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Seabirds and other colonial waterbirds of the Caribbean coast of Panama

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Abstract The status of seabirds and other colonial waterbirds along the Caribbean coast of Panama has never been determined comprehensively. Surveying the entire Caribbean coast of Panama and Lago Bayano, we found six species of seabirds and other colonial waterbirds nesting at eight sites. Brown Boobies (*Sula leucogaster*) nested at five sites, while other seabirds along the coast nested at only one site each. Red-billed Tropicbirds (*Phaethon aethereus*) nested at Isla de los Pájaros and Audubon's Shearwaters (*Puffinus lherminieri*) at Cayos Tigre. Lago Bayano had two nesting sites of Cocoi Herons (*Ardea cocoi*) and Neotropic Cormorants (*Phalacrocorax brasilianus*) and one of Great Egrets (*Ardea alba*). More species and numbers of waterbirds occurred along the coast in April than in June. The Caribbean coast of Panama is clearly an important area for wintering colonial waterbirds. However, it supports limited nesting of seabirds. No nesting was found in coastal wetlands, despite there being extensive areas of apparently suitable habitat. Inland, Lago Bayano supports nesting herons and cormorants, and foraging sites for spoonbills, storks, and other herons. This study is the third in a series aiming to document the nesting status of seabirds and other colonial waterbirds in coastal Panama, allowing a comparison to be made of the two coasts. Colonial waterbird nesting populations on the Caribbean coast are only 2% of those of the Pacific coast, and more species of waterbirds nest on the Pacific. We suggest that differences are due to oceanographic factors and climatic conditions that differ between the two coasts.

Keywords *Ardea cocoi*, Audubon's Shearwater, Brown Booby, Caribbean, Cocoi Heron, Neotropic Cormorant, Panama, *Phaethon aethereus*, *Phalacrocorax brasilianus*, *Puffinus lherminieri,* Red-billed Tropicbird, *Sula leucogaster*

Resumen Aves marinas y otras aves acuáticas coloniales en la costa del Caribe de Panamá—El estado de las aves marinas y otras aves acuáticas coloniales a lo largo de la costa del Caribe de Panamá nunca ha sido determinado de manera exhaustiva. Con el muestreo de toda la costa del Caribe de Panamá y Lago Bayano encontramos seis especies de aves marinas y otras aves acuáticas coloniales nidificando en ocho sitios. *Sula leucogaster* nidificó en cinco de los sitios mientras que las otras aves marinas en la costa nidificaron en un solo sitio cada una. *Phaethon aethereus* nidificó en Isla de los Pájaros y *Puffinus lherminieri* en Cayos Tigre. Lago Bayano tenia dos sitios de nidificación de *Ardea cocoi* y *Phalacrocorax brasilianus* y uno de *Ardea alba*. El número de especies e individuos de aves acuáticas a lo largo de la costa fueron mayores en abril que en junio. La costa del Caribe de Panamá es claramente un área de invernada importante para las aves acuáticas coloniales. Sin embargo, mantiene un número limitado de aves marinas nidificantes. No se encontró ningún nido en los humedales costeros a pesar de ser áreas muy extensas con hábitats aparentemente adecuados. En el interior, en Lago Bayano sí existen nidificaciones de garzas y cormoranes así como sitios de forrajeo para espátulas, cigüeñas y otras garzas. Este estudio es el tercero de una serie dirigida a documentar el estado de la nidificación de las aves marinas y otras aves acuáticas coloniales en la costa panameña lo que permite realizar una comparación entre ambas costas. Las poblaciones de aves marinas coloniales de la costa del Caribe son sólo un 2% de aquellas de la costa del Pacífico y un mayor número de especies de aves acuáticas también nidifican en esta última. Sugerimos que las diferencias son debidas a factores oceanográficos y a condiciones climáticas que difieren entre ambas costas.

Palabras clave *Ardea cocoi*, Caribe, Panamá, *Phaethon aethereus*, *Phalacrocorax brasilianus*, *Puffinus lherminieri*, *Sula leucogaster*

Résumé Oiseaux marins et autres oiseaux d'eau coloniaux de la côte caribéenne du Panama—Le statut des oiseaux marins et des oiseaux d'eau coloniaux le long de la côte caribéenne du Panama n'a jamais été déterminé de manière exhaustive. Lors de l'étude de l'ensemble de la côte caribéenne du Panama et Lago Bayano, nous avons observé six espèces d'oiseaux marins et autres oiseaux d'eau coloniaux nichant sur huit sites. Le Fou brun (*Sula leucogaster*) nichait sur cinq sites, tandis que les autres oiseaux marins le long de la côte nichaient chacun sur un seul site. Le Phaéton à bec rouge (*Phaethon aethereus*) nichait à Isla de los Pájaros et le Puffin d'Audubon (*Puffinus lherminieri*) à Cayos Tigre. Lago Bayano comprenait deux sites de nidification de Héron cocoi (*Ardea cocoi*) et de Cormoran vigua (*Phalacrocorax brasilianus*) et un de Grande Aigrette (*Ardea alba*). Le nombre d'espèces et les effectifs d'oiseaux d'eau présents sur la côte étaient plus importants en avril qu'en juin. La côte

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caribéenne du Panama est clairement une zone importante pour l'hivernage des oiseaux d'eau coloniaux. Cependant, la nidification des oiseaux marins y est assez limitée. Aucune nidification n'a été observée dans les zones humides côtières, malgré l'existence de vastes zones d'habitat apparemment approprié. À l'intérieur des terres, le Lago Bayano accueille des hérons et des cormorans nicheurs ainsi que des sites d'alimentation de spatules, de cigognes et d'autres hérons. Cette étude est la troisième d'une série visant à documenter le statut de nidification des oiseaux marins et d'autres oiseaux d'eau coloniaux sur le littoral du Panama, et à comparer les deux côtes. Les populations nicheuses d'oiseaux marins coloniaux sur la côte caribéenne ne représentent que 2% de celles de la côte du Pacifique sur laquelle un plus grand nombre d'espèces d'oiseaux d'eau nichent. Nous estimons que les différences sont dues aux facteurs océanographiques et aux conditions climatiques qui varient entre les deux côtes.

Mots clés Antilles, *Ardea cocoi*, Cormoran vigua, Fou brun, Héron cocoi, Panama, *Phaethon aethereus*, Phaéton à bec rouge, *Phalacrocorax brasilianus*, Puffin d'Audubon, *Puffinus lherminieri*, *Sula leucogaster*

The status of seabirds and other waterbirds along the Caribbean coast of Panama has never been documented comprehensively. Very few reports of seabirds occur throughout the literature, with most published first-hand observations being 50 or more years old. Statuses of the species in the study area are mentioned in species accounts in Wetmore (1965), Ridgley and Gwynne (1989), Angehr (2006), and Angehr and Dean (2010), and in the site accounts for the region in Angehr (2003) and Angehr *et al.* (2006). There are no reports of colonial waterbirds, other than seabirds, nesting along this coast, but neither had there been a survey until now of the extensive and nearly inaccessible mangrove and fresh-water swamps or of the riparian zones along the numerous rivers crossing the narrow Caribbean coastal plain. The goal of the current study is to provide a comprehensive assessment of nesting seabirds and other colonial waterbirds along the Caribbean coast of the Republic of Panama. The present paper is the third and final part of a long-term study aiming to characterize the nesting seabird and other colonial waterbird populations of coastal Panama (Angehr and Kushlan 2007, Angehr *et al.* 2014). In this paper, we also contrast the results from the Caribbean coast with the very different situation we found along the Pacific.

Methods

Study Area

The study area included the entire Caribbean coast of Panama, covering 580 km of coastline between Panama's borders with Costa Rica and Colombia, including islands and emergent rocks offshore, coastal wetlands, and riverine flood plains. It also included Lago Bayano, a hydropower reservoir located at its nearest points about 23 km inland. The inclusion of Lago Bayano is important as it provides a contrast to the results from the coast, showing that nesting waterbirds were present in the region. Panama's S-shaped Caribbean coast tends west–east, the Costa Rican border being to the west and the Colombian border to the east. The central cordillera of the isthmus (composed, from west to east, of the Cordillera de Talamanca, Serranía de San Blas, and Serranía del Darién) is largely responsible for the climate of the study region. Northeasterly winds carrying moisture from the Caribbean Sea produce prodigious rainfall as they meet the cordillera (from 2,500 to more than 6,000 mm per year on most of the Caribbean slope), creating extensive swamps and numerous short rivers along the Caribbean coast, which could be expected to offer suitable habitat for wetland-nesting colonial waterbirds. Unlike the Pacific slope of Panama, which has a pronounced dry season from mid-December to mid-April, most of the Caribbean slope has a short dry season or none at all, with some rain occurring throughout the year. Also unlike the Pacific, which experiences large tidal ranges, tides on the Caribbean are modest (about 0.6 m), so that extensive intertidal areas are limited.

The most extensive wetlands on the Caribbean slope are found in the west in Bocas del Toro Province and the Comarca Ngäbe-Buglé, especially around Changuinola and Cricamola, and at the base of the Punta Valiente, where the coastal plain in several places is up to 20 km wide. Farther east, the mountains are closer to shore, producing numerous short rivers running from the mountains to the ocean that, depending on topography, create narrow to broad riverine flood plains. The most extensive wetland area on the eastern Caribbean slope is around the Río Mandinga in the western Comarca de Guna Yala (San Blas).

Mangrove swamps (mostly *Rhizophora mangle* and *Avicennia germinans*) line the shorelines of protected coves on islands and mainland bays. Both mangrove swamps and beach shores tend to be backed by freshwater swamps starting just inland of the dune line. In some places these coastal wetlands encircle coastwise linear lagoons. Swamps and marshes occur extensively further inland. They tend to be dominated by raffia palms (*Raphia taedigera*) and mixed evergreen hardwood trees. Herbaceous marshes and bogs also occur inland along the coast.

To the west, Bocas del Toro Province contains an archipelago of several large islands, the largest being Isla Colón at 29 km², as well as many smaller islands. The larger islands support tropical forest inland, and their coasts are lined by mangrove swamps along protected shores and sandy beaches or rocks along exposed shores. Stacks of erosion-resistant igneous rock stand offshore at various locations from Bocas del Toro nearly to the Colombian border. Some of these are bare rock whereas others support trees, shrubs, or grasses on top or along their leeward sides, both of which provide nesting sites (Figs. 1 and 2).

Islands and extensive wetlands are absent between the eastern Comarca Ngäbe-Buglé and central Colón Province in the Panama Canal area. To the east, sandy islands predominate in the Comarca de Guna Yala. Over 360 islands occur in the area, many covered by coconut palm (*Cocos nucifera*) plantations

Fig. 1. Offshore islands along the Caribbean coast of Panama provide nesting sites for seabirds. Isla de los Pájaros, off Isla Colón in Bocas del Toro Province, supports colonies of Red-billed Tropicbirds and Brown Boobies. Photograph by Kirsten Hines.

Fig. 2. Rocky cliffs on offshore islands provide protected nesting sites. Escudo de Veraguas, shown here, supports Brown Booby nesting. Photograph by Kirsten Hines.

tended by the Guna people. Throughout most of the Comarca de Guna Yala, the Serranía del Darién is close to the coast, reaching it in some places to form rocky shorelines or sea cliffs. Where unprotected by reefs, islands, or coves, the surf is relatively high all year, owing to incoming swells from the Caribbean Sea. This restricts foraging areas of wading birds to protected sites.

We also surveyed Lago Bayano, a large hydroelectric reservoir in eastern Panama created in 1976. Lago Bayano is the most extensive inland freshwater wetland in Panama suitable for colonial waterbird nesting. Although it is on the Pacific side of the continental divide, it is equally near to the Caribbean coast and we included it in our surveys for comparison to determine if potentially breeding waterbirds were present in the area (Angehr and Kushlan 2007, Angehr *et al.* 2014).

Bird Surveys

The study was conducted in April–July 2015, timed to overlap the expected nesting seasons of seabirds and other colonial waterbirds. For this study we refer to "seabirds" as the traditional Pelecaniformes and Procellariiformes (tropicbirds, cormorants, pelicans, boobies, and shearwaters) and other "colonial waterbirds" as the traditional Ciconiiformes and Charadriiformes (herons, egrets, storks, ibis, spoonbills, gulls, and terns). Offshore islands in Colón Province (Farallón Sucio, 14 April) and Bocas del Toro Province (Isla de los Pájaros, Cayos Tigre, and Escudo de Veraguas, 18 April; Cayos Valiente, 9 May) were surveyed by boat. We landed on Cayos Tigre to estimate the density of Audubon's Shearwater (*Puffinus lherminieri*) burrows in a 40 m² count area, which was about one quarter of the area available for nesting on the islands. Seabirds and other waterbirds encountered were recorded on a trip by boat between Cartí and Punta Escoces in the Comarca de Guna Yala between 29 June and 1 July. The entire Caribbean coast was surveyed by airplane between 23 and 25 June, including offshore islands (such as Isla de Oro on

Table 1. Locations, species, and numbers of nests of seabirds and other colonial waterbirds along the Caribbean coast of Panama in 2015. The numbers in the first column correspond to sites in Fig. 3.

No.	Location[a]	Red-billed Tropicbird	Audubon's Shearwater	Brown Booby	Neotropic Cormorant	Cocoi Heron	Great Egret
1	Isla de los Pájaros	10		21			
2	Cayos Valiente			23			
3	Cayos Tigre		200[b]				
4	Escudo de Veraguas			58			
5	Farallón Sucio			105			
6	Isla de Oro			70			
7	Lago Bayano 1				2	10	2
8	Lago Bayano 2				51	23	
	Total	**10**	**200**	**277**	**53**	**33**	**2**

[a]Locations (latitude and longitude) of colony sites mentioned. Isla de los Pájaros: 9°27'15"N, 82°17'58"W; Cayos Valiente: 9°11'11"N, 81°55'42"W; Cayos Tigre: 9°12'48"N, 81°55'31"W; Escudo de Veraguas: 9°06'14"N, 81°32'58"W; Farallón Sucio: 9°38'32"N, 79°38'11"W; Isla de Oro: 8°49'42"N, 77°35'38"W; Lago Bayano 1: 9°06'19"N, 78°33'19"W; Lago Bayano 2: 9°05'10"N, 78°32'26"W

[b]Extrapolated count, see text for methods.

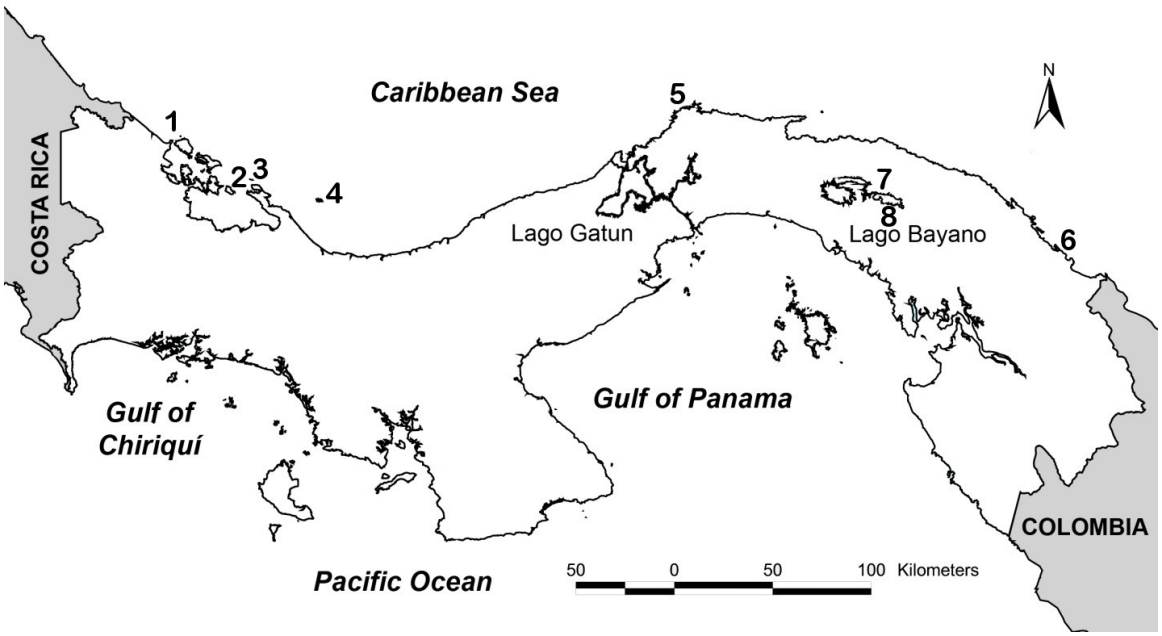

Fig. 3. Panama, showing localities of seabird and other waterbird colonies on the Caribbean coast and in Lago Bayano. Numbers correspond to those listed in the first column of Table 1.

23 June), coastal mangrove swamps, inland wetlands, and coastal rivers inland to the piedmont (580 linear km), and Lago Bayano on 25 June. Boat surveys were conducted using pangas, open 20-ft outboard-engine boats, operated by local captain-guides. Aerial surveys used a Cessna 182S, flying at 150 m at 80–90 knots, descending lower and flying slower as needed. In all cases the numbers of active nests were counted and recorded. Individual birds were also counted.

Results

Colony Sites

We found colonial waterbirds nesting at six sites along the Caribbean coast of Panama (Table 1). All were on offshore islands (Fig. 3). No colonies occurred within the coastal wetlands. In contrast, waterbirds were found nesting at two locations on islands in Lago Bayano.

Species

Six species were found nesting in the survey area. Overall, we estimated 575 nests (Table 1). Except for Isla de los Pájaros (also known as Swan Cay, Swan Key, Cayo Cisne, or Bird Island) and the islands in Lago Bayano, each colony site was occupied by one species.

Brown Boobies (*Sula leucogaster*) were the most widespread, nesting at five sites ranging from about 20 to 100 nests. At Isla de los Pájaros, boobies nested on a small flat islet next to the main island, and at Escudo de Veraguas, on tiny islets north of the main island. At Cayos Valiente, they nested on a set of small stacks with a few trees off Punta Valiente, while at Farallón Sucio, they nested on a large, tall, sparsely vegetated island about 3.2 km off the coast. At Isla de Oro, nests were on a rock stack about 800 m northeast of the main island. (This Isla de Oro is not the island that is referred to in historical accounts as the "Golden Island," which has been identified as the island of Sulet-upo about 12 km to the northwest.) Booby nest sites were quite apparent on the rocky or sparsely vegetated sides of the rock stacks. The colonies were late in the breeding cycle, with large chicks in the nests.

Red-billed Tropicbirds (*Phaethon aethereus*) nested only at Isla de los Pájaros, a tall rock stack with nearly sheer sides, under ledges or in shallow burrows along the leeward rock face of the main island and on a smaller one next to it (see cover photo). We counted 10 nests, mostly birds visible under shallow ledges. We counted an additional 18 birds in flight.

Audubon's Shearwaters nested only at Cayos Tigre (also known as Tiger Rocks), a chain of tiny islets, mostly covered with shrubs and herbaceous vegetation but with a few trees. The birds nested on the middle of the three main islands in densely and uniformly spaced burrows dug into soil held in place by the roots of cane (*Gynerium sagittatum*) growing in a homogeneous stand. Most burrows were evenly spaced, fresh, and well maintained. Fresh foot prints and feathers were found at a few of the burrows but most lacked signs of recent attendance, suggesting that the birds may have mostly completed nesting. These recently used burrows were not explored for young so as not to disturb the highly collapsible substrate. We counted 50 recently used or active burrows in the sample area, implying about 200 active or recently active burrows on the island, or 400 adult birds.

Cocoi Herons (*Ardea cocoi*), Great Egrets (*Ardea alba*), and Neotropic Cormorants (*Phalacrocorax brasilianus*) nested in trees at Lago Bayano on two islands in the easternmost section of the lake, near the entrance of the Río Bayano. Cocoi Heron nests were tightly packed in tall trees. They were in the later stages of nesting, with large young in the nests. Neotropic Cormorants were similarly in late nesting stages or had completed nesting, their nests still being visible. The egrets were early in their nesting cycle.

Other colonial waterbirds and seabirds were also observed

during the surveys (Table 2). Tropicbirds, Brown Pelicans (*Pelecanus occidentalis*), Brown Boobies, White Ibis (*Eudocimus albus*) and two hybrid White x Scarlet Ibis (*E. albus x ruber*), Tricolored Herons (*Egretta tricolor*), Black Terns (*Chlidonias niger*), and Laughing Gulls (*Leucophaeus atricilla*) were observed only along the coast. A small group of about 10 White Ibis was seen near Mulatupo-Sasardi on 30 June, as well as 2 individuals near Ustupo and 3 near Isla de Pinos on 1 July. Wood Storks (*Mycteria americana*), Neotropic Cormorants, and Roseate Spoonbills (*Platalea ajaja*) were observed only on Lago Bayano. Little Blue Herons (*Egretta caerulea*), Snowy Egrets (*Egretta thula*), Cattle Egrets (*Bubulcus ibis*), Green Herons (*Butorides virescens*), and Glossy Ibis (*Plegadis falcinellus*) were observed in both areas. A comparison of the coastal surveys of April and June, either by actual counts or counts rectified by linear extent of coastline covered suggests an overwhelmingly greater abundance and diversity along the coast in April.

Discussion

Of the six nesting colonies of seabirds we found on the Caribbean coast, two sites, Cayos Valiente and Isla de Oro, have not previously been reported. Although Cocoi Herons and Neotropic Cormorants have previously been reported to nest on Lago Bayano (Araúz and Gorrichátgui 2000a, 2000b, Angehr 2003), the sites we found were new.

Isla de los Pájaros is the only known nesting location for Red-billed Tropicbirds in Panama (Wetmore 1965, Ridgely and Gwynne 1989, Angehr 2003, Angehr and Dean 2010), as well as the only one in the southwestern Caribbean, the nearest colonies being in the Islas Los Roques and Islas Los Hermanos, east of Bonaire off the coast of Venezuela (Meyer de Schauensee and Phelps 1978). Panama's colony was first reported by Griscom (1928), based on the collection of nine specimens by R. Benson in 1927 (Peters 1931). Griscom reported the breeding colony size as 30 pairs. Wetmore (1965) visited the site on 26 January 1958, and estimated the colony size as 30 to 35 pairs. W. Martínez estimated that 35–40 pairs were nesting on a visit in 1998 (Angehr 2003). (The statement in Angehr [2003] that Martínez "counted 75 nests" on this visit is in error; the figure actually refers to the number of individuals estimated to be present.) Checklists posted on eBird (2017) record this species as present at the site in every month except June, for which no checklists are available. Most checklist estimates are in the range of 25–40 individuals, with the largest number reported being 100 (Cadman 2009, Fernández 2018).

Although the species has a wide range in the tropical southern Atlantic, Pacific, and Indian Oceans, the Caribbean subspecies (*P. aethereus mesonauta*) nests at few sites, and the population has been declining gradually over decades (Bradley and Norton 2009). Lowrie *et al.* (2012) used the number of birds as an estimate of the size of a breeding colony. However, Bright *et al.* (2014) found that in general the number of flying birds were about twice the number of nests found in a thorough census (although with some variation). As our count of flying adults was about twice the nest count, we use the nest count as the best estimate. The agreement between the number of birds flying and a count of half that number of nests lends confidence to the nest count, but our count is about a third of previous estimates.

Cayos Tigre is the only known nesting site of Audubon's Shearwaters in Panama, and one of only two in the southwestern Caribbean, the other being about 480 km to the north, at Crab Cay near Isla Providencia off the coast of Nicaragua. The

Table 2. Species and numbers of colonial waterbirds counted in April and June 2015. In parentheses is the number of individuals counted per 100 km of shoreline for counts along the coast.

Species	April (coastal)[a]	June (coastal)[b]	June (Lago Bayano)
Laughing Gull	6 (1.5)	0	0
Black Tern	80 (20.5)	0	0
Red-billed Tropicbird	20 (5.1)	0	0
Wood Stork	0	0	65
Brown Booby	122 (31.3)	30 (5.2)	0
Neotropic Cormorant	0	0	53
Brown Pelican	10 (2.6)	2 (0.3)	0
Cocoi Heron	0	2 (0.3)	30
Great Egret	30 (7.7)	12 (2.1)	80
Snowy Egret	1 (0.3)	0	100
Little Blue Heron	34 (8.7)	2 (0.3)	20
Tricolored Heron	1 (0.3)	0	0
Cattle Egret	53 (13.6)	0	40
Green Heron	9 (2.3)	4 (0.7)	4
White Ibis	68 (17.4)	0	0
White x Scarlet Ibis	2 (0.5)	0	0
Glossy Ibis	1 (0.3)	0	2
Roseate Spoonbill	0	0	12
Number of species	**14**	**6**	**10**

[a]April survey was of coast and offshore islands from boat and on land from Bocas del Toro to Escudo de Veraguas and Farallón Sucio, covering 390 km.
[b]June survey was from the air, along the entire Panamanian Caribbean coast including shoreline, wetlands, and coastal rivers, covering 580 km.

colony was first visited on 12 March 1936 by L.H. Miller, when he found four occupied burrows with eggs that ranged from fresh to nearly ready to hatch, and collected two skins and a skeleton (Wetmore 1959a, 1965). Wetmore visited the site on 25 February 1958, examining a roughly 10 x 20 m area of the colony and collecting nine adults and five eggs (Wetmore 1959a, 1965). Although Wetmore described burrows as "numerous," he provided no estimate on the number of nesting birds. S. Olson (in litt.) visited the site on 24 April 1990. He found three nearly adult-size chicks with little down left on them, but thought that all adults and most chicks had already left by this time, so no population estimates were possible. Although we also were unable to count all nests directly, we believe our estimate of 200 nests based on the amount of suitable nesting substrate on the islands is not unreasonable. This would constitute a relatively large colony for the Caribbean (Bradley and Norton 2009). Nesting in the northern winter to early spring is consistent with the situation in other parts of the West Indies and previous observations at this site (Wetmore 1965, S. Olson in litt.).

It is of some importance to clarify the taxonomic identity of this shearwater population, as it has been confused in the past. Wetmore (1959a) described the subspecies *loyemilleri* on the basis of smaller size (wing length of 11 adults from Cayos Tigre ranged from 185 to 195 mm) than *lherminieri* (wing length 193–210 mm; Wetmore did not give the number of specimens examined). Wetmore (1965) stated that specimens (number not given) taken from the Islas Los Roques and in the Islas Los Hermanos had wing lengths 189–192 mm, and a specimen taken 100 km off Guyana (wing length 186 mm) was also consistent with *loyemilleri.* However, wing lengths from birds at nesting sites elsewhere in the southwestern and southern Caribbean overlap with those of the nominate subspecies. Wetmore (1965) found that five specimens from the closest colony to the Cayos Tigres, Crab Cay near Isla Providencia, had wing lengths 195–204 mm, and were thus "within the size range of typical *lherminieri*." Nonetheless, Onley and Scofield (2007) list *loyemilleri* as the form occurring at Isla Providencia. Voous (1983) found that wing lengths of specimens from Curaçao (male, 208 mm) and Bonaire (200, 202, and 203 mm), about 160–200 km west of the Islas Los Roques, agreed with those from the eastern Caribbean rather than with *loyemilleri*. Collins (1969) reported that wing lengths of birds from the colony at Little Tobago Island ranged from less than 190 mm to more than 200 mm, and considered them intermediate between *loyemilleri* and the nominate subspecies. Although it is possible that birds from the southwestern and southern Caribbean might be somewhat smaller on average than those from elsewhere in the range, there is extensive overlap in measurements. The presence of a morphologically diagnosable population in this region is not supported. Likewise, Austin *et al.* (2004), in a study of mtDNA, found that *loyemilleri* was not phylogenetically differentiated from *lherminieri* and was probably not a valid subspecies. The statement by van Halewyn and Norton (1984) that "[t]he population of *P. l. loyemilleri* may be close to extinction" appears to be based mainly on a decline of the breeding colony near Isla Providencia, which Wetmore (1965) excluded from that subspecies. We conclude that the Audubon's Shearwaters nesting on the Caribbean coast of Panama are thus best considered part of the general Caribbean population, *Puffinus lherminieri lherminieri.*

Of the five Brown Booby localities, only those at Isla de los Pájaros, Escudo de Veraguas, and Farallón Sucio were previously reported (Wetmore 1959b, 1965). However, S. Olson (in litt.) observed that rocks off Punta Valiente (referred to by Olson as "Bluefield Point"), probably the Cayos Valiente, were "covered with Brown Boobies" in April 1990. On a March 1958 visit, Wetmore (1959b) estimated that 200 birds were present at Escudo de Veraguas, and noted large down-covered young. Contrary to Wetmore's statement that the nesting islets were off the west coast (which has no islets), we found them off the north coast of the main island. W. Martínez estimated that about 25 pairs of boobies were nesting at Isla de los Pájaros in 1998 (Angehr 2003). Checklists posted on eBird through 2017 record this species as present at the site in every month except June, for which no checklists are available (eBird 2017). Most checklist estimates are in the range of 10–20 individuals, with the largest number reported being 150 (Kratter 2007), although this latter figure almost certainly includes non-nesting birds since the site is too small to support very many nests. There have been no previous estimates of the size of the colony on Farallón Sucio. Wetmore (1965) noted that there was a colony of this species at Tonel Island, Colombia, on the western side of the Gulf of Urabá, a few miles beyond the eastern boundary of the Comarca de Guna Yala. To the west of Panama, a colony of 50–100 pairs has been documented at Uvita Island off the Caribbean coast of Costa Rica (Stiles 1984).

Cocoi Herons were previously reported nesting on Lago Bayano by Araúz and Gorrichátgui (2000a), who found a colony of 67 nests on four small islets in the western part of the lake (about 20 km west of the colonies we found) on a survey during 20–22 March 1999. Most nests they found were in the incubation stage, although at least one had small chicks. The only other nesting sites reported for this species in Panama have been smaller colonies in mangroves near the Pacific coast (10 nests) and near Río Bayano (3 nests) (Angehr and Kushlan 2007).

Neotropic Cormorants were first noted nesting in Lago Bayano, at a small colony in dead trees near Isla Majé at the western end of the lake, in late May 1978 (GRA pers. obs.), only 2 yr after the creation of the reservoir. On a survey between 20 and 22 March 1999, Araúz and Gorrichátgui (2000b) found a colony of about 50 nests, with nearly grown chicks, near the western end of the lake (about 30 km west of the colony we found). They estimated that 200 cormorants were present at the colony, and a total of 500 cormorants (including those at the colony) in the western part of the lake as a whole. The main nesting areas for this species in Panama are on offshore islands and in mangroves around the Gulf of Panama, where Angehr and Kushlan (2007) found 3,649 nests.

It was surprising not to have found significant nesting by other species of herons or of Wood Storks at Lago Bayano. Such a colony might have been missed, or perhaps they nest on a different annual schedule than expected. Given the numbers of birds observed foraging, it remains clear that, whether it supports nesting or not, the lake is one of the more important areas for colonial waterbirds in Panama. Lago Bayano was considered a Nationally Important Bird Area by Angehr (2003).

Even more surprising was not finding any waterbird colonies

Table 3. Comparison of seabird and other colonial waterbird nesting populations (expressed as number of nests) in Panama on the Pacific coast (Gulf of Panama and Gulf of Chiriquí), Caribbean coast, and Lago Bayano.

Species	Gulf of Panama[a]	Gulf of Chiriquí[b]	Caribbean Coast[c]	Lago Bayano[c]
Brown Noddy (*Anous stolidus*)	50			
Sooty Tern (*Onychoprion fuscatus*)	3,000			
Bridled Tern (*O. anaethetus*)	50	16		
Red-billed Tropicbird			10	
Audubon's Shearwater			200	
Wood Stork		50		
Magnificent Frigatebird (*Fregata magnificens*)	2,216	640		
Blue-footed Booby (*Sula nebouxii*)	281			
Brown Booby	233	2,445	277	
Neotropic Cormorant	3,649			53
Brown Pelican	4,877	466		
Cocoi Heron	13			33
Great Egret	1,366	199		2
Snowy Egret	175			
Tricolored Heron	101			
Cattle Egret	6,262	170		
Black-crowned Night-Heron (*Nycticorax nycticorax*)	509			
Yellow-crowned Night-Heron (*Nyctanassa violacea*)	173			
White Ibis	2,756			
Glossy Ibis	200			
Total	**25,911**	**3,986**	**487**	**88**

[a]Angehr and Kushlan (2007)
[b]Angehr *et al.* (2014)
[c]This paper

in the extensive wetlands of the Caribbean coast, despite very complete aerial coverage. The swamps and marshes were well flooded, and many seemingly appropriate nesting sites were seen along the coast in June. White Ibis (including two hybrid White x Scarlet Ibis individuals) showing the beginning of breeding coloration were seen flying to night roosts in April, yet no colony was found in the same area 2 months later despite intensive examination; and in fact no White Ibis were seen. No nesting of colonial waterbirds, other than seabirds, had been reported previously from the Caribbean coast. Our observations support the proposition that there are no nesting colonial wading birds there. Nor do sand-nesting colonial waterbirds such as gulls and terns nest in the region, as these are known to occur only in winter (Table 2). Although the absence of these wintering species in June is understandable, that is not necessarily the case for other colonially nesting waterbird species, which we found in numbers at Lago Bayano, only about 20 km away.

Admittedly, counts of birds from boats in April and aircraft in June were not very comparable, even when rectified by a measure of effort (i.e., linear distance). Given that aerial surveys cover the entire potential habitat comprehensively, it would be expected that our aerial surveys in June would have much higher chances of observing birds compared to the ground surveys in April, and so any comparison should favor the summer data. Yet over the complete June aerial survey along the entire coast, only a few colonial waterbirds were observed. The overall impression from the survey, which was not contradicted by the data (Table 2), was that wading birds were generally absent from the coast in summer. It would appear that many of the birds (clearly the terns and gulls, which do not nest in Panama) observed in April were wintering birds that had departed by June.

The paucity of nesting colonial waterbirds and of non-nesting colonial waterbirds on the Panamanian Caribbean coast in summer is in stark contrast to the situation on the Pacific coast (Table 3). Whereas seabird and other colonial waterbird nesting populations on the Pacific coast totaled nearly 30,000 pairs, the population sizes are two orders of magnitude less on the Caribbean coast. Whereas 18 species nested on the Pacific coast, only 3 nested on the Caribbean coast. We previously showed that the Gulf of Panama and Gulf of Chiriquí have exceptional populations of nesting seabirds and other colonial waterbirds (Angehr and Kushlan 2007, Angehr *et al.* 2014). However, in the present study we found that seabird nesting along the Caribbean coast is relatively circumscribed, and nesting of colonial wading birds appears to be non-existent. The contrasts between coasts are likely attributable to the availability of food resources. The Gulf of Panama is endowed with significant upwelling of deep, cool Pacific waters generated by easterly spring and summer winds that pass between a gap in the mountain ranges (not by coincidence the location of the Panama Canal) (Jackson and D'Croz

1997). Along these lines, the Gulf of Chiriquí experiences reduced upwelling in contrast with the Gulf of Panama due to the blocking of easterly winds by the mountain ranges (Jackson and D'Croz 1997), and we found fewer than one-fifth the number of nesting birds along the Gulf of Chiriquí. The Caribbean experiences no upwelling, despite the strong easterly winds, principally because the ocean is relatively warm and its deep waters are unproductive. Reduced seabird nesting on the Caribbean side of Panama relative to the Pacific side supports the understanding of the Caribbean as a relatively unproductive region with respect to seabird nesting.

These observations of the effect of differing oceanographic conditions on seabird nesting suggest one reason why other colonial waterbirds do not nest along the coast and in coastal wetlands, yet do nest on the Pacific coast (Table 3). Another likely factor is tidal amplitude. The 3–5 m tidal range on the Pacific exposes substantially more feeding areas and provides a greater diurnal opportunity to access prey concentrated by falling waters (Morrison *et al.* 1998) than does the 0.6 m tide on the Caribbean side.

The limited use and lack of nesting in interior wetlands of the Caribbean coast, however, cannot be explained by the coastal processes of upwelling and tidal amplitude alone. Regional climate may be a factor as well, particularly the high, near year-round rainfall. Given the high regional rainfall, these wetlands are flooded year-round, likely experiencing little in the way of seasonal fluctuations in water depth or coverage. Wading birds in many tropical wetlands tend to nest during the dry season, when falling water levels concentrate fish and other aquatic prey in densities sufficient to provide relatively efficient foraging to support nesting (Kushlan 1978, 1986). It may be that the prey base made available by a limited seasonal pulse of flooding and receding water depths may be insufficient for nesting, but is sufficient to meet wintering requirements.

Supporting this argument is the presence of herons nesting and other wading birds feeding in Lago Bayano, a few dozen kilometers inland from the coast. They were feeding at sites along the edge of the reservoir experiencing water level recession, which concentrated fish and other prey, making them available to foraging birds. The water level in this lake rises and falls regularly through the year with variation in rainfall (being on the Pacific slope) and water demand for hydropower. The presence in the lake of foraging Wood Storks, a species highly dependent on falling waters to concentrate prey (Ogden *et al.* 1976), supports the notion that the presence of variable water levels in Lago Bayano compared with more stable water levels on the coastal plain wetlands may help explain the lack of nesting we observed for colonial wading birds along the Caribbean coast.

This is not to say that these habitats are unimportant to colonial waterbirds. The tropicbird, shearwater, and even the booby colonies make significant contributions to Caribbean total populations. Lago Bayano is clearly one of the most important wading bird habitats in Panama and supports the largest colonies of Cocoi Herons yet reported in Panama. The Caribbean coast and its inland wetlands appear to support significant numbers of wintering birds, likely from both North America and South America. For this reason alone, they are important areas for waterbirds in Panama.

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