Shorebird counts in the Upper Bay of Panama highlight the importance of this key site and the need to improve its protection

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We present data from aerial and ground shorebird counts in the Upper Bay of Panama during fall migration 2003. From 7 to 27 September 2003, we conducted three aerial and 12 ground surveys. Aerial surveys resulted in a cumulative total of 630,613 shorebird observations. These were dominated by small shorebirds (91.2%), with relatively small numbers of medium shorebirds (2.7%) and large shorebirds (6.1%). Shorebirds were concentrated along 30 km of shore east of Panama City, an area of broad mudflats with soft fine sediment. Ground surveys at five sites east of Panama City resulted in a cumulative total of 298,454 shorebird observations and provided valuable information about the importance of non-intertidal habitats for species diversity.

We make the following research and management recommendations:
1. Studies on the effects of urbanization, particularly a project to locate new high tide roosts – if any exist – that may have replaced previous roost sites lost to development.
2. A thorough reassessment of existing survey data.
3. Shorebird surveys should be extended to cover the entire migration period.
4. As the tidal flats within 30 km east of Panama City are extremely important for small shorebirds, we recommend that protection be extended to several areas not included in the existing Ramsar and proposed Western Hemisphere Shorebird Reserve Network sites; especially the mudflats of Costa del Este, the Panama Viejo area, and the mangroves at Juan Díaz.
5. In some areas, protection needs to be enforced, especially in the mangroves of the Río Bayano.
6. Studies of productivity, nutrient input, etc. in the intertidal zone to determine why the mudflats between Panama City and Río Pacora are so attractive to shorebirds.
7. As non-intertidal habitats such as flooded grasslands, rice fields, and flooded cattle pastures are important as roost sites for shorebirds and refuges for herons and ducks, they merit protection from further development.
8. Because sites further east of Panama City are difficult to access by ground, local residents who know the area and its wildlife well should be trained as future collaborators in the collection of information on shorebird numbers, fish stocks, crab stocks, fish kills, and other information.

INTRODUCTION

Shorebirds are among the most migratory of all birds and spend the majority of the year in a small number of essential wintering and migratory staging areas. As these birds take no notice of political borders, their conservation represents an international challenge (Myers 1983, Myers *et al.* 1987, Morrison & Myers 1989), one whose importance is emphasized by recent declines in North American shorebird populations (Donaldson *et al.* 2000, Morrison *et al.* 2001).

Panama occupies an important geographical position connecting North and South America and, because of suitable intertidal habitats on its coasts, hosts a large number of migratory shorebirds in a restricted area. Aerial surveys by the Canadian Wildlife Service have documented the importance of Panama as a wintering and staging area for these birds (Morrison *et al.* 1998). In January 1993, they counted 255,000 shorebirds in the whole country of which 80% were in the Upper Bay of Panama. These numbers, concentrated in a small area and representing nearly 10% of the wintering populations of the whole of South America, highlight the crucial importance of Panama for shorebirds. During southward migration in October 1991, counts were even higher with over 369,000 shorebirds in the Upper Bay alone (Morrison *et al.* 1998). Aerial and ground surveys by Watts (1998) found 370,000 shorebirds in a single day during fall migration in 1997. These numbers, by exceeding 100,000 birds regularly, qualify the area as an International Reserve under the Western Hemisphere Shorebird Reserve Network (WHSRN) (Morrison *et al.* 1995). Taking turnover into account, Watts (1998) estimated that about 1.1 million Western Sandpipers alone pass through the area during fall migra-

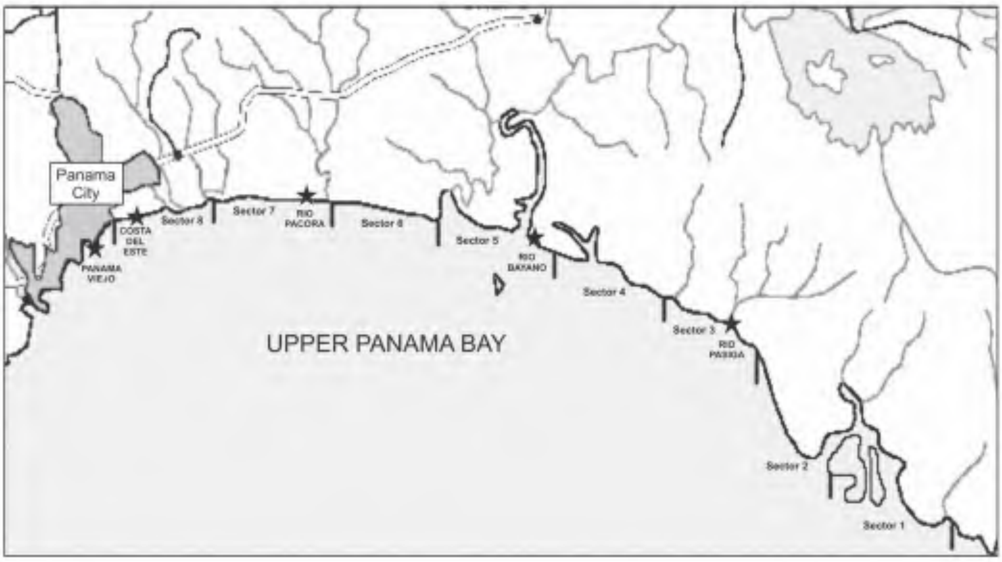

Fig. 1. Location map of the Upper Panama Bay showing the numbered aerial transect sectors and ground survey sites (★). Each aerial sector covered 10 km of shoreline.

tion every year. This far exceeds the WHSRN criteria of 500,000 birds annually, thus qualifying the area as a Hemispheric Reserve, the highest status under WHSRN (Morrison *et al.* 1995).

Based on criteria established by Birdlife International, the Upper Bay of Panama has been designated as an Important Bird Area (IBA) of global importance (Angehr & Jordán 1998, Angehr 2003). This includes 17,000 ha of mangroves and 22,000 ha of mudflats. With a tidal range of 7 m, the mudflats extend several kilometres from the shore at low tide. The mangroves lie to the east of the mudflats that are most heavily used by shorebirds, and there is a strong alongshore current flowing from east to west, suggesting that the mangroves may provide much of the nutrients found in the mudflats (Watts 1998). The western end of the Upper Bay of Panama IBA, a 30-km stretch between the eastern edge of Panama City and the mouth of the Bayano River, supports the highest density of birds. This area, adjacent to Panama City, is under the most serious threat of development.

Since 1998, the Panama Audubon Society (PAS) has been working to protect this area and, at its instigation, Panama's National Authority for the Environment designated part of it as a Wetland of International Importance under the Ramsar Convention. On 20 October 2003, it was officially declared a Ramsar Site (No. 1319), giving it international recognition as a globally important wetland. This was based on assessment criteria that included endangered species, waterbird numbers (minimum: 20,000), fish, and hydrology. This status obligates the government to take all steps necessary to ensure the maintenance of the site's ecological character (Ramsar 2003). In addition, the PAS is currently negotiating with the WHSRN to designate the Upper Bay of Panama as a Hemispheric Reserve with protection extending over the same area as the current Ramsar site. Although these designations are of great value for the conservation of the area, significant parts of the Upper Bay of Panama were not included within the official Ramsar or proposed WHSRN sites. These include the mudflats of Costa del Este and Panama Viejo, as well as the mangroves at Juan Díaz, the latter area being designated for development.

The purpose of this study was to conduct additional aerial surveys of the Upper Bay of Panama during the fall migration of 2003, in order to build on the abundance, distribution, and phenology data previously collected by Morrison *et al.* (1998) and Watts (1998), and to monitor shorebird numbers, especially in the recently developed Costa del Este area. In addition, we conducted extensive ground surveys at five sites to expand on ground survey data collected by Buehler (2002).

METHODS

This study was conducted along the 80-km northern shore of the Upper Bay of Panama from Panama Viejo at the eastern edge of Panama City to the Río Maestra Estuary (Fig. 1). The study area encompasses the new Ramsar and proposed WHSRN sites, which protect all remaining mangroves between Río Tapia and the Río Maestra Estuary as well as all mudflats between the eastern edge of the new Costa del Este housing complex (just west of the Río Juan Díaz) and the Río Maestra Estuary. We surveyed this area intensively, dividing the shoreline into eight 10-km sectors (Fig. 1) which correspond approximately to those used by Watts (1998). The area falls within sectors 61 and 62 of Morrison *et al.* (1998), and consists of mangroves and extensive intertidal mudflats, primarily composed of fine silt and organic compounds, backed by a narrow coastal plain. A detailed description of the habitats in the eight count sectors is set out in Table 1.

Ground surveys

We conducted ground surveys at five sites during 8–27 September 2003 (Fig. 1). Where possible we visited the sites on a rotating basis. However, due to difficult access, we visited Río Pasiga only once and Río Bayano only twice. At each site, both DMB and AIC conducted surveys using binoculars and telescopes when the tide was 70–100% high. The same stretch of shore was surveyed each time.

The **Panama Viejo** site (9°00'21"N, 79°29'14"W) is on the eastern edge of Panama City and comprises a broad mudflat with soft fine sediments, flanked to the east by a tourist centre and to the west by a rocky outcrop. An elevated highway, the Southern Corridor, runs offshore over the outer mudflats, and may have changed tidal circulation patterns since its construction in the late 1990s. We surveyed a 1-km strip of this intertidal mudflat and the adjacent rocks.

The **Costa del Este** site (9°00'40"N, 79°27'31"W) is 3 km east of Panama Viejo. Buehler (2002) included both Costa del Este and Panama Viejo as a single site, but here we consider these separately since they have different shorebird communities (Panama Viejo tends to support more medium and large shorebirds whereas Costa del Este supports huge numbers of small shorebirds). Costa del Este comprises broad mudflats, flanked to the west by the Río Matías Hernández and to the east by mangroves. The landward side of the mudflat is flanked by a concrete seawall built to protect a new housing development which began construction in 1997. During surveys conducted in 1997 by Watts (1998), the area now covered by houses was an extensive area of wet grassland, marsh, and bare ground. We surveyed a 3-km stretch of intertidal mudflat plus a 700 × 300 m area of temporary grassland which will soon be converted into condominiums.

The **Río Pacora** site (9°01'24"N, 79°18'09"W) is 25 km east of Costa del Este and comprises broad mudflats of soft fine sediments, flanked inland successively by savannah-like grassland with scattered trees and extensive rice fields. To the east is the mouth of the Río Pacora. We surveyed a 2-km stretch of intertidal mudflat, plus those irrigated rice fields that we were able to observe from the road.

The **Río Bayano** site (8°59'54"N, 79°06'18"W), 25 km east of Río Pacora, was accessed by boat, a 15-km trip taking 2 hours. The site, at the mouth of the Río Bayano, comprises a sandy beach with a small fishing village nearby. We surveyed a 2-km stretch of the beach on foot, and we traversed the 15-km stretch of mangrove forest along the Río Bayano en route by boat.

The **Río Pasiga** site (8°55'16"N, 78°55'14"W) is 25 km east of Río Bayano site. We accessed it via the Río Bayano and then a 2-hour trip at sea by boat. The site comprises a 1-km undisturbed intertidal flat composed of gravel, sand, and silt at the mouth of Río Pasiga.

All five sites are subject to upwelling during the dry season, when westerly winds blow warm surface water offshore and draw cooler nutrient-rich bottom water to the surface near the coast. Upwelling increases invertebrate activity and reproduction, so that intertidal areas that experience it are particularly rich in invertebrates used as food by shorebirds (Morrison *et al.* 1998).

We used these surveys to ground-truth our aerial counts (see below). From the air, we found some species difficult to distinguish so we counted them by size-class: small, medium and large. We then estimated the number of each species by extrapolating from the proportions in the ground counts. However, even on the ground two very similar species, Semipalmated and Western Sandpiper, are difficult to distinguish (scientific names of the study species are listed in the Appendix). We therefore treated them as a single category, 'peeps'. 'Small' shorebirds included peeps, Least Sandpipers, Semipalmated Plovers and Wilson's Plovers; 'medium' shorebirds included Short-billed Dowitchers (Long-billed Dowitchers *Limnodromus scolopaceus* are rare in Panama and have not been recorded in intertidal habitats), Red Knots, Black-bellied Plovers, and Ruddy Turnstones; 'large' shorebirds included Whimbrels, Marbled Godwits, and Yellowlegs spp. (we did not distinguish Greater and Lesser Yellowlegs in our counts, but most individuals in intertidal habitats in Panama are Greater). Some species within each category (for example Willets) were identifiable from the air and for these we used aerial counts without adjustment based on ground surveys. Some rarer species such as Collared Plovers and Red Knots may have been present in larger numbers than we recorded, since single individuals tend to be missed in large flocks. Because of habitat similarities, we used ground survey proportions from Río Pasiga to extrapolate counts for Sectors 1–3, proportions from Río Bayano for Sectors 4–6, proportions from Río Pacora for Sector 7, and proportions from Costa del Este for Sector 8.

Aerial surveys

Aerial shorebird counts were carried out on 7, 18 and 26 September 2003, dates chosen to represent bird numbers at the beginning, middle, and end of the survey period (Table 2). Flights were timed so that they took place when the tide was 70–90% high, a time when shorebirds are concentrated in a narrow band along the shore and easily counted (Watts 1998). Although we planned for flights to be separated by an

Table 1. Major habitats present in aerial survey sectors of the Upper Panama Bay, Panama. Breaks in habitat are indicated with diagonal strokes with the first section describing the intertidal habitat, the second section describing the habitat immediately behind the intertidal zone heading inland, and the third section describing habitats further inland if necessary. Sectors are listed from west to east. Sectors 1 to 8 correspond approximately to those used by Watts (1998), and fall within sectors 61 and 62 of Morrison *et. al.* (1998).

Sector	Habitat description
8	Broad mudflat with very soft fine sediments / concrete seawall and housing complex on western edge and mangroves to the east / housing complexes, industrial buildings and Tocumen Airport.
7	Broad mudflat with very soft fine sediments / savannah scrub forest and grassland with scattered small houses / agricultural land (mainly rice fields). Note: Almost all sandy beaches have been removed. Only a small sandbar at the mouth of Río Pacora remains undisturbed.
6	Broad mudflats with firmer mud, sand beach / cow pasture with scattered trees.
5	Sand and mudflats with some sand beach at the west end of the sector, mangroves right up to the water at the mouth of Río Bayano, sand beach at the east end of the sector / some cow pasture with savannah scrub forest and grassland at the east end of sector.
4	Sand beach, flooded mangroves / mostly mangroves, some cow pasture with savannah scrub forest and grassland at the west end of the sector.
3	Sand beach, flooded mangroves / mostly mangroves, some cow pasture with savannah scrub forest and grassland at the west end of the sector.
2	Muddy flats, sand beach, flooded mangroves / mangroves and some low forest.
1	Muddy flats, sand beach, flooded mangroves / mangroves and some low forest.

equal number of days, weather conditions and the timing of tides prevented this.

All aerial surveys followed methods described by Morrison *et al.* (1998). We began at the mouth of Río Matías Hernández, to the west of the Costa del Este housing development in Panama City and then flew east along the coast as far as the Río Maestra Estuary (Fig. 1). The aircraft, a high-winged Cessna 152, flew at 180 kmph 20–30 m above the ground and 25 m offshore from the tide edge. One observer (DMB) looked inland from the rear left seat, the other (AIC) forward and seaward from the front right seat. Qualitative habitat descriptions were recorded for each count sector. These were later used to evaluate habitat changes since the surveys of Morrison *et al.* (1998) and Watts (1998). All observations were dictated into tape recorders and transcribed later.

Small flocks (<20) were counted individually; larger flocks were estimated. We estimated to the nearest 10 for flocks of 20–200 birds, 50 for flocks of 200–1,000, 100 for flocks of 1,000–5,000, 1000 for flocks of 5,000–20,000, and 5,000 for flocks >20,000. We identified species where possible, but when flocks were large and diverse or contained similar species, we used the size categories described above.

We generated total shorebirds for each sector by pooling the counts of each observer. In many cases of high density large flocks, birds that flushed early flew over the sea and were counted by AIC, while birds that flushed late flew inland and were counted by DMB. We maintained constant communication between observers and made every effort not to make duplicate counts.

RESULTS

Habitats

Apart from Sectors 7 and 8 near Panama City, the major habitats in our study area (Table 2) are largely unchanged compared with those reported during the surveys of Morrison *et al.* (1998) in 1988, 1991, and 1993 and of Watts (1998) in 1997. In sector 8, the greatest change is the replacement of the Costa del Este marshlands with a housing complex. Other changes include the loss of most of the sandy beach in Sector 7 due to sand extraction, and the construction of the Southern Corridor highway, which now runs across the seaward side of the Panama Viejo mudflat. In addition, the area inland from the Juan Díaz and Tocumen mangroves has become more urbanized. This has increased pressure on coastal ecosystems although development has not yet reached the coast itself. Local residents report subtle effects of urbanization that can be detected even in remote areas. In the Bayano Estuary, for example, a fisherman informed us of recent illegal cutting of mangroves for the expansion of a cattle farm. Regulations to prevent this are difficult to enforce, especially in remote areas. Elsewhere, fishermen in the Río Pacora area reported fish kills that probably arose from effluent of factories along the river. Farther east changes have been minimal and the area remains a mosaic of agricultural land, cattle pasture, mangroves, and scattered fishing villages.

Abundance

Ground surveys

The 12 ground surveys at five sites resulted in a cumulative total of 298,454 shorebird observations (Table 3). Small shorebirds were by far the most numerous (93.6%) with only low numbers of medium shorebirds (3.8%) and large shorebirds (2.6%). Within small shorebirds, peeps (Western and Semipalmated Sandpipers) were by far the most abundant (90.8%). Using mist-netting data, Watts (1998) calculated that Western Sandpipers accounted for 86.9% of peeps in Panama. Applied to our counts, this proportion suggests that Western Sandpipers make up 79% of small shorebirds and 74% of all the shorebirds we counted. Other small shorebirds we encountered included Least Sandpipers, Semipalmated Plovers, Wilson's Plovers, Spotted Sandpipers, and Sanderlings. Medium shorebirds were dominated by Short-billed Dowitchers and Black-bellied Plovers, with small numbers of Ruddy Turnstones and Red Knots. Large shorebirds were dominated by Willets and Whimbrels, with Marbled Godwits and Yellowlegs spp. also relatively common.

Aerial surveys

The three aerial surveys resulted in a cumulative total of 630,613 shorebird observations (see Table 4 for shorebird counts by sector and date, and Appendix 1 for details). These

Table 2. Summary of aerial surveys of the Upper Panama Bay in September 2003.

Date	Survey time	Time of high tide	Predicted tide height (m)	Weather
7 Sept.	11:58–13:03	13:14	4.5	Light haze, light wind, 30°C
18 Sept.	7:16–7:50	8:17	4.1	Overcast, light wind, 22°C
26 Sept.	15:00–15:33	16:39	5.3	Clear, light wind, 32°C

Table 3. Summary of ground counts of shorebirds at five sites in Panama during 8–27 September 2003. Cells with dashes indicate sites and dates where no count took place.

	8 Sept.	9 Sept.	10 Sept.	11 Sept.	12 Sept.	15 Sept.	16 Sept.	17 Sept.	22 Sept.	24 Sept.	25 Sept.	27 Sept.
Costa del Este	13,765	–	–	12,822	–	16,197	–	6,447	–	25,947	–	60,867
Panama Viejo	1,730	–	–	137	–	–	–	1,980	–	1,161	–	190
Río Pacora	–	26,243	–	–	27,884	–	28,363	–	–	–	73,924	–
Río Bayano	–	–	147	–	–	–	–	–	151	–	–	–
Río Pasiga	–	–	–	–	–	–	–	–	499	–	–	–

were dominated by small shorebirds (91.2%), with only low numbers of medium shorebirds (2.7%) and large shorebirds (6.1%).

Distribution

Ground surveys

The greatest concentrations of shorebirds occurred at Costa del Este and Río Pacora, which together accounted for 98% of the total (45.6% and 52.4% respectively). All shorebird size classes were concentrated in these two sites, though this was most pronounced in small shorebirds (99%), whereas medium and large shorebirds were slightly more dispersed (85.3% and 84.5% respectively).

Species composition varied between the five sites. Small shorebirds comprised over 90% of the total shorebirds at Costa del Este and Río Pacora, but only 50% at the other three sites. Panama Viejo had a high percentage of medium shorebirds (30%) in comparison with the other sites, and Río Bayano and Río Pasiga were important for large shorebirds which comprised 40% of shorebirds at those sites. Available habitat at each site was important for species composition. Río Bayano, with its sandy beach, was the only site with Sanderlings and American Oystercatchers. Moreover Buff-breasted Sandpipers, Pectoral Sandpipers, Upland Sandpipers, and Southern Lapwings were only seen in the flooded grassland of Costa del Este.

Aerial surveys

Shorebirds reached their highest concentrations between Panama City and the mouth of the Río Pacora. This area (Sectors 7 and 8) contained 73 % of all shorebirds (Fig. 2a) and the concentration was most pronounced in small shorebirds (79%). Medium shorebirds were distributed differently with the majority (35.7%) in Sector 4. This arose because a large flock of mixed medium and small shorebirds was counted on a sandbar in Sector 4 on 26 September. Because there are proportionally fewer medium shorebirds, this flock skewed the distribution for them more than for small species. Large shorebirds were distributed more evenly along the aerial transect with the only significant concentration occurring in Sector 2 on 7 September.

In terms of time and space, the distribution of small shorebirds appears to be relatively fixed with the main concentration being associated with the soft, fine sediments of the 30-km stretch of shore adjacent to Panama City on all three flights (Fig. 2b). In contrast, the distribution of medium and large shorebirds changed between sectors on different flights (Fig. 2c & d).

Phenology

Shorebird numbers increased with date over the three flights, as well as over the ground surveys at Costa del Este and Río Pacora (where most were concentrated). This was also true for small, medium and large shorebirds considered separately. This is consistent with a survey in 1997 when medium and large shorebirds peaked in late September, and small shorebirds increased throughout the season until early November (Watts 1998). DMB carried out an additional survey at the Costa del Este ground site on 26 November 2003 and found that all shorebird categories and most shorebird species had decreased substantially since the peak counts obtained on 27 September. Only Common Snipe and Wilson's Plover numbers had increased (Common Snipe had not arrived by 27 September, and were found only in the flooded grassland area in the November survey).

DISCUSSION

Habitats

The six years between the fall migration of 1997, when Watts (1998) conducted his surveys, and 2003 have seen large changes in shorebird habitat on the edge of Panama City as urbanization has sprawled eastward, bringing housing complexes, roads, and factories. Changes have included the in-filling and paving over of the Costa del Este marshes for housing, the building of the Southern Corridor highway across the seaward side of the Panama Viejo mudflats, and construction of new factories on the rivers that feed the Upper Bay. The ecological impact of these developments has not yet been fully evaluated, and our counts, though important for monitoring shorebird numbers, are insufficient by themselves. Further studies on the effects of urbanization are needed. For example, sediment studies are necessary to assess whether the paving-over of marshes changes the chemical make-up of the adjacent mudflats, and radio-tracking studies would help to discover the locations (if they exist) of new high tide roost sites when former sites such as at Costa del Este have been lost to development. Furthermore, studies on the waste products of factories located on rivers which feed into the Upper Bay are needed to investigate possible reasons for the fish kills reported by local people.

Abundance and phenology

Our aerial counts correspond well with those of Watts (1998). In terms of species composition our figures are nearly identical, with small shorebirds making up over 90%, large shorebirds around 6%, and medium shorebirds 2%. Our total

Table 4. Shorebird counts according to size-class and date along 80 km of coast east of Panama City in the Upper Bay of Panama during September 2003.

Shore-birds	Counts			Cumulative total	Average count
	7 Sept.	18 Sept.	26 Sept.		
Small	127,411	183,122	265,589	576,122	192,041
Medium	2,267	3,525	11,096	16,888	5,629
Large	12,260	12,067	13,276	37,603	12,534
TOTAL	141,938	198,714	289,961	630,613	210,204

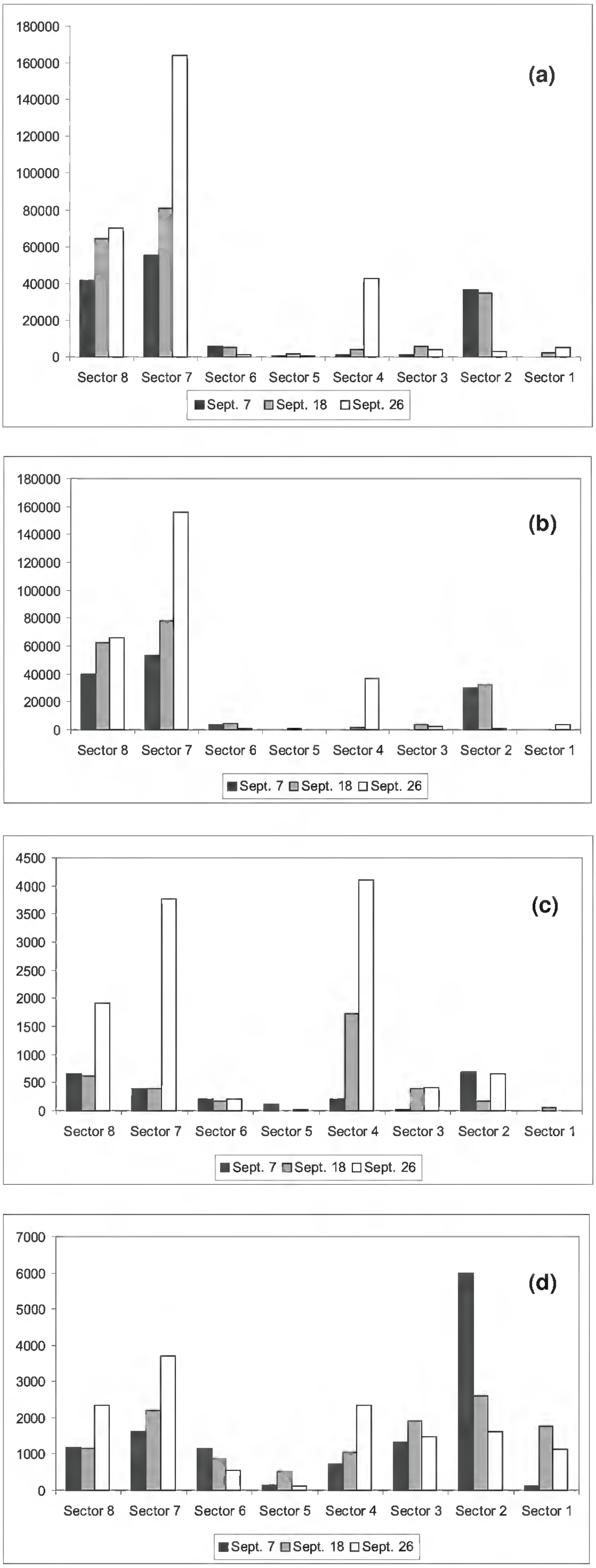

Fig. 2. Temporal and spatial distribution of shorebirds in the Upper Panama Bay, Panama, according to aerial counts on 7, 18 and 26 September 2003:
(a) all shorebirds,
(b) small shorebirds,
(c) medium shorebirds and
(d) large shorebirds.
Each sector is 10 km of shore located as shown in Fig. 1.

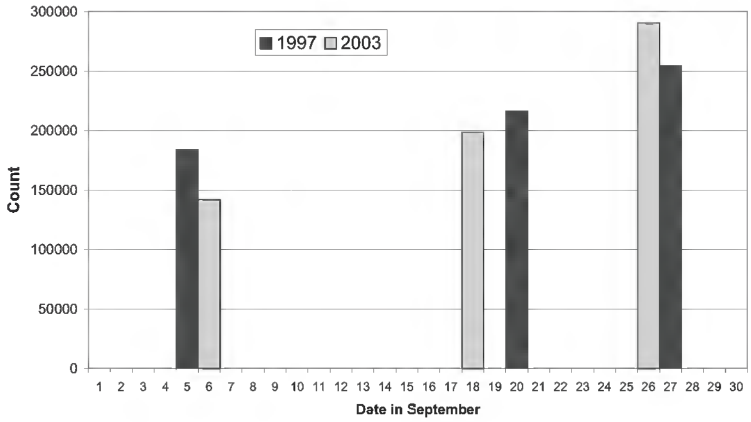

Fig. 3. Counts of shorebirds in the Upper Bay of Panama in September 1997 from Watts (1998) and September 2003 (this study) compared.

counts also match well (Fig. 3). As a whole, the Upper Bay supported approximately the same number of shorebirds in September in 2003 as it did in 1997. However, in 2003 migration apparently started more slowly than in 1997, and there was a large increase in numbers between 18 and 26 September.

Our counts, combined with data from Watts (1998), DMB's additional survey on 26 November 2003, and January counts from Morrison *et al.* (1998), all indicate that small shorebird numbers peak in early to mid-November in Panama. This is the reason why our peak count was lower than that of Watts' 1997 survey which covered the peak of Western Sandpiper migration in November. Our peak counts for medium and large shorebirds were also slightly lower despite the fact that our survey covered the 1997 peak dates for all medium and large species except Willet (which peaked on 4 October in 1997).

Morrison *et al.* (1998) carried out their aerial surveys at different times of year to ours (late February 1988, late October 1991 & mid-January 1993) so the datasets are not directly comparable. However, our peak shorebird count of 290,536 on 26 September 2003 falls between Morrison *et al.*'s winter (January) count of 209,703 and their fall (October) figure of 332,838, indicating that our survey covered a period of active migration when numbers are not far short of the seasonal peak.

Similarly, the ground surveys by Buehler (2002) are not directly comparable since they also took place at other times of year (January–April 2002). Her peak counts for Costa del Este and Río Pacora were higher than ours probably because she caught the spring peak of Western Sandpiper migration, whereas we did not cover the peak of Western Sandpiper fall migration.

We recommend that future aerial surveys should cover the whole fall migration (August–November) and the whole spring migration (January–April). This will facilitate a better understanding of phenology, particularly when peak numbers occur. Repetition of such whole-season counts will allow us to draw conclusions about inter-year variability. We chose our flight dates to cover peak migration for most shorebird species (except Western Sandpipers, which do not peak until October). However, because of differences in the timing of surveys, the only direct comparison possible is with the data of Watts (1998), and then only for September. Future whole-season surveys will provide a better means for monitoring shorebird abundance in the Upper Bay of Panama.

Distribution

Our shorebird distribution data corresponds well with that of Watts (1998). Both studies demonstrate the crucial importance for small shorebirds of the 30-km stretch of coast east of Panama City. This is probably linked to feeding opportunities available on the extensive soft, fine sediment mudflats that occur in this area. Further east, the mud becomes firmer and shorebird numbers drop steeply.

The shorebird concentrations are almost certainly linked to high food productivity due to high nutrient input into the mudflats. The sources of this input are not definitely known. They may include sediments from rivers, adjacent mangrove forests, and dry-season upwelling (Butler *et al.* 1997, Morrison *et al.* 1998). Mangroves are legally protected in Panama, and most of those in the Upper Bay of Panama have received additional protection through inclusion within the new Ramsar site. However, recent cutting of mangroves was evident during aerial surveys in the Bayano area. Therefore additional effort needs to be directed to the enforcement of existing legislation.

Another possible nutrient source is Panama City. It has a population of over 800,000 and sewage is generally discharged into the Bay without treatment. This could be the main source of nutrients in the mudflats immediately east of the city. Studies to determine the organic and chemical content of these mudflats and their productivity are necessary to understand why they are so attractive to shorebirds. Chemical pollutants and other contaminants from urban and agricultural areas may also be present and these could have an impact on populations throughout the flyways for which Panama is a major crossroads.

Our ground surveys demonstrate fine-scale differences in shorebird distribution which highlight the need to protect a variety of habitats to maintain species diversity. Small shorebirds were the most abundant at Costa del Este and Río Pacora, whereas Panama Viejo had more medium shorebirds compared with other sites, and Río Bayano and Río Pasiga were important for large shorebirds. The mudflats at all of our ground-survey sites are protected as part of the Ramsar site except those at Panama Viejo. The latter, though not important in terms of overall abundance, is attractive to medium shorebirds. A flock of 100–200 Red Knots, for example, occurred there regularly from January to mid-April 2001 and 2002 and reappeared again in November 2003 (D. Buehler pers. obs.). This species was not seen consistently in such numbers at any other ground survey site. Bird abundance at Panama Viejo varied widely according to tide height and it appears that the area may be used as a refuge under certain tidal conditions.

The Panama Audubon Society is currently negotiating with the new Panamanian government to have the Juan Díaz mangroves and the mudflats of Costa del Este and Panama Viejo legally protected, as these areas are not included within the Ramsar/WHSRN site. This study strongly supports their efforts.

Although the mudflats east of Panama City support the highest numbers of shorebirds, flooded grasslands, rice fields, sandy beaches, and even wet cattle pastures are particularly important for species diversity. Some kinds of development have less impact than others and some are beneficial. Rice farms and damp cattle pastures, for example, provide roosting or feeding sites for herons, ducks and some shorebirds and so may have an overall beneficial effect on waterbird diversity as long as they do not involve destruction of mangroves, and agrochemicals and pesticides are used with care. Much more damaging is the complete drainage of land for agricultural purposes. Drained grassland at Costa del Este and dry cattle pastures, for example, are not used by any shorebirds, herons, or ducks. Most detrimental of all is the development of land near mudflats for buildings and other paved areas. Waterbirds do not use such places, and shorebirds are particularly affected during spring tides. In the dry season of 2002, Buehler (2002) observed large flocks, mainly Western Sandpipers, flying continuously during a spring tide. The mudflats were submerged and the marshes that had been used as a roost site in the past (Watts 1998) had been filled for housing. As the tide receded and the birds resumed feeding, a Peregrine was seen attacking the flock. Instead of flying off in tight formation, as they normally would, the birds were hardly disturbed and seemed more concerned with feeding than avoiding predation. This flying throughout the high water period is almost certainly due to lack of suitable, safe roosting sites. It wastes energy, increases food requirement and indirectly may increase the risk of predation.

Population growth in Panama means that continuing development is unavoidable. However, there are options that can minimize the damage arising from certain types of development. Our observations on flooded grassland at Costa del Este suggest one such option. In fall 1997, this was a relatively undisturbed freshwater marsh, but by spring 2002 the area had been drained and was dried mud. In fall 2003, however, wet season rains had flooded areas of the mud, wetland grasses had recovered, and shorebirds, herons and ducks were again using the area. This shows that disturbed lands can recover relatively quickly and that birds can and will use flooded grasslands even in the midst of pavement and housing. Although not an optimal solution, the damage of development can be minimized if, for example, grassy areas within housing developments close to the mudflats are allowed to flood and recover a measure of their natural state. This type of compromise would provide green areas for residents and roosting sites for shorebirds.

The Upper Panama Bay is an extremely important area for shorebirds and other coastal species and the sheer number of birds that the area supports gives it international importance. The region is diverse and beautiful. To the west, urbanization is encroaching, but to the east it remains one of a few relatively undisturbed habitats in Panama. The bay is important not only biologically, but also socio-economically, providing, among other things, fish and shrimp that are used not only directly by humans as food, but also as feed for the country's chicken industry. Continued monitoring as well as further studies on the effects of urbanization will be needed to understand and protect the Upper Panama Bay for future generations of shorebirds and humans alike.

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APPENDIX

Species population estimates of shorebirds in the Upper Panama Bay, Panama, on 7, 18 & 26 September 2003. For Sanderling, Willet, Spotted Sandpiper, Black-necked Stilt and American Oystercatcher the figures presented are actual (aerial) counts; for the remainder, the figures are estimates based on aerial counts of small, medium and large shorebirds divided between species according to ground count data as described in the text.

a) 7 September 2003

	Sector 8	Sector 7	Sector 6	Sector 5	Sector 4	Sector 3	Sector 2	Sector 1	Total
Short-billed Dowitcher *Linodromus griseus*	337	268				5	328		**938**
Red Knot *Calidris canutus*	1						1		**2**
Least Sandpiper *Calidris minutilla*	448	530	248	12	7		1,566		**2811**
"Peeps"[a]	36,906	47,852	1,303	60	33	3	24,404		**110,561**
Sanderling *Calidris alba*				10					**10**
Marbled Godwit *Limosa fedoa*	70	23							**93**
Yellowlegs spp. *Tringa melanoleuca* and *T. flavipes*	19	29							**48**
Willet *Catoptrophorus semipalmatus*	1,000	1,500	603	123	657	702	3,343	25	**7,953**
Spotted Sandpiper *Actitis macularia*	6	8	5	2					**21**
Whimbrel *Numenius phaeopus*	111	70	549	17	69	620	2,650	80	**4,166**
Black-bellied Plover *Pluvialis squatarola*	298	126	194	102	194				**914**
Semipalmated Plover *Charadrius semipalmatus*	2,628	4,451	1,241	58	32	1	3,358		**11,769**
Wilson's Plover *Charadrius wilsonia*	12	159	1,303	60	33		672		**2,239**
Ruddy Turnstone *Arenaria interpres*	14	8	6	3	6	5	371		**413**
TOTAL	**41,850**	**55,024**	**5,452**	**447**	**1,031**	**1,336**	**36,693**	**105**	**141,938**

b) 18 September 2003

	Sector 8	Sector 7	Sector 6	Sector 5	Sector 4	Sector 3	Sector 2	Sector 1	Total
Short-billed Dowitcher *Linodromus griseus*	321	266				188	75	24	**874**
Red Knot *Calidris canutus*	1								**1**
Least Sandpiper *Calidris minutilla*	698	783	255	56	69	180	1,612	12	**3,665**
"Peeps"[a]	57,535	70,696	1,361	298	368	2,952	26,445	205	**159,860**
Sanderling *Calidris alba*				13					**13**
Marbled Godwit *Limosa fedoa*	105	127							**232**
Yellowlegs spp. *Tringa melanoleuca* and *T. flavipes*	29	158							**187**
Willet *Catoptrophorus semipalmatus*	857	1,535	619	452	892	658	100	567	**5,680**
Spotted Sandpiper *Actitis macularia*	8	10	5	6					**29**
Whimbrel *Numenius phaeopus*	167	375	250	62	162	1,242	2,511	1,199	**5,968**
Black-bellied Plover *Pluvialis squatarola*	284	126	165	4	1,668				**2,247**
Semipalmated Plover *Charadrius semipalmatus*	4,096	6,576	1,277	278	345	396	3,548	28	**16,544**
Wilson's Plover *Charadrius wilsonia*	19	235	1,361	298	368	72	645	5	**3,003**
Ruddy Turnstone *Arenaria interpres*	14	8	5		53	212	85	26	**403**
TOTAL	**64,134**	**80,895**	**5,298**	**1,467**	**3,925**	**5,900**	**35,021**	**2,066**	**198,706**

c) 26 September 2003

	Sector 8	Sector 7	Sector 6	Sector 5	Sector 4	Sector 3	Sector 2	Sector 1	Total
Black-necked Stilt *Himantopus mexicanus*	25	105							**197**
Short-billed Dowitcher *Linodromus griseus*	995	2,509				197	310		**4,011**
Red Knot *Calidris canutus*	4	4							**8**
Least Sandpiper *Calidris minutilla*	735	1,562	30	14	2,185	100	26	200	**4,852**
"Peeps"[a]	60,568	141,049	160	74	11,653	1,640	427	3,280	**218,851**
Sanderling *Calidris alba*				60					**60**
Marbled Godwit *Limosa fedoa*	311	326							**637**
Yellowlegs spp. *Tringa melanoleuca* and *T. flavipes*	85	408							**493**
Willet *Catoptrophorus semipalmatus*	1,454	2,000	373	93	1,436	715	814	522	**7,407**
Spotted Sandpiper *Actitis macularia*	8	12	7	4					**31**
Whimbrel *Numenius phaeopus*	496	966	189	26	912	761	794	595	**4,739**
Black-bellied Plover *Pluvialis squatarola*	879	1,183	203	10	3,979				**6,254**
Semipalmated Plover *Charadrius semipalmatus*	4,313	13,121	150	70	10,924	220	57	440	**29,295**
Wilson's Plover *Charadrius wilsonia*	17	468	160	74	11,653	40	10	80	**12,502**
Ruddy Turnstone *Arenaria interpres*	42	74	7		127	223	350		**823**
American Oystercatcher *Haematopus palliatus*		3	2	48	134	250		6	**443**
TOTAL	**69,932**	**163,790**	**1,281**	**473**	**43,003**	**4,146**	**2,788**	**5,123**	**290,603**

[a] Western Sandpiper *Calidris mauri* and Semipalmated Sandpiper *Calidris pusilla*