

Seabird and Colonial Wading Bird Nesting in the Gulf of Panama

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Abstract.—The Gulf of Panama is a highly productive marine ecosystem at the southern edge of North America. Although the Gulf's aquatic bird populations have been remarked upon by ornithologists for over 50 years, nesting populations have been neither systematically studied nor completely characterized. In 2005 and 2006, the entire Gulf of Panama was inventoried to document the nesting status of seabirds and other colonial waterbirds. Over 50,000 birds of 20 species nesting at 57 sites were documented. Seabirds nested during the dry season, the period of oceanographic upwelling. Coastal colonial waterbirds nested at the end of the dry season and in the early wet season, when inland feeding habitats were optimal. Brown Pelicans (*Pelecanus occidentalis*) were the most numerous seabird with over 4,800 nests and 10,000 individuals counted. Over 3,600 Neotropic Cormorant (*Phalacrocorax brasilianus*) nests and over 2,200 Magnificent Frigatebird (*Fregata magnificens*) nests were documented. Cattle Egrets (*Butor ibis*) were the most abundant colonial wading birds, followed by Great Egrets (*Ardea alba*). Great Egrets were the first wading birds to nest, Cattle Egrets the last. Seven sites contained over 1,000 nests. Colony locations and numbers differed markedly from the historic literature. Some historic information is erroneous, but other differences reflect changes in distribution. More nesting Brown Pelicans and Sooty Terns (*Sterna fuscata*) and fewer Neotropic Cormorants were found than expected from the literature. New sites documented included some of global or regional conservation importance. This paper presents the first breeding records for Panama of Little Blue Heron (*Egretta caerulea*), Glossy Ibis (*Plegadis falcinellus*), and Bridled Tern (*Sterna anaethetus*), and third record for Cooi Heron (*Ardea cocoi*). There is no evidence for long-term declines of seabirds or colonial wading birds in the Gulf of Panama. Populations reaching conservation thresholds globally or biogeographically include Brown Pelican, Bare-throated Tiger-Heron (*Tigrisoma mexicanum*), White Ibis (*Eudocimus albus*), Glossy Ibis, and Bridled Tern. The Black-crowned Night-Heron (*Nycticorax nycticorax*) exceeded conservation thresholds for Central America. Six new sites of global importance for bird conservation were identified and the continued importance of another site confirmed. The continued health of the waterbird populations of Panama will depend on environmental education and protection of important colony sites from disturbance and development. *Received: 29 September 2006, accepted 25 May 2007.*

Key words.—Bay of Panama, booby, colonial wading birds, colonial waterbirds, colonies, cormorant, distribution, egret, frigatebird, Gulf of Panama, heron, ibis, Important Bird Areas, Panama, Pearl Islands, pelican, populations, Ramsar, seabirds, tern.

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Lying at the cross-roads of much of the New World's avifauna and supporting a number of racially distinctive birds on its many isolated islands, the Gulf of Panama has played an important role in ornithological history. Despite a half-century of recognition of its biological and conservation importance, the Gulf's nesting aquatic bird populations have remained surprisingly little documented. There has never been a comprehensive survey of seabird and colonial waterbird nesting sites, nor much information at all along the coast or on near shore islands. The best known aquatic birds of the Gulf of Panama are the migratory shorebirds, a million or more of which use the upper Bay of Panama annually (Morrison *et al.* 1998; Watts

1998; Angehr 2003; Buehler *et al.* 2004). As a result this area is considered a Wetland of International Importance under the Ramsar Convention, a component of the Western Hemisphere Shorebird Reserve Network, and a globally Important Bird Area.

Knowledge of other aquatic birds is another matter. Incidental observations on seabirds and colonial waterbirds were made as part of general avifaunal studies by Bovallius in the Pearl Islands in 1882 (Rendahl 1920), Brown in the Pearls in 1900 and 1904 (Bangs 1901; Thayer and Bangs 1905), Wetmore in various places from 1944-1963 (Wetmore 1946, 1952, 1965; Olson 1997), Butler as part of coastal shorebird surveys (Butler *et al.* 1992, 1998), and Angehr (2003) as part of his

Important Bird Area studies in 2000. Ridgely, Delgado, and Angehr also summarized aspects of existing nesting site information (Delgado 1985; Ridgely and Gwynne 1989; Angehr 2003). Angehr determined 49 sites in Panama to be of global importance to bird conservation and 39 sites to be of national importance. Birds at sea have been surveyed by Murphy in 1925, 1944, and 1956 (Murphy 1936, 1944a, b, c, 1956; Wetmore 1965), Robins (1958) in July 1957, Loftin (1991) in 1968-1969, and Spear and Ainly (1999). The best known waterbird species is Brown Pelican (*Pelecanus occidentalis*), especially those nesting in the Taboga island group (Maridueña 1979; Montgomery 1982; Montgomery and Martínez 1984; Martínez 1981, 1983, 1984; Daguerra 2000). Batista (1981) censused pelicans at sea in the Pearls during the breeding season. Few of these data documented actual breeding numbers. Other seabirds and colonial wading birds have been far less studied (Villalaz 1987; Tejera 1989).

The purpose of the present study was to delineate definitively the status and distribution of seabirds and other colonial waterbirds of the Gulf of Panama. This study was the first complete census in the Gulf and

adjacent shores, determining breeding sites, breeding numbers, and estimating overall nesting population sizes. The study reports new records of nesting species for Panama, identifies sites of global and national importance for conservation, compares these findings to the literature, and evaluates implications of these findings.

STUDY AREA

The study area was the Gulf of Panama inside a line from Punta Mala in Los Santos Province to Punta Garachiné in Darién Province, plus the Islas Frailes just to the south of Punta Mala. The study area was divided into the following subregions: 1) eastern Azuero Peninsula; 2) Parita Bay; 3) western Bay of Panama from Chame Bay to the Panama Canal, including the Otoque and Taboga island groups; 4) eastern Bay of Panama from the Panama Canal to Punta San Lorenzo; 5) Gulf of San Miguel from Punta San Lorenzo to Punta Garachiné, extending inland as far as the confluence of the Ríos Tuira and Balsas; and 6) the Pearl Islands (Fig. 1). The study included offshore waters within the Gulf, near shore and offshore islands, and the coastline including rivers flowing into the Gulf and their associated marshes and swamps. Habitats included marshes and mangrove swamps, shallow bays, sandy beaches, rocky shores, intertidal mud flats, and offshore islands, salinas, wet pastures, shrimp farms, and coastal areas next to Panama City and other built-up areas.

The oceanography of the Gulf of Panama is key to understanding its bird communities. Semi-diurnal tides on

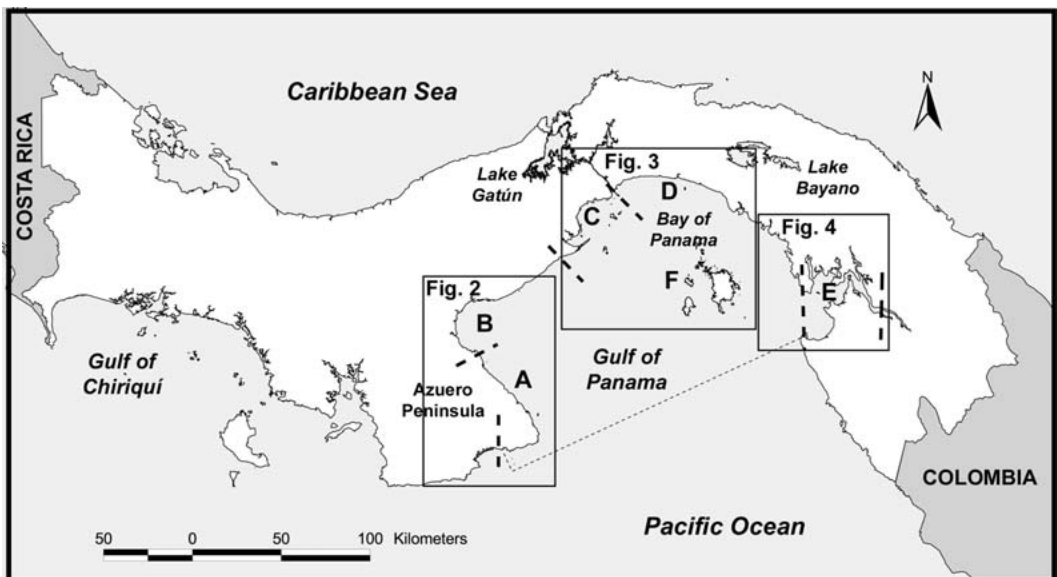


Figure 1. Panama. Survey area boundary indicated by a dotted line, and the boundaries between subregions by dashed lines. Subregions: A. eastern Azuero Peninsula; B. Parita Bay; C. western Bay of Panama; D. eastern Bay of Panama; E. Gulf of San Miguel; F. Pearl Islands. Nesting sites in the insets are shown in Figures 2-4.

average flux five meters, peaking seasonally at over seven meters. Such tides expose enormous coastal mud flats abutting the mainland in the eastern and western Bay of Panama and in the Bay of Parita. In some places these extend out several km at low tide. Here and along outer shores and islands, sandy and rocky beaches and rocky bars are made available for bird foraging twice a day. The Gulf of Panama covers 12,880 km² and features a submarine valley running from the Río Bayano to the Pacific Ocean, deepening to the edge of the continental shelf (Delgado 1998). During the dry season, from late December through April, steady northeast trade winds blow across the Isthmus of Panama and push surface waters away from the coast, creating upwelling conditions by allowing colder nutrient-rich water to rise and support phytoplankton blooms. These blooms nourish large populations of Pacific Anchoveta (*Cetengraulis mysticetus*) and other small fishes, which tend to move toward shore in the Bay of Panama (Schaefer *et al.* 1958; Delgado 1998). Large fishes, especially Albacore (*Thunnus alalunga*) and Yellow-fin Tuna (*Thunnus albacares*), feed on these baitfish. Seabirds feed by diving and plunging onto the fish shoals, especially over tuna. As a result of the abundance of food, pelagic seabirds tend to nest on offshore islands in the mid to late dry season. Most colonial wading birds (herons and ibises), on the other hand, nest along the coast or near-shore islands starting towards the end of the dry season and early wet season. A massive inflow of freshwater from the Panama Canal occurs year round, providing foraging habitat along the Bay of Panama coast for colonial waterbirds and coastal seabirds, especially pelicans, cormorants, and boobies. Thus influenced by seasonal deep water upwelling and by fresh water inflow from rivers and the Panama Canal, the Gulf provides an extremely rich environment for waterbirds.

METHODS

A complete inventory was made of waterbirds along shores, islands, and coastal wetlands of the Gulf of Panama in 2005 and 2006. Survey periods were chosen to encompass the early and later parts of the nesting seasons of seabirds, the early parts of the nesting season of terns, and most of the nesting season of colonial wading birds. Aerial surveys were conducted on 17-20 April and 2-27 July 2005, flying a Cessna 172 over 1,900 km at altitudes below 300 m, covering the entirety of the Gulf of Panama and adjacent wetlands. All previously-known nesting sites were over-flown, as were all islands and all coastal streams. All islands within the Gulf of Panama more than five kilometers offshore were visited by boat. We counted the numbers of nests from the boat, from the ground, or, for those colonies not otherwise accessible, from the airplane. Foraging and roosting birds also were tallied from the air or boat. We visited colony sites by boat or ground on 20-30 April 2005, 18-19 June 2005, 28-30 July 2005, and 20-25 February 2006. Some sites in the Gulf of San Miguel were visited by C. Montañez on 15-17 August 2006.

Nesting sites, nesting populations, and total populations are reported. Nesting sites were determined from the inventory results. The greatest number of nests counted at each site during the April-August period was used to estimate the breeding population. Data from February, the beginning of a new nesting cycle for seabirds was used for comparative purposes. Total populations for calculating conservation population thresh-

olds were estimated conservatively as three times the number of nests, that is, a pair plus one young (Delaney and Scott 2002). A main goal of our study was to identify or confirm sites of importance to conservation of congregatory waterbirds in Panama, compared to the results of Angehr (2003). Criteria for identification of global IBAs included the presence of >1% of a biogeographic population of a congregatory waterbird species, or >1% of the global population of a seabird population, and for identification of national IBAs the presence of >1% of the national population of a congregatory waterbird or seabird species. Under the definitions used by BirdLife International, of the species nesting in Panama shearwaters, boobies, tropicbirds, and frigatebirds are considered to be seabirds, and the remainder waterbirds. Total population figures from Kushlan *et al.* (2002) and BirdLife International and Conservation International (2005) were used to calculate 1% levels for global or biogeographic populations. Reference populations for species reaching the 1% threshold in our study area include Brown Pelican (290,000 global, 175,000 neotropical), Bare-throated Tiger-Heron (*Tigrisoma mexicanum*) (10,000 global and neotropical), White Ibis (*Eudocimus albus*) (100,000 neotropical), Glossy Ibis (*Plegadis falcinellus*) (10,500 neotropical), and Bridled Tern (*Sterna anaethetus*) (15,500 neotropical). In addition, Black-crowned Night-Heron (*Nycticorax nycticorax*) exceeded the 1% level for Central America (10,000).

RESULTS

Colony Sites

Seabirds and other colonial waterbirds nested at 57 sites (Table 1, Figs. 2-4). Most colonies were in the Pearl Islands and the western Bay of Panama (19 and 13, respectively). The largest was at the Islas Frailes del Sur off the coast of the Azuero, with over 3,100 nests of a total of three species. Other sites with more than 1,000 combined nests were Isla Pacheca (with over 2,100 nests), Chepo, and Islas Pedro González, Iguana, Pelado, Gallo, Taborcillo, and de Coco. Four sites each held over 1,000 nesting pairs of a species: Sooty Terns (*Sterna fuscata*) on Islas Frailes del Sur; Magnificent Frigatebirds (*Fregata magnificens*) on Isla Iguana; Brown Pelicans on Isla Pedro González; and Neotropical Cormorants (*Phalacrocorax brasilianus*) on Islas Pacheca and de Coco. Pelagic terns and frigatebirds nested mainly along the southern Azuero coast. Most colonial wading birds (herons and ibises) nested in coastal wetlands or on near-shore islands along the Bay of Panama. Cormorants, pelicans and boobies, as well as some herons and ibises,

Table 1. (Continued) Seabird and colonial wading bird nesting sites in the study area. Column 1: code numbers for sites are keyed to Figs. 2-4. Column 2: coordinates are given to the nearest minute for the approximate center of the colony or island. Column 3: principal habitats used by nesting birds at each site: R = rocks and cliffs, S = scrub and herbaceous vegetation; W = freshwater wetland; F = tall non-mangrove forest; M = mangroves. Figures given for each species are the number of nests or pairs counted at the site. Of the species recorded breeding on our surveys, Anhinga, Little Blue Heron, and Boat-billed Heron are not included.

Code	Sites	Coordinates	Habitats	Blue-footed Booby	Brown Booby	Brown Pelican	Neotropic Cormorant	Magnificent Frigatebird	Cocoi Heron	Great Egret	Snowy Egret	Tricolored Heron	Cattle Egret	Black-crowned Night Heron	Yellow-crowned Night Heron	White Ibis	Glossy Ibis	Bridled Tern	Sooty Tern	Brown Noddy	Total
13	Isla Estivá	08°35'03"N 079°36'45"W	R	29																	29
14	Isla Gallo	08°48'26"N 079°44'44"W	S							30			1,100								1,130
15	Isla Cocoví	08°51'49"N 079°35'39"W	S							2			11	13	47	39					112
16	Isla Tortolita	08°51'44"N 079°33'26"W	S							63			87	15		49					214
17	Isla Changamé	08°53'29"N 079°32'58"W	S							5	55	4	14	34	21	85					218
18	Isla Chamá	08°44'13"N 079°34'42"W	S/R	25		62															87
19	Isla Taboga	08°47'17"N 079°33'26"W	F			578				52											630
20	Isla Uravá	08°46'29"N 079°32'04"W	F			145	347			28											520
21	Isla Taboguilla	08°48'26"N 079°30'58"W	F			95				1				4	16						116
22	Farallón de Taboguilla	08°47'439"N 079°34'52"W	R		7									6							13
Eastern Bay of Panama																					
23	Río Tranca	09°05'51"N 079°08'54"W	M						3												3
24	Estero Brinco	09°05'09"N 079°08'18"W	M				700			40											740
25	Chepo	09°09'52"N 079°06'56"W	W										1,900			20					1,920
26	Chinina	98°58'16"N 078°59'43"W	W										500								500

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27	Pasiga	08°1'20"N 078°54'38"W	W										100								100
28	Ensenada de Corral	08°50'31"N 078°51'22"W	M						10	600											610
29	Isla Pelado	08°37'59"N 078°42'17"W	S/R		10							43	10			1,160					1,223
30	Isla Majé	08°38'14"N 078°37'55"W	F			679				7											686
31	Isla Majagual	08°39'34"N 078°38'01"W	F			204				9					8						221
32	Isla Pajaros Norte	08°32'40"N 078°32'47"W	F			79				10	3				3	113					208
33	Isla Pajaros Sur	08°31'58"N 078°32'18"W	F			69															69
Gulf of San Miguel																					
34	Isla Josepha	08°22'42"N 078°21'57"W	F/S							5	60		20		5	120					210
38	Isleta El Cedro	08°20'15"N 078°12'48"W	S													100					100
36	Isla Estero Pavón	08°26'09"N 078°11'06"W	F/S							20						400					420
35	Taimati	08°04'39"N 078°14'44"W	W													100					100
34	Quebrada Celorito	08°04'25"N 078°19'47"W	M							55											55
Pearl Islands																					
39	Isla Pachequilla	08°40'14"N 079°3'48"W	F/R	167	55	207															429

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40	Isla Pacheca	08°39'57"N 079°03'19"W	F/R	44		303	1,521	314		3				4	4						2,193
41	Isla Bédico Norte	08°38'52"N 079°03'32"W	S		1																1
42	Isla Bartolomé	08°40'33"N 079°02'10"W	S											51		6					57
43	Isletilla Culo de Mono	08°31'208"N 079°03'41"W	S							1	4	1		2	4	8					20
44	Isletilla del Pero	08°28'56"N 079°03'19"W	S								4			1	9	6					20
45	Isla Señora	08°26'41"N 079°06'29"W	F			124				2											126
46	Isla Pedro González	08°24'01"N 079°06'23"W	F			1,265	56														1,321
47	Isla de Coco	08°21'49"N 079°00'44"W	F				1,025														1,025
48	Isla Caña Brava	08°20'57"N 079°00'02"W	S			5									2	78					85
49	Isla Moreno	08°20'08"N 079°00'25"W	S			4															4
50	Isla Aposentro	08°20'11"N 078°59'15"W	R		5																5
51	Isla San Pablo	08°27'339"N 078°51'14"W	F			197				3											200
52	Isleta Espiritu Santo	08°25'08"N 078°50'45"W	S							1	5	5		3	5	104					123
53	Isla Elephante	08°23'46"N 078°48'10"W	S	4	43																47
54	Isla Monte	08°19'38"N 078°48'20"W	S		4																4

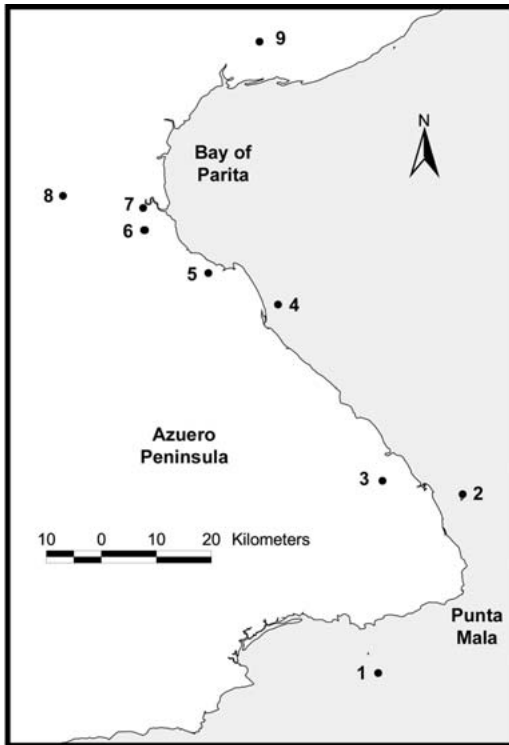


Figure 2. Waterbird nesting sites in the eastern Azuero Peninsula and Parita Bay. 2005-2006. See Table 1 for code numbers.

nested in the Pearl Islands and on the Taboga, Otoque-Boná, and Majé-Majagual groups.

Nesting Populations

Overall 25,911 nests were found, accounting for almost 52,000 seabirds and other colonial waterbirds nesting in and near the Gulf of Panama. The most abundant species was Cattle Egret (*Bubulcus ibis*); the next most numerous in order being Brown Pelican, Neotropic Cormorant, and Sooty Tern.

Blue-footed Boobies (*Sula nebouxi*) nested in very small numbers at five sites, on cliffs and small rocky stacks. Interestingly, no Blue-footed Boobies were found nesting during February 2006, even at sites where they had bred in 2005. Although commonly seen roosting on the outer islands of the Pearls, Blue-footed Boobies are relatively rare, scattered, and perhaps irregular as breeders.

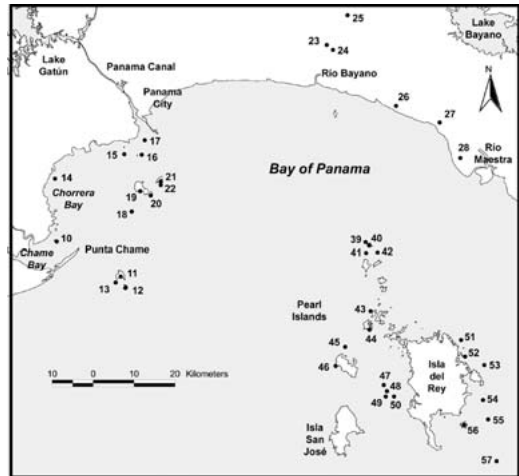


Figure 3. Waterbird nesting sites in the western Bay of Panama, eastern Bay of Panama (part), and Pearl Islands 2005-2006. See Table 1 for code numbers.

Brown Boobies (*Sula leucogaster*) nested in similar sites as Blue-footed Boobies but were more widely distributed, at eleven colony sites in April. The following February, many non-breeding birds were found, including many young from the previous year. Male Brown Boobies in the western Pacific are distinctive in having silvery heads, a character that is very obvious in the Gulf birds during the early nesting period.

Brown Pelicans were strikingly abundant in the Gulf. Brown Pelicans nested at 18 sites supporting 4,877 nests. Additionally, in April 2005, 10,003 individuals were counted away from nesting sites. Since nearly all nests had an adult bird in attendance, adding the totals suggest that the total number of adult birds was about 14,000. The largest concentrations were on Islas Pedro González and Señora in the Pearl Islands (1,389 nests), Isla Majé and nearby islands (Majagual and Pajaros Norte and Sur) in the eastern Bay of Panama (1,031 nests), and the Taboga group (including Taboga, Uravá, Taboguila, and Chamá) in the western Bay of Panama (880 nests). Most sites were on large to medium-sized, well-forested islands. In late June all nesting in the Pearl Islands had terminated. But nesting began again in February, when birds in all nesting stages from eggs through very large young were found, suggesting the

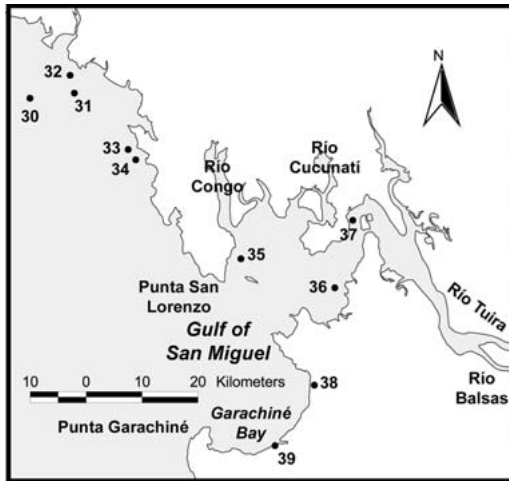


Figure 4. Waterbird nesting sites in the eastern Bay of Panama (part) and Gulf of San Miguel, 2005-2006. See Table 1 for code numbers.

extreme prolongation of the nesting season in Panama. Greatest numbers of foraging and roosting pelicans were observed in the Bay of Panama, especially near the Panama Canal and Panama City, where they no doubt benefit from the nutrient-rich waters.

Neotropical Cormorants were also abundant throughout the Gulf. Over 3,600 nests were found at five sites in 2005. These birds occurred by the hundreds and even thousands in some locales. Over 1,600 were counted feeding and roosting along the eastern Bay of Panama including along the shores of Panama City. Cormorants used various nesting sites, including large and small forested offshore islands and coastal mangroves. Colonies at two sites, Islas Pacheca and de Coco, totaled over 1,000 nests each. Nesting had finished by June but was beginning again in February 2006. Nesting at that time had not begun on Isla Pacheca but was underway in Islas de Coco and Moreno, the latter a site where they had not nested in 2005. Even so early in the season in 2006, 2380 nests were on these two islands alone. These data suggest that the size and location of cormorant colonies may differ from year to year.

A few Anhinga (*Anhinga anhinga*) nests were found at colonies in the Parita Bay region in July, at Laguna de Cerro Negro and Ciénaga del Rey. Eight females were seen at

the Laguna de Pocrí on 24 April, and males and females there and at Chitré Airport in July, but no nests were found at these sites.

Over 2,000 Magnificent Frigatebird (*Fregata magnificens*) nests were found at four sites, the largest at Isla Iguana along the southern Azuero Coast. On Isla Iguana, most nests were in tall grass and scrub, but elsewhere they were in trees. Frigatebirds are a common sight throughout the Gulf, especially feeding in association with gulls and pelicans in the Bay of Panama, terns on the southern Azuero coast, and with pelicans and herons on inland freshwater ponds in the eastern Azuero.

Cocoi Heron (*Ardea cocoi*) has only recently been documented to nest in Panama, extending to Central America the range of this South American species. Three Cocoi Heron nests were found in April and ten nests in July at Ensenada de Corral, and also three nests in August at Río Tranca near the Río Bayano, both sites in the eastern Bay of Panama. At Ensenada de Corral the nests were in the tops of tall mangroves within the large colony of Great Egret (*Ardea alba*) at this site, while the nests at Estero Tranca were not associated with other species.

Great Egret was a common bird throughout the Gulf of Panama, the second most abundant heron after Cattle Egret. Within the Bay of Panama, near the city, they frequent mudflats during low tide, while nesting and roosting on the offshore islands of Changamé and Taboga. Great Egrets occurred year-round off the city of Panama: over 50 were counted along the shore there in April and overall over 250 birds were counted away from nesting sites. Great Egrets (along with Cocoi Herons) were clearly the earliest of the herons to nest, starting in February in the Pearl Islands and toward the end of the dry season near shore. Great Egrets fed not only in mangroves and along mudflats but also not uncommonly in the surf along sandy and on rocky beaches. They nested in small numbers on many small islands within the Gulf and in larger numbers in mangroves and inland wetlands; 1,366 nests were found at 27 sites. The largest colony, 600 nests, was in an extensive area

of mangroves just west of the Ensenada de Corral, where the egrets occupied a line of tall trees along a river channel. The second largest colony, 180 nests, was at Ciénaga del Rey, a small marsh near Santa María, some 16 km inland along the Río Santa María in the Parita Bay region. Nesting was well underway during the April census, with most birds incubating or with small young. By July most birds had large young.

Snowy Egrets (*Egretta thula*) were thinly but widely dispersed along the coast. They were found nesting in small numbers at eight sites, all but one (Chitré Airport) on small islands, either near-shore or in the Pearl Islands. The largest colony was 55 nests on Isla Changamé.

Adults and young of the year Little Blue Herons (*Egretta caerulea*) were present along the eastern Azuero coast and Parita Bay during the April and June surveys. On 29 July, we observed a large juvenile perched in a tree begging from an adult at the El Rosario colony. At dusk, five adults and five juveniles changing into adult plumage flew in to roost in the colony. These observations document the nesting of the species in the area.

Tricolored Herons (*Egretta tricolor*) were common in small numbers all along the coast. They were found nesting at seven sites, all but one of them (Laguna de Cerro Negro) on small nearshore islands.

Cattle Egrets (*Bubulcus ibis*) were common throughout the region, especially in the cattle-raising and agricultural areas inland of the eastern Azuero coast. This was the most numerous waterbird, with over 6,200 nests recorded at 17 sites. Cattle Egrets were only beginning to nest in April but were fully nesting in July. Most sites were in small shallow freshwater ponds or marshes, including the largest colony at Chepo, 19 km inland, with 1,900 nests. Some colonies were on near-shore islands, including the second largest colony at Isla Gallo, 1,100 nests, 1.3 km offshore. The farthest offshore they were observed nesting was a surprising 9 km at Isla Pelado.

Black-crowned Night Herons nested at 14 sites, usually in small numbers at each. The exception was Isla Taborcillo, where 349 nests were found in April. Birds appeared to

leave this site soon after breeding, since only about ten adults and 20 juveniles were there by late July. Most sites were on small near-shore or offshore islands, although a few were in freshwater marshes.

Yellow-crowned Night Herons (*Nyctinassa violacea*) fed commonly on the mud flats near Panama City and may be one of the most abundant herons in the area. They bred in tight groups, and this species was found nesting at 13 sites, all on small near-shore or offshore islands. The largest colonies were at Islas Taborcillo, with 49 nests, and Cocoví, with 47. Like Black-crowned Night-Herons, they appeared to leave Taborcillo after breeding, since none were found there in July.

Two juvenile and two adult Boat-billed Herons (*Cochlearius cochlearius*) were seen at Cenegón del Mangle, where nesting had previously been documented by F. Delgado (pers. comm.).

White Ibis was a common bird, especially in the eastern and western Bay of Panama and along the eastern Azuero Coast, but also on many small islands. Nesting was beginning in the western Bay of Panama during April, but was already underway in the eastern Bay. Most nesting had finished by July. They were found nesting at 17 sites, the largest, with 1,160 nests, being on Isla Pelado, a rocky island 9 km off the mainland. Otherwise they nested in colonies of 10s to low 100s of nests. Ibises very typically nested on very small islets covered with cactus, as well as in the more usual freshwater wetlands.

Glossy Ibis, 450 adults, in near-breeding condition plumage were seen in rice fields near Santa María in April. Breeding was clearly documented for the site as on 29 July we observed and photographed a large nestling at the Ciénaga del Rey colony. Glossy Ibis remained common at the colony site and widespread in rice fields for several km surrounding this colony in late July.

Bridled Terns nested on the tops of rock cliffs of the larger island of Frailes del Sur in April. About 50 pairs were found occupying niches suitable for nesting and some also were observed copulating.

A large colony of Sooty Terns (*Sterna fuscata*), 3,000 nests, occupied the bare flat

rocky tops of both the larger and the smaller islands of Frailes del Sur in April. Visible nests appeared to be at egg stage in April.

About 50 Brown Noddies (*Anous stolidus*) were found nesting in niches below the cliff tops around the north end of the larger island of Frailes del Sur in April.

Incidental observations were made of several non-breeding seabird and waterbird species during the study. One Great Blue Heron (*Ardea herodias*) was seen on 23 April at Playa Venado on the southern Azuero coast, and another at Punta Chame on 30 July. Bare-throated Tiger-Herons were frequently observed foraging along beaches in the Pearl Islands, and two nests were found in February on Isla San José. Densities in the archipelago may exceed a pair for every two kilometers of coastline, suggesting a total population of over 350 individuals. Two foraging groups of Roseate Spoonbills (*Platalea ajaja*) were seen, containing about a dozen adults each, in shallow ponds just east of the mouth of the Río Tocumen and just north of the mouth of the Río Chico 24-27 July. A single individual spoonbill was seen near the mouth of the Río Congo in Darién on 7 July. A nesting colony may exist in the mangroves at the mouth of the Río Bayano. A group of 40 Wood Storks (*Mycteria americana*) were observed foraging in a small pond on the Río Salado at the head of the Estero de Mensabé in the eastern Azuero on 19 April. On 27 July three groups, of about 30 storks each, were observed roosting at various sites around the edge of the mangroves at the mouth of the Río Bayano. Laughing Gulls (*Larus atricilla*) (1,740 individuals) were recorded along the coast during surveys. A flock of more than 200 Common Terns (*Sterna hirundo*) was seen feeding between Islas Mogo Mogo and Casaya in the Pearl Islands on 27 April.

DISCUSSION

Distribution of Nesting Waterbirds in Panama

Beyond the Gulf of Panama, seabirds and other waterbirds nest in Panama in several areas: along the Caribbean coast, inland,

and in the Pacific in the Gulf of Chirique. Birds nesting in Panama only on the Caribbean coast include Red-billed Tropicbird (*Phaethon aetherus*) and Audubon's Shearwater (*Puffinus lherminieri*) at one site each; Brown Boobies nest at three Caribbean sites (Griscom 1928; Peters 1931; Wetmore 1959a, b, 1965; Angehr 2003). Surprisingly, there are no known breeding sites for colonial wading birds anywhere on the Caribbean slope of Panama. The reason for the scarcity of seabirds along the Caribbean coast is that trade winds blow toward shore and prevent upwelling. A few colonial waterbirds nest in inland Panama, notably Neotropic Cormorant and Cocoli Heron at the Lake Bayano reservoir in eastern Pacific Panama, (Ridgely and Gwynne 1989; Araúz and Gorachátegui 2000). Anhinga and Boat-billed Heron also nest inland in hard-to-find monospecific colonies. In the Gulf of Chiriquí, like the Caribbean, upwelling is restricted, because mountains block the trade winds. Seabirds known to nest in the Gulf of Chiriquí are Brown Pelican, Magnificent Frigatebird and perhaps Brown Booby (Wetmore 1965; Ridgely and Gwynne 1989; Olson 1997). Anhinga, Great Egret, Cattle Egret, Black-crowned Night-Heron, Boat-billed Heron, Wood Stork and White Ibis also nest in the Gulf of Chiriquí (Delgado 1985; F. Delgado in Ridgely and Gwynne 1989; Angehr 2003; Jiménez and Aparicio 2002).

Due to the restricted nesting of seabirds elsewhere in Panama, the censuses reported in this paper, in the Gulf of Panama, appear to account for 95%-100% of the known populations of colonial waterbird species nesting in Panama, except those restricted to the Caribbean. That the Gulf of Panama supports the preponderance of waterbirds in Panama is due to a combination of its seasonal upwelling, inflow of extensive rivers and mangrove swamps, and the availability of foraging opportunities in agricultural areas, shrimp ponds, and salinas along the coast.

Inactive Sites

Several colony sites reported in the literature were not found to be active in this study.

These include *Islas Cangrejo* and *Saboga* in the Pearl Islands, *Farallón de Chirú*, *Peñón de la Honda* (also known as *Isla Villa*), and the *Río Pedasí*. On *Isla Cangrejo* (08°29'56"N, 078°57'16"W), 'several hundreds' of Magnificent Frigatebirds were reported breeding in 1882 (Rendahl 1920). If this did occur as reported, the site was evidently abandoned before 1960, as it was not reported by Wetmore on his visit to *Isla del Rey* that year nor found on surveys by Maridueña in 1979. On *Farallón de Chirú* (08°21'14"N, 080°06'41"W), Wetmore recorded pairs of Blue-footed Boobies, Brown Pelicans and Magnificent Frigatebirds in 1957 (Olson 1997), but we found no nesting. On *Peñón de la Honda*, off the eastern Azuero coast, Wetmore in 1957 found a colony of 75-100 pairs of Frigatebirds, as well as Brown Pelicans and Black-crowned Night-Herons (Olson 1997). By the mid 1980s, it seems that only Cattle Egrets and White Ibis nested there (Delgado 1985) and this study found only 20 Cattle Egrets nesting in July. The condition of these islands today appears to be similar to that described by Wetmore in 1957, so the reason for their abandonment is not obvious. However, *Cangrejo* and *Farallón de Chirú* are both close to towns (*San Miguel* and *Farallón*, respectively) and may have been subject to disturbance. A colony of Neotropic Cormorant, Great Egret, and Cattle Egret on the *Río Pedasí* (07°33'48"N, 080°01'45"W) (F. Delgado, pers. comm. in Angehr 2003) was not found by us. Nesting by boobies, cormorants, and frigatebirds was reported on *Saboga* (08°37'20"N, 079°03'40"W) but not *Pacheca* in 1904 (Thayer and Bangs 1905). However, given descriptions of a major colony on *Pacheca* in 1882 (Rendahl 1920) which still persists, and the lack of any evident reason for abandonment of *Saboga*, which retains extensive forest, we think it likely that the latter never supported a colony but was confused with *Pacheca* by Thayer and Bangs.

Priority Sites for Conservation

Many sites censused satisfy global or national criteria for Important Bird Areas for the conservation of seabirds or congregatory

waterbirds in Panama. These are discussed in geographical order below.

Along the Eastern Azuero Coast, the *Islas Frailes del Sur*, recognized as a national IBA by Angehr (2003), are of outstanding importance as the only breeding site for Bridled Tern and Brown Noddy in Panama, and for Sooty Tern in Panama or Central America. Its 3,000 nests make it the largest single waterbird or seabird colony in Panama. With a population of 150 individuals of Bridled Tern, the site supports one percent (within the range of error of our estimate) of the neotropical population and is of global importance. The islands are not legally protected and should become wildlife refuge, although it seems they are under little threat due to the difficulty of landing. *Isla Iguana* continues to hold the largest colony of Magnificent Frigatebird in Panama. It is protected as the *Isla Iguana Wildlife Refuge*.

Parita Bay holds several important sites. Although decreasing in size, *Cenegón del Mangle*, recognized as a national IBA by Angehr (2003), continues to be an important nesting site and is fortunately protected as a wildlife refuge. The newly found sites of *Ciénaga del Rey* and *Laguna de Cerro Negro* are on private land, as is the previously known *El Rosario* colony. *Ciénaga del Rey* and the area around it, with 450 Glossy Ibis, support 4.3% of the neotropical population and is of global importance. These sites may best be protected by working with landowners to ensure the sites are not drained and the colonies are not molested.

In the western Bay of Panama, *Isla Taborcillo* is of outstanding importance, containing the third-largest colony of White Ibis, 358 nests, and by far the largest colony, 349 nests, of Black-crowned Night-Herons—almost 70% of all the nests of the latter species we found on our surveys. For White Ibis, with 1,074 individuals, it exceeds one percent of the neotropical population, and for Black-crowned Night-Heron, with 1,047 individuals, the site exceeds one percent of the Central American population. It also had the most Tricolored Herons and Yellow-crowned Night-Herons, the third largest count of Snowy Egrets, and was used by three other

species as well. It was recognized as a national IBA by Angehr (2003), but now qualifies at the global level. A small tourist development, including a hotel and other attractions, has been built in the central part of the island. The heron colony, which occupies scrub at the island's southeastern end, is being managed as a private reserve, and entry into the colony and disturbance of the colony is prohibited by the owner (R. Hübner, A. Albrecht, pers. comm.). The greatest threat to the colony is sand-dredging offshore, the sand being used in construction. Maps from the 1960s indicate that the island, which is essentially a large sandbar, has been reduced from 40 ha at that time to only 25 ha today, most likely due to uncontrolled extraction of sand. Trees at the edge of the colony have been undermined by erosion. If sand extraction in the vicinity of the island is not controlled, it is likely this important site will not survive long.

In the Otoque group, Isla Boná, recognized as a national IBA by Angehr (2003) contains the second largest colony of Magnificent Frigatebirds in Panama and together with Otoque itself and Estivá is an important site for pelicans and boobies. Except for two small fishing villages on Otoque, the island remains well forested. Forested Boná and rocky Estivá are uninhabited and little altered. Although little threatened at present, the southern part of Otoque, where the pelican nesting area is located, together with Boná and Estivá, should be recognized as a national IBA and merit formal protection.

Although the size of its colonies has declined, the Taboga group remains the third-largest site for Brown Pelicans in Panama, and Uravá contains an important colony of Neotropical Cormorants. The Taboga Wildlife Refuge (including Uravá) and Taboguilla were recognized as global level IBAs, and Chamá as a national level IBA, by Angehr (2003). With a current population of 2,640 Brown Pelicans, the group has 1.5% of the neotropical population, and continues to be of global importance. (Taboguilla, however, no longer qualifies globally by itself, although Taboga-Uravá does.) There is small town that is a popular tourist destination on the north

side of Taboga, but the forested southern side and all of Uravá are contained in the Taboga Wildlife Refuge. The reserve is affected to some extent by fires set by iguana hunters, and garbage from the town has been dumped in part of it (Daguerra 2000), but the nesting area for pelicans is generally intact. There is a large fishmeal processing plant on Taboguilla, but the forest on the rest of the island is mainly intact. It would be worthwhile to incorporate the presently unprotected southern part of Taboguilla, Farallón de Taboguilla (a nesting site for boobies), and Chamá into the Taboga Wildlife Refuge.

Three small islands to just to the west of the Pacific entrance of the Panama Canal, Changamé (recognized as a national IBA by Angehr 2003), Tortolita, and Cocoví, contain small but diverse heron colonies, which together include 35% of all Snowy Egrets and 27% of all Yellow-crowned Night-Herons on our count, as well as five other species. Despite heavy marine and pleasure and fishing-boat traffic in the area, the colony on Changamé has existed since at least 1941 (Wetmore 1965). Protection would be warranted for Changamé and its neighboring islets, which should be incorporated in the IBA.

The upper Bay of Panama, extending from just east of Panama City to the Río Maestra, as has been noted before, is an area of global importance for migratory and wintering shorebirds (Angehr 2003). Several nearby sites are also critical for several species of colonial waterbirds. Isla Majé and the associated islands of Majagual and Pajaros Norte and Sur are in aggregate a globally important site for Brown Pelican, with a population of 3,093, or 1.7% of the neotropical population. Nearby Isla Pelado contained 43% of all the nesting White Ibis on our counts, as well as Brown Boobies. This is an intriguing colony site. It is as surprising that White Ibis and Cattle Egrets nest so far off shore as it is that Brown Boobies nest so close to the coast. The group as a whole had 1,273 White Ibis nests, or 3,819 individuals, totaling 3.8% of the neotropical population. These islands are jointly of global importance and well worthy of preservation as a wildlife refuge. The mangroves and mudflats

of the adjacent mainland, including the Ensenada de Corral with its major colony of Great Egret and Cooi Heron, were recognized as a global IBA for migratory shorebirds, the Chimán Wetlands, by Angehr (2003). The Río Bayano mangroves, recognized as a national IBA by Angehr (2003), contains the third-largest colony of Neotropic Cormorant in Panama at Estero Brinco. The upper Bay of Panama, with the incorporation of the Ensenada de Corral and the Río Bayano mangroves as well, was declared a Wetland of International Importance under the Ramsar Convention in 2003. Threats are many. It is likely not a coincidence that ibis have chosen small, distant Isla Pelado, covered by spiny plants, as a nesting site, suggesting that protection from human disturbance is hard to find in the region. Draining for agriculture has destroyed much of the freshwater wetlands surrounding the Bayano mangroves, and over-use of pesticides and agrochemicals in this area may also be a problem. Fortunately the colony at Ensenada de Corral is so inaccessible that at least at present it is little threatened.

The colony at Chepo, the third largest waterbird nesting site in Panama, was partially cleared in early 2006 by the local landowner (W. Adsett, pers. comm.). It remains to be seen how this will affect nesting in this colony. Although most of the birds were Cattle Egrets, a widespread and abundant species, this event illustrates the vulnerability of colonies on private land in that there are no regulations to protect them.

In the Gulf of San Miguel, Islas Josepha and Estero Pavón on the north side of the Gulf of San Miguel together contain 520 nests of White Ibis, or 22% of the Panama total, and with 1,560 individuals exceed 1.5% of the neotropical population of this species. The adjacent Congo and Cucunatí Estuary Mangroves were recognized as a potential IBA by Angehr (2003) on the basis of occurrence of migratory shorebirds, and inclusion of these nesting sites would confirm this area as a global-level IBA. Quebrada Celorito and Taimati lie within the Ensenada de Garachiné Wetlands IBA (Angehr 2003), a globally important site for migratory shorebirds.

The Pearl Islands in aggregate are of global importance for both Brown Pelican (14,142 individuals, or 8.2% of the neotropical population) and Bare-throated Tiger-Heron (>350 individuals, or >3.5% of the global population). The most important sites within the archipelago are discussed individually below.

Isla Pacheca is the single most important nesting site in the archipelago, supporting the highest total number of nests, 2,143, including the largest single colony of Neotropic Cormorants in Panama in 2005 as well as significant numbers of Brown Pelicans and Magnificent Frigatebirds. The island is privately owned, and the owner protects the forest and the birds. Pacheca, together with nearby Pachequilla and Bartolomé were recognized as a national IBA by Angehr (2003).

Pedro González and neighboring Señora currently have the single largest concentration of nesting Brown Pelicans in Panama. The population of 4,167 represents 2.4% of the neotropical population and is thus of global importance; the islands were recognized as national IBAs by Angehr (2003). The islands are privately owned, and there is a small fishing village on Pedro González. The forest on both islands has been extensively disturbed by shifting agriculture, and much of the coastal area is occupied by tall second growth. This does not seem to have been detrimental to nesting by pelicans, which often placed their nests in tall *Cecropia* and other second-growth trees. All nests on Pedro González were on the coast of the western half; this area and nearby Señora merit protection. Isla de Coco is the site of the second largest colony of Neotropical Cormorants in Panama (largest in the February 2006 survey). This small, forested island is uninhabited and does not appear to be under any immediate threat. Nonetheless it and nearby Islas Aposentro and Moreno merit protection as a reserve for cormorants and boobies. Isla San Telmo, which has the fourth largest colony of Brown Pelican in Panama, is partly owned by ANCON, Panama's largest non-governmental conservation organization. There are some buildings and other structures on the island which are not

currently in use, and the island is uninhabited and mostly forested. The site, which was recognized as a national IBA by Angehr (2003), deserves protection. Isla Galera, recognized as a national IBA by Angehr, is of importance as one of only five known colonies of Magnificent Frigatebird in Panama. It is uninhabited, little disturbed, and very scenic. Isla San Pablo contains four percent of Panama's nesting Brown Pelicans, and is also uninhabited and little disturbed. Although relatively few boobies were found on Islas Camote and Monte, recognized as a national IBA by Angehr (2003), they probably continue to nest there. Isla Elephante had 21% of the nesting Brown Boobies on our surveys. All these islands merit full protection.

The Pearl Islands are at present sparsely inhabited. Other than heavily-developed Isla Contadora, there are only a few fishing villages of a few hundred to a few thousand inhabitants each; most of the smaller islands are either uninhabited or have at most a few houses. There is substantial interest on the part of both the Panamanian government and private individuals in large-scale tourism development in the archipelago, so this benign situation is not expected to last. At present there are no officially protected areas in the archipelago, but proposals for the protection or conservation management of certain areas are currently being formulated (H. Guzmán, pers. comm.). Formal protection of the most sensitive sites in this globally important region is urgently needed.

Based on information from the present study, the following national-level IBAs identified in Angehr (2003) would not qualify for that status on the basis of presence of colonially nesting species: Pablo Arturo Barrios Wildlife Refuge (site of the former nesting colony on the Río Pedasí), Peñón de la Honda Wildlife Refuge (although it still qualifies for migratory shorebirds), Farallón de Chirú, Isla Saboga, and Isla Cangrejo.

Species Status

The status of Blue-footed Booby in Panama has been somewhat unclear in that they have reported only to have nested in small

numbers in several localities (Ridgely and Gwynne 1989). In 2005, we were able to confirm breeding on seven islands, three of which (Islas Estivá, Chamá, and Elephante) were not previously known. Although Wetmore (1965) reported the largest colony to be at Boná, in 2005 the largest concentration was at Pacheca and Pachequilla, whereas Boná had only twelve nests. Some previously reported (Farallón de Chirú, Peñón de la Honda, Monte) and suspected (Farallón de Taboguilla, Pacheca, Galera) nesting sites (Sturgis 1928; Wetmore 1965; Olson 1997; M. Allen, pers. comm. in Angehr 2003) were not active. In February 2006, we revisited most of the sites active in 2005, finding no nesting and few birds in high color. Our data together with historical information suggest why the status of Blue-footed Boobies was unclear, since they appear to nest irregularly in the Gulf of Panama, both in location and timing.

The Brown Booby has been considered the most widespread booby of the Gulf of Panama (Ridgely and Gwynne 1989), and this seems to be the case; we found them nesting at ten sites and individuals certainly were overall more abundant and more widespread than were Blue-footed Boobies. Of the nine previously reported sites (Thayer and Bangs 1905; Hallinan 1924; Rendahl 1924; Wetmore 1965; Maridueña 1979), we confirmed six (Farallón de Taboguilla, Galera, Boná, Pachequilla, Monte, and Camote) but did not find nesting at three (Pacheca, Saboga, and Bartolomé) in either 2005 or 2006. As noted previously, we think the record of nesting on Saboga was in error. But we did find them nesting at five unreported sites (Islas Frailes del Sur, Bédico Norte, Pelado, Palenque, and Elephante). Generally, the numbers of nests found early in the nesting season in 2006 mirrored those of the late nesting season in 2005, suggesting that our totals of about 230 pairs is a reasonable estimate of the nesting population. In February 2006, about half the roosting birds we saw were juveniles, suggesting that the 2005 season was successful.

Ornithologically, the Gulf of Panama is the Gulf of Pelicans. They seem to be everywhere, and our counts suggest a population exceeding 14,000 adult birds, or 21,000 if

juveniles are taken into account, 7.2% of the global population. One can scarcely travel the waters of the Gulf without encountering flocks of Brown Pelicans. Most of the pelicans we saw actively foraging were in the upper Bay of Panama. Pelicans traveled between colonies and roosts in the western Bay and Pearl Islands to the upper Bay of Panama to feed, distances of 35-50 km. If these pelicans are of the subspecies *carolinensis*, the Gulf is its largest concentration. However based on both morphology and behavior (E. Schreiber, pers. comm.), we suspect that this is a taxonomically distinct population, which, if confirmed, increases the conservation importance of the nesting islands of the Gulf. Our census of pelican colonies at the beginning of the nesting season in 2006 was one third to half of the nests of the late 2005 season, suggesting our 2005 estimate is realistic for the Gulf of Panama. Our population estimate does pale in comparison to the oft-cited estimate of 100,000 pelicans in the Gulf, based on 30-50,000 birds reported as nesting on Taboga-Uravá, and another 30,000 nesting in the Pearl Islands in 1981 (Montgomery 1982). These past figures are puzzling, however, because estimates of Maridueña (1979), Daguerre (2000) and our own surveys all found numbers an order of magnitude lower. We do not regard Montgomery's estimates as likely—he provided no information on his methodology, no detailed figures on individual sites, and no indication that he counted only nests. It would seem he included counts of all individuals from an area and of course, estimates of individuals should not be transformed into a nesting population estimate. Montgomery and Martínez (1984) reported that the number of pelicans in the Gulf increases several-fold during the northern winter, and Maridueña estimated 10,000 pelicans at sea near Isla Pedro González on 22 March 1979, but found only 139 nests there on 4 May. We believe our estimate of about 14,000 nesting birds is appropriate likely at historic levels, and still a meaningful number of pelicans.

It is clear from a comparison of our data with that of published information that Brown Pelicans have a tendency to shift nest-

ing sites and concentrations within the Gulf. Taboga and its satellites Taboguilla and Uravá, with up to 1,476 nests (Maridueña 1979, Daguerre 2000), was historically the largest known colony, but together with Chamá had only 880 nests in 2005. The largest colony we found, 1,389 nests, was on Isla Pedro González and its satellite Señora, where Maridueña found only 270 nests in 1979. The next largest concentration we found, 1,031 nests, was at the previously unreported site of Islas Majé, Majagual and Pajaros Norte and Sur near Chimán. It is likely Wetmore would have seen some of these colonies during his field work in the area in February 1950 had they existed then. A colony on Galera was seen by Wetmore in 1960 but not by Maridueña in 1979 nor by us. Wetmore did not observe a colony on San Telmo in 1960, but Maridueña found 113 nests there in 1979, and by 2005 the colony had grown to 577 nests. Similarly, Maridueña surveyed Pachequilla and San Pablo in 1979 finding no pelican nests, while we found about 200 nests at each of these sites. These changes show the capacity of pelicans to shift their nesting sites over time within the Gulf. It is difficult to assess any long term changes in numbers throughout the Gulf, in that no previous study has censused the entire area. The most extensive previous survey, by Maridueña, included just the Taboga group and the Pearl Islands, recording 2,119 nests. Our total for these same areas was almost 70% greater, so any decrease at Taboga has been more than compensated for by increases in the Pearl Archipelago.

Reasons for changes in Pelican nesting distribution are far from clear. They do not seem to be related to human disturbance as Taboga and Uravá, where nesting numbers have decreased, are protected as the Taboga Wildlife Refuge and the forest in the nesting area appears largely intact. Perhaps subtle effects of human co-occupancy of the island have a cumulative effect. Pedro González and Señora, the largest present colonies, are in second-growth forest on unprotected islands. Changes in local nesting populations seem more likely to be due to patterns of productivity within the Gulf.

We found fewer Neotropic Cormorants than reported previously. Our numbers are less than half that reported by Maridueña (1979) for the Pearls as a whole and far less than the 30,000 reported for Taboga-Uravá by Montgomery (1982), although we do not think this latter estimate likely as nesting numbers. We found nesting at four sites previously reported (Pacheca, Pedro González, Taboga-Uravá, and Estero Brinco), but not Saboga, a record which we think to be in error (see above), or Río Pedasí (Thayer and Bangs 1905; Rendahl 1924; Montgomery 1982; Maridueña 1979; Aparicio and Jiménez 2002; F. Delgado, pers. comm. in Angehr 2003), and found an unreported colony at Isla de Coco. It is possible that the birds at Isla de Coco had shifted from Pacheca, where we found fewer than a third of previously reported numbers. It may be that cormorant nesting was somewhat retarded in 2005 due to the mild El Niño conditions. Observations of the beginning of nesting in 2006 seem to confirm this view. The species also nests inland on Lake Bayano (Ridgely and Gwynne 1989; Angehr, pers. obs.) in a colony of unknown size.

Aningas have previously been reported breeding in our survey area at Chitré Airport, Cenegón del Mangle, and El Rosario (Delgado 1985; Tejera 1989), and it is likely that small numbers probably nest at marshes and ponds throughout this region. Our record for Laguna de Pocrí is the first of the species for Los Santos province (although they were not found nesting there). The species has only recently been documented for Chiriquí province as well (Angehr, pers. obs.). The fact that this species can breed on small farm ponds in pastureland may be enabling it to expand its distribution in Panama.

Our finding of over 2,200 Magnificent Frigatebird nests is difficult to compare to earlier estimates due to the lack of previous numerical data from several sites. We found more nests, 1,300, on Isla Iguana than the 1,000 reported by Wetmore (1965). Maridueña (1979) reported 178 nests at Pacheca, where we found 314, and 232 at Galera, where we found 148. We found 454 nests at Boná, where nesting was reported by Wet-

more (1965) without an estimate of numbers. We found no nests at the previously reported sites of Taboguilla, Chamá, Farallón de Chirú, Peñón de la Honda, and Cangrejo; a report from Saboga was likely an error (Thayer and Bangs 1905; Rendahl 1924; Wetmore 1965; Maridueña 1979; Olson 1997). Although it appears some former colony sites have been abandoned, there is no evidence for a long-term decrease in nesting numbers.

We found Bare-throated Tiger-Herons to be rather common along the rocky shores of the Pearl islands. We found two nests on Isla San José (Kushlan and Angehr 2007), where nesting had previously been reported by Wetmore (1985). Nesting has also been reported on the Río Chico and Río Martinambo in the Río Bayano mangroves (Wetmore 1965; Aparicio and Jiménez 2002). Although Ridgely and Gwynne (1989) reported the species to be declining over much of its Panama range, numbers remain high in the Pearl Islands, which support globally-important numbers.

We did not find Great Blue Herons nesting, although we saw several on our surveys. They occur commonly in Panama in the northern winter and some, especially juveniles, remain in summer (Eisenmann 1952; Ridgely and Gwynne 1989). Wetmore (1965) identified birds in Panama as *A. h. lessoni*, described as a darker form occurring from Mexico through Central America. Although this race is no longer recognized (Kushlan and Hancock 2005), the presence of birds in the breeding season suggests the potential for their nesting in Panama.

For Cocoi Heron we confirmed one previously known colony (Ensenada de Corral, Watts 1998; Angehr 2003) and found one new one at the Río Tranca. The only other site at which the species has been reported to nest in Panama is Lake Bayano (Araúz and Gorrichátegui 2000).

Of all the waterbirds, Great Egrets seem especially well regarded within Panamanian culture. The residential palace is named *Palacio de los Garzas*, and Great Egrets are kept prominently in the courtyard there. The local egret population appears to be enhanced substantially by migrants in the

northern winter (Butler *et al.* 1992). We found them nesting at 27 sites, the most for any species on our survey. Great Egrets have previously been recorded nesting at El Rosario near Penonomé, Cenegón del Mangle, the mouth of the Río Pedasí, Chitré Airport, Taborcillo, Changamé, Taboga, Pacheca, and Ensenada de Corral (Wetmore 1965; Maridueña 1979; Ridgely and Gwynne 1989; Tejera 1989; Watts 1998; Delgado 1985 and pers. comm. in Angehr 2003; Angehr 2003). We found nests at all these sites, except the Río Pedasí, plus many previously unreported colonies. By far the largest colony, with 600 nests, was that at the Ensenada de Corral, larger than the previously reported largest colony (Delgado 1985).

Snowy Egrets have previously been reported nesting only at Changamé, Taborcillo, and Chitré Airport (Wetmore 1965; Ridgely and Gwynne 1989; Angehr 2003; F. Delgado, pers. comm. in Angehr 2003). We found them at all these sites plus five others. Because they nest in small numbers in mixed colonies, they tend to be difficult to distinguish from Cattle Egret at a distance. They likely are more numerous and widespread than our survey data indicate.

We found Tricolored Herons at two sites previously known (Taborcillo, Changamé) as well as five new sites. They have previously been recorded nesting at two other sites, El Rosario and Chitré Airport (Delgado 1985; Ridgely and Gwynne 1989; Tejera 1989; Angehr 2003). We found fewer nests at Taborcillo, 47, than the 130 found by Ridgely in April 1976 (Ridgely and Gwynne 1989). They were common along the coasts.

Little Blue Herons have previously been reported breeding in Panama by Delgado (cited in Butler *et al.* 1998), but this interpretation turns out to be an error (F. Delgado, pers. comm., 2005). Our record from El Rosario therefore provides the first report of nesting in Panama. Very small numbers are reported to breed in northwestern Costa Rica (Stiles and Skutch 1989). Little Blue Herons are most abundant during the northern winter, when migrants occur. During the Panama nesting season most Little Blue Herons are birds in white immature plumage

(Wetmore 1965; Ridgely and Gwynne 1989). It must now be suspected that some of these are locally-bred birds.

The largest colonies of Cattle Egrets reported previously have been at the Chitré Airport, with 2,000 nests, and Cenegón del Mangle, with 1,600 (Delgado 1985). We found fewer at these localities. Some of the Cattle Egrets formerly breeding at Cenegón del Mangle may have shifted to the new colonies at Ciénaga del Rey and Laguna de Cerro Negro, with 900 nests combined. Cattle Egrets forage largely in pastures and are not closely tied to the marine environment as most of the other species in our survey. This is reflected by the largest colony we found, of 1,900 nests, being 19 km inland in the midst of cattle country.

We found Black-crowned Night-Herons at five sites from which they had previously been reported (Chitré Airport, Taborcillo, Changamé, Farallón de Taboguilla, and Pacheca) and did not find them at three others (El Rosario, Peñón de la Honda, and the Río Pedasí) (Wetmore 1965; Maridueña 1979; Delgado 1985; Tejera 1989; F. Delgado, pers. comm. in Angehr 2003). We also found many unreported colonies at Ciénaga del Rey and on small nearshore islands in the Taboga group and in the Pearl Islands.

Yellow-crowned Night-Herons have previously been recorded breeding at only four sites, Taborcillo, Changamé, Pacheca, and the Bayano mangroves (Wetmore 1965; Maridueña 1979; Ridgely and Gwynne 1989; Aparicio and Jiménez 2002). We found them at all these sites except the Bayano mangroves, plus many small inshore islands, on Taboguilla, and in the Pearl Islands.

White Ibis were locally common along all shores from Panama City through the Pearls, where they feed even along rocky shores. The most unusual finding was the colony on Isla Pelado, so far offshore from their mainland feeding sites. This suggests they are avoiding disturbance on closer islands. We found them at four sites previously reported (Chitré Airport, Taborcillo, Changamé, near Isla Espiritu Santo), but not at three others (El Rosario, Cenegón del Mangle, and Peñón de la Honda) (Wetmore 1965; Del-

gado 1985; Ridgely and Gwynne 1989; Tejera 1989; Angehr 2003, N. G. Smith, cited in Maridueña 1979), as well as at many new sites on small islets in eastern and western Panama Bay, the Gulf of San Miguel, and the Pearl Islands. They almost always nested within cactus or similar plants, again suggesting their need to avoid predation or disturbance, likely from people. With 2,756 nests, or 8,268 individuals, the Gulf of Panama as a whole has 8.2% of the neotropical population of this species.

Our breeding record of Glossy Ibis from Ciénaga del Rey is the first definite confirmation for Panama. Four juveniles were also seen at the heronry just west of Chepo, eastern Panamá province, on 5 November 2004, by W. Adsett (in litt.) and D. and K. Wade, suggesting a further nesting site here. F. Delgado (pers. comm.) believes Glossy Ibis to have been breeding at Ciénaga del Rey for about three years, and based on congregations of 400-500 birds seen in the marsh soon after dawn and near dusk he has suggested that the colony consists of about 200-250 pairs, which is consistent with our sighting of 450 breeding condition birds near the colony in late April. The first record of Glossy Ibis in Panama was in 1949 (Wetmore 1965) and by 1989 the species was being recorded regularly in Herrera and eastern Panama province and less frequently from the Caribbean slope of the Canal Area, most often in the northern fall and winter (Ridgely and Gwynne 1989). Some continue to occur into the breeding season (Ridgely and Gwynne 1989), and such records now should be more closely examined for breeding.

We did not find Roseate Spoonbills nesting. It has been reported breeding by Delgado (1985) in mangroves near the mouth of the Río Grande in southern Coclé, but without identifying a specific locality. The species is reported to have bred up until about 1930 at Cocolí in the Canal Area (Wetmore 1985).

The status of pelagic terns breeding in Panama has never been very clear. They are known to nest at only one site in the country, Islas Frailes del Sur. Wetmore (Wetmore 1965; Olson 1997) visited the Frailes del Sur in 1956, 1957, and 1962. In February 1956,

Wetmore identified some birds as Bridled Terns, but supposed that Sooty Terns were also present. In March 1962 he estimated about 100 pairs of Sooty Terns, both adults and immatures. Wetmore noted no Brown Noddies on any of his visits, although they were photographed there in 1949 (Wetmore 1965). In June 1996, Delgado (pers. comm.) found 500-750 pairs of Sooty Terns with chicks, 50 nests of Brown Noddies, and no Bridled Terns. In contrast, we found all three species nesting, including what constitutes the first record of Bridled Tern nesting in Panama. Our count of 3,000 pairs of Sooty Terns increases the previous record fourfold. Wetmore's and Delgado's records together with our own suggest that breeding at this site may take place on other than a twelve month cycle, with large numbers breeding in some years and fewer or none in others. The continental shelf plunges sharply to great depths off the southern coast of the Azuero Peninsula, providing conditions suitable for large schools of tuna close to land. Breeding of these three pelagic terns in Panama is apparently limited to Los Frailes because it is the only suitable nesting island that provides access to such tuna schools. The nearest breeding site for Sooty Tern in the Pacific is the Galapagos Islands (Harrison 1983). Bridled Tern and Brown Noddy breed on islets off the Pacific coasts of Costa Rica and Colombia (Hilty and Brown 1986; Stiles and Skutch 1989).

Conservation Issues

There is no evidence for any long-term declines in any species of seabird or colonial wading bird in Panama and, fortunately, there seem to be few serious direct threats to nesting colonies. There are potential long-term threats. These include pollution, contamination from agricultural and urban areas, and urbanization, tourist and agricultural development. Perhaps potential development of breeding islands is the most critical issue. There is little tradition of human exploitation of seabirds or other colonial waterbirds in Panama, although cormorants are sometimes eaten, and herons and other spe-

cies may occasionally be shot for raiding shrimp ponds. Formerly extensive freshwater wetlands in eastern Panama province at Tocumen and La Jagua, and at the edge of the Río Grande mangroves and in the valley of the Río Santa María in the Parita Bay region, have been drained for conversion to rice and sugar cane plantations. (Rice fields still provide habitat for some aquatic species, however.) Some mangroves have been cut for timber, charcoal, or conversion to pasture, urban areas, or shrimp farms (although most shrimp farms in Panama are in former areas of salt pans rather than mangroves). Sewage and waste water from Panama City and its suburbs enters Panama Bay untreated, introducing large amounts of nutrients as well as industrial effluents and other pollutants. It might be, however, that the nutrients in the freshwater from the Panama Canal and from the urban center of Panama City are having a positive effect on food availability for fish-eating birds in the Bay of Panama.

Most offshore islands are little disturbed. On inhabited islands with colonies, villagers rely mostly on fishing and tourism and do not disturb the birds, although their pets likely do. Iguana hunters set fires during the dry season on both large and small islands in order to drive their quarry from cover, and sometimes leave dogs behind that prey on low-nesting species. Development of some islands for tourism could be a problem in the future, particularly in the Pearl Islands. Conservation agreements related to the protection of sites, reduction of tourism impact, burning and management of domestic animals might be used to ameliorate threats from private developments on islands. The principal needs for seabird and waterbird conservation are twofold—environmental education and site protection.

The seabirds and colonial waterbirds of the Gulf of Panama are important aspects of the Panamanian national patrimony, as epitomized by the presidential palace itself. Tens of thousands of water birds can be seen on the mudflats off Panama City. The meaning of recent official recognition of the upper Bay of Panama as a site of international importance to bird conservation is becoming

appreciated by the local people and government, as perhaps is the increasing value of the ecotourism industry. Seabird populations of the Gulf are a critical component of its ecosystem as well as an indication of the health of the fish populations, which in turn support the near-shore and offshore fisheries of Panama. Providing information to the people of Panama on the value of their waterbird populations is perhaps the fundamental long term need.

Sites identified as being globally and nationally important deserve and require site specific conservation action, and this needs to be done relatively soon before development pressures increase. Depending on the site, this might mean setting up a private conservation easement or incorporation of the site into existing or future national parks and reserves. In addition, each site has its own special needs for posting, protection, and monitoring, as well as its own opportunities for use as an environmental educational resource. These important sites should become part of an expanded network of protected places that together secure for posterity the seabird and colonial waterbird resource of Panama.

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LITERATURE CITED

- Angehr, G. R. 2003. Directory of Important Bird Areas in Panama. Panama Audubon Society, Panama City.
- Aparicio, K. and B. Jiménez. 2002. Componente aves. Pages 83-107 in *Humedales de la Bahía de Panamá* (B. Jiménez and K. Aparicio, Eds.). Panama Audubon Society, Panama City.
- Araúz, J. and K. Gorrichátegui. 2000. Una colonia de anidación de Garza Cocoi (*Ardea cocoi*) en Panamá. *El Tucán* 25: 1, 3-4.
- Bangs, O. 1901. Birds of San Miguel Island, Panama. *Auk* 18: 24-32.

- Batista, V. E. 1981. Estudio de la población del Pelicano Chocolate, *Pelecanus occidentalis*, durante el periodo de anidación en el Archipiélago de las Perlas. Exxon Student Report, Smithsonian Tropical Research Institute, Panama City.
- BirdLife International and Conservation International. 2005. Áreas Importantes para la Conservación de las Aves en los Andes Tropicales: sitios prioritarios para la conservación de la biodiversidad. BirdLife International, Quito.
- Butler, R. W., R. I. G. Morrison and F. Delgado. 1992. The distribution of fish-eating, wading and raptorial birds in the Gulf of Panama, October 1991. Progress Notes No. 198: 1-3, Canadian Wildlife Service, Ottawa.
- Butler, R. W., R. I. G. Morrison and F. Delgado. 1998. The distribution and abundance of coastal seabirds, wading birds, and birds of prey on the coast of Panama. Pages 69-89 in Atlas of Nearctic Shorebirds and Other Waterbirds on the Coast of Panama (R. I. G. Morrison, R. W. Butler, E. S. Delgado and R. K. Ross, Eds.) Canadian Wildlife Service, Ottawa.
- Buehler, D. M., A. I. Castillo and G. Angehr. 2004. Shorebird counts in the Upper Bay of Panama highlight the importance of this key site and the need to improve its protection. Wader Study Group Bulletin 105: 56-64.
- Daguerre, N. 2000. La conservación del Refugio de Vida Silvestre Taboga y un reconocimiento del área de anidación del *Pelecanus occidentalis carolinensis* (Pelicano Marrón). Thesis (licenciatura), Universidad de Panamá, Panama City.
- Delany, S. and D. Scott. 2002. Waterfowl population estimates (Third Edition). Wetlands International Global Series No 12, Wageningen.
- Delgado, F. S. 1985. Panama. Pages 420-438 in A Directory of Neotropical Wetlands (D. A. Scott and M. Carbonel, Compilers). IUCN, Cambridge, UK.
- Delgado, F. S. 1998. Geography, physical oceanography, and climate of the Gulf of Panama. Pages 19-25 in Atlas of Nearctic Shorebirds and Other Waterbirds on the Coast of Panama (R. I. G. Morrison, R. W. Butler, E. S. Delgado and R. K. Ross, Eds.) Canadian Wildlife Service, Ottawa.
- Eisenmann, E. 1952. Annotated list of birds of Barro Colorado Island, Panama Canal Zone. Smithsonian Miscellaneous Collections 117: 1-62.
- Griscom, L. 1928. New birds from Mexico and Panama. American Museum Novitates 293: 1-6.
- Hallinan, T. 1924. Notes on some Panama Canal Zone birds with special reference to their food. Auk 41: 304-326.
- Harrison, P. 1983. Seabirds: An Identification Guide. Houghton Mifflin Company, Boston, MA.
- Hilty, S. L. and W. L. Brown. 1986. A Guide to the Birds of Colombia. Princeton University Press, Princeton, NJ.
- Jiménez, B. and K. Aparicio. 2002. Aves del área de Bahía Honda (Veraguas, Panama). Unpublished report, LiquidJungleLab, Isla Canal de Tierra, Veraguas.
- Kushlan, J. A. and J. A. Hancock. 2005. The Herons. Oxford University Press, Oxford, UK.
- Kushlan, J. A. and G. E. Angehr. 2007. Seaside tiger herons. Waterbirds 30: 278-283
- Kushlan, J. A., M. J. Steinkamp, K. C. Parsons, J. Capp, M. A. Cruz, M. Coulter, I. Davidson, L. Dickson, N. Edelson, R. Elliot, R. M. Erwin, S. Hatch, S. Kress, R. Milko, S. Miller, K. Mills, R. Paul, R. Phillips, J. E. Saliva, B. Sydeman, J. Trapp, J. Wheeler and K. Wohl. 2002. Waterbird Conservation for the Americas: The North American Waterbird Conservation Plan, Version 1. Waterbird Conservation for the Americas. Washington, D.C.
- Loftin, H. 1991. An annual cycle of pelagic birds in the Gulf of Panama. Neotropical Ornithology 2: 85-94.
- Maridueña, L. 1979. Distribución de aves marinas en el Archipiélago de Perlas y estado de las aves en Isla Pacheca, Golfo de Panamá. Exxon Student Report, Smithsonian Tropical Research Institute, Panama City.
- Martínez, M. L. 1981. Nidación del Pelicano Chocolate en las Islas de Taboga y Uravá, Bahía de Panamá. Exxon Student Report, Smithsonian Tropical Research Institute, Panama City.
- Martínez, M. L. 1983. Biología reproductiva de *Pelecanus occidentalis* en relación con el afloramiento de la Bahía de Panamá. Thesis, Universidad del Valle, Colombia.
- Martínez, M. L. 1984. Parental care and reproductive failure of Brown Pelicans, *Pelecanus occidentalis*, on Taboga Island, Panama. Exxon Student Report, Smithsonian Tropical Research Institute, Panama City.
- Montgomery, G. G. 1982. Creación de un refugio nacional Panameño para aves marinas en las Islas de Taboga y de Uravá. Revista Médica de Panamá 7: 97-104.
- Montgomery, G. G. and M. L. Martínez 1984. Timing of pelican nesting on Taboga Island in relation to upwelling in the Bay of Panamá. Colonial Waterbirds 7: 10-21.
- Morrison, R. I. G., R. W. Butler, E. S. Delgado and R. K. Ross. 1998. Atlas of Nearctic Shorebirds and Other Waterbirds on the Coast of Panama. Canadian Wildlife Service, Ottawa.
- Murphy, R. C. 1936. Oceanic Birds of South America, Vol. 2. American Museum of Natural History, New York, NY.
- Murphy, R. C. 1944a. To the Chocó in the schooner "Askoy." Natural History 53: 274-281.
- Murphy, R. C. 1944b. In the Pearl Islands. The second installment in the story of the "Askoy" expedition. Natural History 53: 200-208.
- Murphy, R. C. 1944c. To the continental shelf: The third installment in the story of the "Askoy" expedition. Natural History 53: 303-309
- Murphy, R. C. 1956. The vertebrates of SCOPE, November 7-December 16. Birds. Pages 121-140 in Physical, Chemical, and Biological Observations in the Eastern Tropical Pacific, November-December 1956 (R. W. Holmes, Ed.). Scripps Institute of Oceanography, La Jolla, CA.
- Olson, S. L. 1997. Avian biogeography in the islands of the Pacific Coast of western Panama. Pages 69-82 in The Era of Allan R. Phillips: A Festschrift (R. W. Dickerman, Compiler). Horizon Communications, Albuquerque, NM.
- Peters, J. L. 1931. Additional notes on the birds of the Almirante Bay region of Panama. Bulletin Museum of Comparative Zoology 71: 310-345.
- Rendahl, H. 1920. A list of the birds of the Pearl Islands, Bay of Panama. Arkiv för Zoologi 13: 1-57.
- Ridgely, R. S. and J. A. Gwynne. 1989. A Guide to the Birds of Panama. Princeton University Press, Princeton, NJ.
- Robins, C. R. 1958. Observations on oceanic birds in the Gulf of Panama. Auk 60: 300-302
- Schaefer, M. B., Y. M. Bishop and G. V. Howard. 1958. Some aspects of upwelling in the Gulf of Panama. Bulletin of the Inter-American Tropical Tuna Commission 3: 79-131.
- Spear, L. B. and D. G. Ainley. 1999. Seabirds of the Panama Bight. Waterbirds 22: 175-198.

- Stiles, F. G and A. F. Skutch. 1989. A Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, NY.
- Sturgis, B. B. 1928. Field Book of Birds of the Panama Canal Zone. G. P. Putnam's Sons, New York, NY.
- Tejera, V. H. 1989. Aspectos bioecologicos de una colonia de aves in la Laguna El Rosario, Panama. Ph.D. Thesis, Universidad Nacional Autonoma de Mexico, Mexico DF.
- Thayer, J. E. and O. Bangs. 1905. The mammals and birds of the Pearl Islands, Bay of Panama. Bulletin of the Museum of Comparative Zoology. 46: 137-160.
- Villalaz, M. 1987. Historia natural de la colonia de aves acuáticas del aeropuerto de Chitré, Provincia de Herrera. Thesis, Universidad de Panamá, Facultad de Ciencias Naturales y Exactas, Chitré, Panama City.
- Watts, B. D. 1998. An investigation of waterbirds within the Panama Canal Area and the Upper Bay of Panama. Center for Conservation Biology, College of William and Mary, Williamsburg, VA.
- Wetmore, A. 1946. Birds of San José and Pedro González Islands, Republic of Panamá. Smithsonian Miscellaneous Collections 106: 1-60.
- Wetmore, A. 1952. The birds of the islands of Taboga, Taboguilla, and Uravá, Panamá. Smithsonian Miscellaneous Collections 134: 1-105.
- Wetmore, A. 1959a. The birds of Isla Escudo de Veraguas, Panamá. Smithsonian Miscellaneous Collections 139: 1-27.
- Wetmore, A. 1959b. Description of a race of the shearwater *Puffinus lherminieri* from Panama. Proceedings of the Biological Society of Washington 72: 19-22.
- Wetmore, A. 1965. The Birds of the Republic of Panamá. Part 1. Tinamindae (Tinamous) to Rynchopidae (Skimmers). Smithsonian Miscellaneous Collections 150: 1-483.