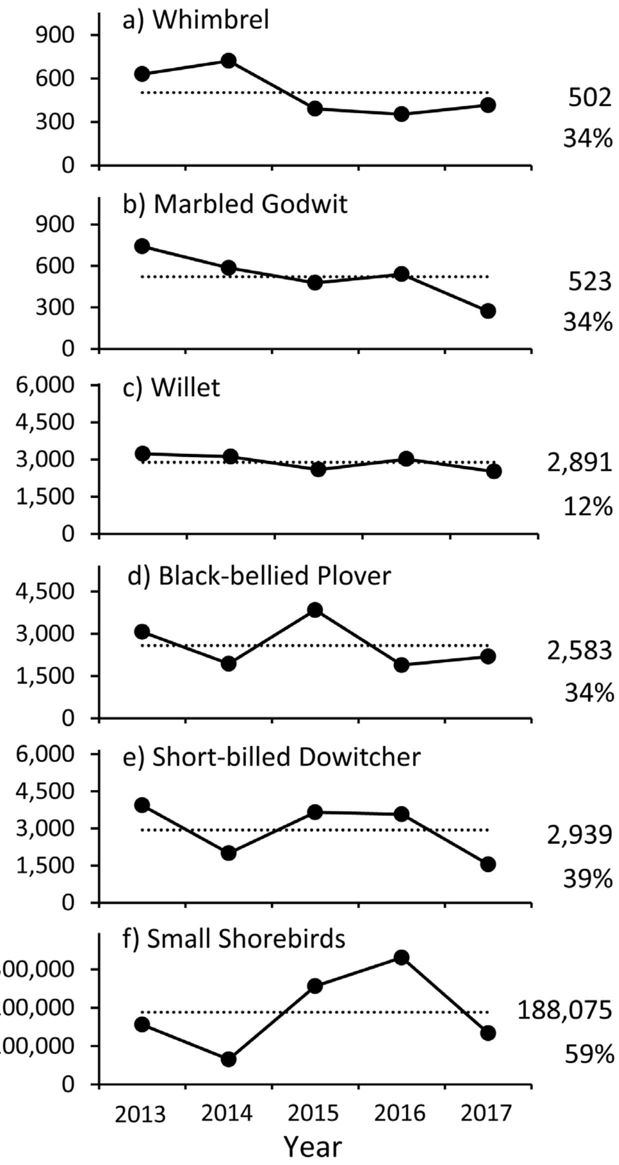

Fig. 2. Annual totals of the five most abundant large and medium sized species (a–e) and the three Small Shorebirds pooled (f) for 2013–2017. To the right of each panel is the annual mean with the CV below. Across panels, the scale of the vertical axis is proportional to the mean (dotted horizontal line) to show the relative magnitude of annual variation among species (variation was largest for Small Shorebirds, f).

Because of the variable number of subsites missing from each annual census (Table 1), the number of birds of each species totaled over only the censused sites was not a valid index of the population size of the entire site each year or of the bird density across sites over the five-year census period. To remedy this for the five most common medium and large species, we assumed that a reasonable estimate for the population in a missing subsite was the mean count for that species of the remaining years that were sampled for that subsite. We prepared a table of imputed counts for each of the five large and medium shorebirds based on this assumption and used it to calculate the annual mean for each year (Fig. 2). The total number of missing birds added for missing subsites in the five years of censuses comprised 16% of the totals for those five species in the imputed data set. For individual species, the added birds ranged from 10% to 22% of the five-year totals. However, in 2015, the year with the highest number of missing subsites (Table 1), the added birds for some of the five species comprised as much as 63% of that year's count. This method of imputing missing data would be expected to slightly reduce the variance of the annual totals for each site (Donders *et al.* 2006).

The great majority of Small Shorebirds were recorded from just one or two large flocks at each site. Because of

Table 1. Number of species counted at each subsite in each year, length of each subsite parallel to the shoreline, and percent of shoreline length censused in each year. '--' indicates subsites that were inaccessible in a given year and not surveyed. 'X' indicates subsites not part of the survey protocol for that year. Grouped species categories (unidentified Greater/Lesser Yellowlegs and Small Shorebirds) are not included in number of species counted.

Area	Subsite	Length (km)	Survey year				
			2013	2014	2015	2016	2017
Panama-Juan Diaz	Pan A	0.76	4	10	8	9	6
	Pan B	0.59	--	6	--	6	9
	Pan C	0.31	9	8	5	9	3
	Pan D	0.39	5	8	--	8	10
	Pan E	0.6	7	5	--	2	7
	Pan F	0.33	6	9	11	8	6
	Pan G	0.42	8	9	10	8	7
	Pan H	1.03	7	9	--	--	6
	Pan I	0.21	4	--	--	--	6
	Pan J	0.39	3	--	6	6	8
	Pan K	1.19	10	--	--	2	9
	Pan L	0.54	7	--	3	6	0
	% length censused		91%	66%	41%	82%	100%
Pacora-West	PW01	1.58	X	3	9	4	0
	PW02	1	X	8	--	4	10
	PW03	1	X	8	--	4	4
	% length censused		0%	100%	44%	100%	100%
Pacora-Chico	PC01	1	5	5	--	7	5
	PC02	1	7	2	0	5	8
	PC03	1	7	8	0	7	6
	PC04	1	2	7	0	4	3
	PC05	1	2	7	0	7	4
	PC06	1	5	2	1	4	4
	PC07	1	4	6	1	2	1
	PC08	1	3	3	3	5	9
	PC09	1	3	5	0	2	4
	PC10	1	5	9	0	3	7
	PC11	0.86	11	6	4	8	7
	% length censused		100%	100%	91%	100%	100%

the tendency of Small Shorebirds to gather into huge flocks which could be spread over one or several subsites during a census, we considered the number counted as representative of the entire site rather than assigning the total to particular subsites. Consequently, we do not estimate the number that may have been missed at uncensused subsites to obtain an imputed site total. Instead, we report only a site total for the number of Small Shorebirds observed at the accessible subsites (Fig. 2). The one exception is that in 2013 we had no site estimate for Small Shorebirds at Pacora-West, and we used the mean of the following four years, only 4,719 birds, as an imputed site total for that year. Other than listing annual totals, no further analysis of any of the less-common sandpipers (Table 2) is presented here. Annual totals for the five common medium and large species and the Small Shorebirds (all three counted as one group) were log transformed to reduce heteroscedasticity before calculating individual regressions of counts *vs* year for each. Coefficients of variation (CV) for untransformed annual totals were adjusted for small sample size by multiplying by (1+1/4n) and expressed as a percent of the mean.

To determine the proportions of the three common species comprising the large flocks of Small Shorebirds at Pacora-Chico (Fig. 3), we identified and counted multiple samples of 50 birds on 6 February 2016, approximately a month after our regular census. We assume that this date is too early for migration to have substantially changed the proportions of the Small Shorebirds present. On that day the birds were spread out evenly along approximately 5 km of coast during a falling neap tide, which provided ideal conditions for measurement of ratios. To avoid the natural impulse to select only birds close to the observer to identify, we sampled three subpopulations along each of seven transects, each perpendicular to the beach line and spaced 500–1,000 m apart, spanning a distance of 4.14 km and including subsites PC05 to PC09. All birds at the site were within 200 m of the beach. At each transect location, the group of birds along the transect line was visually divided into thirds at increasing distances from the beach, labeled Near, Middle, and Far sectors. In each of the Middle and Far sectors a sample of the first 50 birds to be seen in a scope were identified and tallied by a single observer. The Near sector in each transect was tallied once each by two different observers and the mean count was used when calculating the overall mean ratio. Semipalmated Sandpipers were distinguished from Western Sandpipers by their generally shorter bill, steeper angle of their forehead and crouched foraging position (Watts 1998). Semipalmated Plovers were distinguished by their different plumage and shorter bills.

At Panama-Juan Diaz, we were not able to drive along the beach to record species ratios of Small Shorebirds. Instead, we sampled from three transects arranged radially from one position at subsite G and one transect at subsite F on 8 and 9 January 2016. A total of 50 birds from near to far along each transect were selected and identified as they appeared in the scope. Semipalmated Plovers were present in low numbers but did not appear in the tallies.

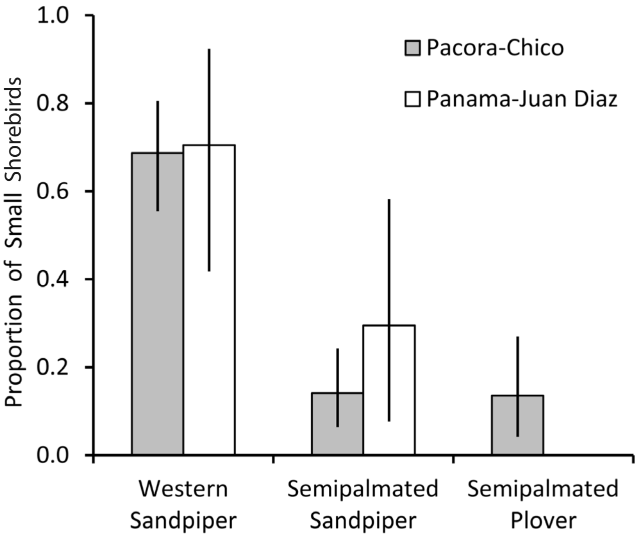

Fig. 3. Proportion of the surveyed individuals composed of each of the three Small Shorebird species at sites Pacora-Chico and Panama-Juan Diaz in January 2016. Means and 95% CI bars are back-transformed values from arcsine square root transformed ratios for each species. Pacora-Chico proportions calculated from subsites PC05 to PC09, Panama-Juan Diaz proportions from subsites F & G. No data were collected for Pacora-West. No Semipalmated Plovers were tallied at Panama-Juan Diaz when recording these data.

Because the ratio data were proportions, we applied an arcsine square root transformation before calculating the mean ratio and 95% CI for each species at each of the two sites where the ratios were determined. To check for interaction between species and sectors at Panama-Juan Diaz, a two-way ANOVA was calculated after pooling data in adjacent transects. Using the mean ratio at each site, an adjusted mean total for 2016 was determined for each of the Small Shorebird species at Pacora-Chico and Panama-Juan Diaz. The ratio for Pacora-Chico was also applied to the very small Pacora-West total.

To compare the annual usage of the three sites by each of the five common larger species and by the Small Shorebirds, we calculated the linear density, or the number of birds divided by the site length in kilometers, using imputed data for the larger species and actual data for the Small Shorebirds. Log transformed counts were used to reduce heteroscedasticity and one-way ANOVAs were computed for each species or group (Fig. 4) to test for differences in linear density between sites over the five-year census period.

The type of shoreline within the census area varied among mangroves advancing seaward over mudflats, mangroves growing behind a sandy beach grading into mudflats, and upland agricultural areas or rocky ledges behind a sandy beach grading into mudflats. Based on historical records, aerial photos dating back to 1968, old maps, historical imagery from Google Earth, and direct observations of the shoreline, we tabulated changes in the shoreline type and the rate of advance of the shoreline over the past 30 years.

RESULTS

Population size and distribution

A total of 23 shorebird species was recorded during the five annual census counts from 2013 to 2017 (Table 2). The group of three Small Shorebird species comprised 95.5% of all shorebirds counted over five years. The next five most common species comprised 4.0% and were all medium or large birds. Their means ranged from 502 to 2,939 (Fig. 2). In individual regressions of the log transformed totals against year, only Marbled Godwit *Limosa fedoa* showed a statistically significant trend, a decrease ($P = 0.047$). Trends for the remaining species or for the Small Shorebirds were not significantly different from zero. Willet *Tringa semipalmata* populations were remarkably stable from year to year (CV = 12%), while the Small Shorebirds showed the greatest annual variation (CV = 59%), ranging from 64,954 in 2014 to 330,429 in 2016. The CVs for the other species ranged from 34% to 39%.

The species composition of the Small Shorebirds was estimated only in 2016, the year when the largest total count, 330,429, was recorded. At Pacora-Chico, Western Sandpipers comprised 68.7%, Semipalmated Sandpipers 14.1% and Semipalmated Plovers 13.5% of the flocks of Small Shorebirds scanned (Fig. 3). The interaction between species and sector (distance from shore) was significant ($P = 0.022$, df = 4) which validates our use of stratified sampling along transects to estimate ratios. At Panama-Juan Diaz, Western Sandpipers comprised approximately the same proportion of the total (70.5%) but no Semi-

Table 2. List of species or species groups of shorebirds, including the five-year total, counted during winter surveys 2013–2017, ordered by frequency encountered. The group Small Shorebird as used in this paper includes Western Sandpiper, Semipalmated Sandpiper, and Semipalmated Plover, but does not include the five less-common small shorebirds.

Size	Common name	Scientific name	2013	2014	2015	2016	2017	Five-year total	% of total
Medium	Pectoral Sandpiper	*Calidris melanotos*	1	0	0	0	0	1	0.00
Medium	Surfbird	*Calidris virgata*	1	0	0	0	0	1	0.00
Medium	Solitary Sandpiper	*Tringa solitaria*	3	3	15	0	0	21	0.00
Medium	Lesser/Greater Yellowlegs	*Tringa flavipes/melanoleuca*	9	12	0	0	0	21	0.00
Medium	Lesser Yellowlegs	*Tringa flavipes*	1	6	10	1	11	29	0.00
Small	Collared Plover	*Charadrius collaris*	21	1	0	11	11	44	0.00
Large	American Oystercatcher	*Haematopus palliatus*	1	90	0	27	19	137	0.01
Medium	Red Knot	*Calidris canutus*	30	36	0	35	55	156	0.02
Medium	Greater Yellowlegs	*Tringa melanoleuca*	26	10	13	62	75	186	0.02
Medium	Ruddy Turnstone	*Arenaria interpres*	65	14	44	17	52	192	0.02
Large	Southern Lapwing	*Vanellus chilensis*	18	0	113	87	25	243	0.02
Large	Black-necked Stilt	*Himantopus mexicanus*	274	45	68	0	82	469	0.05
Small	Wilson's Plover	*Charadrius wilsonia*	1	34	270	15	183	503	0.05
Small	Spotted Sandpiper	*Actitis macularius*	117	130	112	188	117	664	0.07
Small	Least Sandpiper	*Calidris minutilla*	110	59	67	474	68	778	0.08
Small	Sanderling	*Calidris alba*	119	93	825	61	153	1,251	0.13
Large	Whimbrel	*Numenius phaeopus*	514	650	143	326	416	2,049	0.21
Large	Marbled Godwit	*Limosa fedoa*	612	512	192	540	272	2,128	0.22
Medium	Black-bellied Plover	*Pluvialis squatarola*	2,579	1,516	2,696	1,127	2,188	10,106	1.03
Large	Willet	*Tringa semipalmata*	2,693	2,630	1,402	2,729	2,511	11,965	1.22
Medium	Short-billed Dowitcher	*Limnodromus griseus*	3,425	1,871	2,961	3,459	1,548	13,264	1.35
Small	Small Shorebird	Small *Calidris* or *Charadrius*	155,695	64,954	255,910	330,429	133,386	940,374	95.51
Total			**166,315**	**72,666**	**264,841**	**339,588**	**141,172**	**984,582**	**100**

palmated Plovers were tallied and Semipalmated Sandpipers made up the remaining 29.5%.

The individual totals from the 2016 census for the three common Small Shorebirds at all sites combined, as estimated from the calculated ratios, were 227,349 Western Sandpipers, 49,715 Semipalmated Sandpipers, and 41,974 Semipalmated Plovers, giving a total of 319,038 Small Shorebirds. The total of adjusted means does not exactly match that in Fig. 2 because it was calculated using back-transformed mean ratios.

We found a difference between sites in linear density at high neap tide roosting areas (Fig. 4) for four of the five common medium and large species, Marbled Godwit, Willet, Black-bellied Plover *Pluvialis squatarola*, and Short-billed Dowitcher *Limnodromus griseus* ($F_{2,12}$ and P are: 103, <0.001; 4.46, 0.036; 5.30, 0.022; and 11.1, 0.002 respectively for log-transformed densities). Each of these four species had the highest linear density at Panama-Juan Diaz. The group of three Small Shorebirds had the opposite distribution, with a linear density at Pacora-Chico almost 15 times greater than that at Panama-Juan Diaz ($F_{2,12}$ = 7.91, P = 0.006). Whimbrels *Numenius phaeopus* showed no difference between sites ($F_{2,12}$ = 1.40, P = 0. 284).

Changes in type of shoreline

The distribution of mangroves and sandy beaches and changes over the past 30 years may help explain the current distribution and abundance of shorebirds. In 1987, 51% of the coast between Panama City and the Río Pacora, a distance of 23 km and encompassing our Panama-Juan Diaz and Pacora-West census sites, consisted of mangroves adjacent to mudflats, sometimes with a narrow sandy beach. By 2000 mangrove shorelines had increased to 63%. Between 2003–2004 and 2013 the entire shoreline in this section of coast advanced seaward by 150–300 m, a rate of 15–30 m per year as compared to sporadic advances of <8 m per year with long periods of stability previously from at least 1968. This coincided with filling and development of some low-lying areas along the coast close to Panama City and sand mining farther west up to and including the channel of the Río Pacora. After 2013, the coastline advance slowed substantially or even stopped. In 2016 the proportion of mangrove coastline was 89%. In contrast, the next 12 km to the east, encompassing our Pacora-Chico site, were relatively unchanged over this period. It had 14% mangrove coast in 2000 and 12% mangrove coast in 2016. The mangroves were close to the mouths of the rivers at each end and outside of our census area. We can find no indication of any different shoreline type in that section as far back as 1987. Since the shoreline advance was absent east of the Río Pacora, including at our Pacora-Chico site, but was uniformly distributed to the west, downstream from a persistent east to west long-shore current, it is likely that much of the source of the sediment causing the coastline advance was from construction, landfill and sand mining.

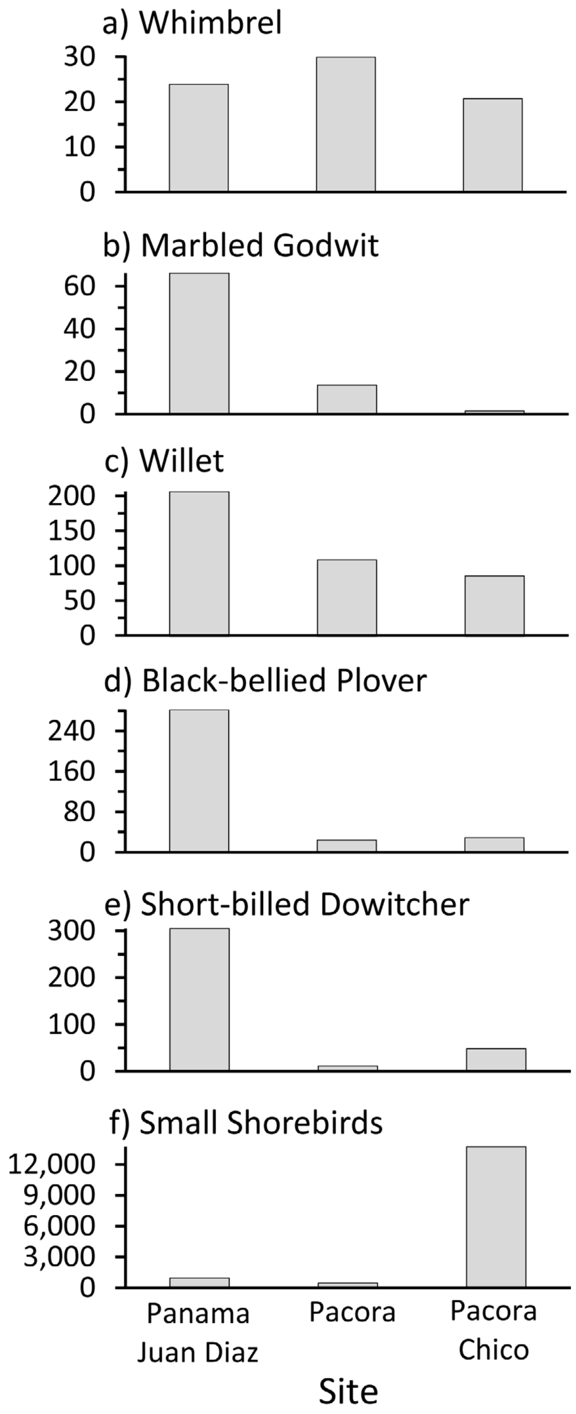

Fig. 4. Five-year mean linear density (number of birds per linear km of shoreline) of the most abundant shorebirds for each site. Scales of vertical axes vary among species.

DISCUSSION

Current shorebird populations

In our five-year study, we found no change in the populations of any species, except for Marbled Godwit, which decreased. Because we only censused about half of the coastline between Panama City and the Río Bayano, our counts are subject to variability from differences in site fidelity at high tide from year to year. The most variable species were the Small Shorebirds (CV = 59%) probably because of their frequent lateral movements on rising neap tides, their tendency to flock together in huge groups, and the difficulty of counting such large numbers. With this high CV, a relatively large number of years might be required to detect a change in population. By contrast, the low CV of Willets (12%) indicates a higher site fidelity and suggests that a change in their annual count could provide an earlier warning of habitat change for that species.

The global populations of the three species comprising our category Small Shorebird are estimated to be 3,500,000 for Western Sandpipers, 1,450,000 for Semipalmated Sandpipers, and 200,000 for Semipalmated Plovers (Andres *et al.* 2012). The overwintering population for each of these species in 2016, as estimated from proportions determined in that year, are 6.4%, 3.4%, and 21% of their global populations respectively. Our mean annual counts of larger species, based on imputed data, represented 1.8% of the global population for Short-billed Dowitcher, 1.2% for Willet, and 0.3% for Marbled Godwit, as well as 0.7% of the North American population for Black-bellied Plover and 0.6% for Whimbrel.

The high value of 21% of the global population for Semipalmated Plovers underlines the importance of our census area as an overwintering site for that species. The lower percentages for the winter populations of other species do not necessarily indicate a lesser importance of the Bay of Panama for them because much higher numbers use these wetlands as a stopover site during migration. This includes 1,100,000 Western Sandpipers, or 30% of the world population (Watts 1998; global population updated with Andres *et al.* 2012).

Spatial differences in density

The marked difference between the sites in linear density, with four species preferring the site closest to Panama City and Small Shorebirds preferring the site 20 km to the east (Fig. 2), suggests specific local high tide habitat preferences for each. Understanding local habitat preferences will help us interpret population changes in the future in the face of a constantly changing shoreline.

Panama-Juan Diaz is essentially an urban site and had high numbers of medium and large shorebirds using it at high tide. While the current habitat appears to attract them, it may also expose them to higher levels of pollution than they would experience farther from the city. The mangroves at that site may provide attractive roosting areas for Willets and Whimbrels at high tide. Except for three viewing areas, the mudflats seaward of the mangroves are often inaccessible and less subject to human disturbance than the beach at Pacora-Chico, which commonly has fishermen driving along it, and at Pacora-West with an active sand extraction operation. Some species at Panama-Juan Diaz may also be attracted to foraging areas of fine mud along the channels leading from the mouths of the five small rivers entering that site. The only rivers near Pacora-West and Pacora-Chico are larger and their outflow channels are outside of or adjacent to the edges of the area we censused (Fig. 1). The type of watershed of these rivers, urban at Panama-Juan Diaz and agricultural at the other two, could also determine the type of pollution and sediment size in river outflow to the offshore mudflats, which would affect the prey available to the birds. The tall buildings in Panama City adjacent to Pacora-Juan Diaz, but absent at the other two sites, provide roosting areas for overwintering Peregrine Falcons *Falco peregrinus* often seen preying on smaller shorebirds. This can drive small shorebirds away from otherwise acceptable sites (Ydenberg *et al.* 2007, Dekker & Drever 2016).

Population sizes compared to historical records

We estimated mean abundances for medium and large shorebirds that were more than 2.8 times larger than estimates from an earlier aerial winter survey done on 14 January 1993 (Morrison *et al.* 1998) in their sector 62 (Table 3). This sector encompasses 44.2 km of shoreline and includes all 21.2 km of our census areas. Although the five-year mean for Small Shorebirds was only slightly more than the 1993 count, two of the five years surpassed the 1993 total by a wide margin (Fig. 2). Because an aerial count covers the entire shoreline, it theoretically would record all of the birds roosting along the shore at high tide, unlike our ground-based census covering less than half of sector 62. Our census then should usually record considerably fewer birds, assuming no other

Table 3. Winter population surveys of shorebirds in comparable sections of the Bay of Panama. For the Morrison *et al.* survey in January 1993, the totals for each size class are tabulated. For the current paper, the sum of the five-year means for the birds in each size class are tabulated using the imputed data for the five most common medium and large shorebirds and the three most common Small Shorebirds. These species comprise 99.5% of all shorebirds counted, and use the same classification into size categories as previous studies.

Reference	Type	Coastal extent	Length (km)	Number of shorebirds		
				Small	Medium	Large
Morrison *et al.* (1998)	Aerial	Panama Viejo to Río Bayano (Sector 62)	44.2	166,345	1,953	1,350
Current paper	Ground	Panama Viejo to Río Chico	21.2	188,075	5,522	3917

methodological factors affected the count. The sizes of our largest two census counts, in 2015 and 2016, suggest that the Small Shorebird population currently using Morrison's sector 62 is substantially larger than it was in 1993, as for the larger shorebirds.

A methodological factor that may have contributed to the higher numbers we recorded is the different tide levels at which each survey was conducted. Unlike the 1993 survey of sector 62, our censuses were conducted under lower tides, *i.e.* during rising neap tides when the water level was between 3.2 m and 4.2 m and before birds were pushed off the mudflats. According to our calculations from their flight data and tide charts (Morrison *et al.* 1998, Pentcheff 2018), the flight during which sector 62 was counted on 14 January 1993 occurred at a tide level between 4.2 m and 4.8 m when the mudflats would have been largely covered. If birds that had been forced off the mudflats had remained on the sandy beaches or flown to adjacent areas such as sandbars at the mouths of large rivers, they would still have been counted and there would be little effect on the species totals. However, if they had flown inland to an open field or freshwater wetland as many of the species do at high tide (Watts 1998), or if they had failed to flush out of roosts in the mangroves, they would have been missed in 1993.

If the substantially higher numbers in our census results are not entirely due to differences in methodology, then populations may have significantly increased since 1993, likely by movement of overwintering birds into our census area rather than a flyway-wide population increase, since populations in general are thought to be stable or declining (Andres *et al.* 2012). The reasons for attracting more birds could have been a change in the quality or quantity of sediment or the increase in the amount of mangrove shoreline as a result of the rapid advance of parts of the shoreline between 2004 and 2013. Another possibility is that birds have been forced off their habitat in other parts of the flyway and moved to our area, similar to what has happened in Bohai Bay off the Yellow Sea in China (Yang *et al.* 2011). However, we are not aware of any large-scale degradation of habitat in other parts of Pacific Panama.

For at least one species, the increase in the Bay of Panama between 1993 and our study does not seem attributable to differences in methodology. Marbled Godwits have been expanding their overwintering range southward (Melcher *et al.* 2006). Anecdotal accounts (Wetmore 1965, Ridgely & Gwynne 1989) report few of these birds in Panama. Marbled Godwits were absent from Christmas Bird Counts for the Pacific Count Circle in 13 out of 22 years between 1973 and 1994, but have been recorded every year after that (Panama Audubon Society pers. comm.). Neither Morrison *et al.* (1998) nor Watts (1998) recorded Marbled Godwits in their aerial surveys, although Watts reported they were present in small numbers in the fall. Our census records an annual geometric mean of 498, approximately the same as for Whimbrels. Evidently the winter Marbled Godwit population has increased substantially from the time of the earlier surveys.

Recognition of the importance of the wetlands of the Bay of Panama for shorebirds (Buehler 2002, Angehr 2003, Ramsar 2003, Kaufmann 2012) is based mostly on aerial surveys during fall migration (Morrison *et al.* 1998, Watts 1998, Buehler *et al.* 2004), but also on Morrison's 1993 winter survey (Table 3). The higher winter numbers we recorded may be due either to a difference in methodology or to an actual population increase, but in either case they show that these wetlands host more winter birds than previously thought.

Value of aerial and ground-based surveys in the wetlands of the Bay of Panama

There are advantages to both aerial and ground censuses, and both could be used in Panama to inform conservation priorities. Ground-based censuses can be conducted at a finer grain so that local changes in habitat type, if correlated with local population change, can help determine if mitigation measures are necessary. Our protocol, monitoring by foot at high neap tides, is inexpensive, requiring only a few staff and volunteers, and can be maintained for many years by a small institution such as ours. The disadvantage is that the census area is limited to accessible parts of the coast and cannot distinguish a change in population, over days or years, from movements of birds in and out of the census area. Aerial surveys can cover a much larger area, including otherwise inaccessible parts of the coast, so that most of the birds are recorded each time, but at a greater cost both in air flights and observer training. A valuable adjunct to our annual ground-based monitoring would be an occasional winter aerial survey covering the entire Gulf of Panama, or better, the entire Pacific coast of Panama. The wider coverage would give a better estimate of the current use of the Bay of Panama by shorebirds.

In conclusion, we have documented the sizes of winter populations of shorebirds over five years along 21 km of dynamic shoreline partly influenced by urban growth in the wetlands of the Bay of Panama (Fig. 2). Mean annual counts of the eight most common shorebirds were equal to or higher than previously recognized from an aerial survey conducted in 1993 but which had included an additional 23 km of prime coastal shorebird habitat. Whether this is from methodological differences or an increase in local winter populations is unknown. Four of the species preferred roosting at high neap tides at the closest site to Panama City while the three Small Shorebirds preferred the farthest site. These results should facilitate interpretation of future changes in census counts and their implication for changes in the inaccessible offshore foraging areas.

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