

AVIAN BIOGEOGRAPHY IN THE ISLANDS OF THE PACIFIC COAST OF WESTERN PANAMA

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ABSTRACT.—Distributional data on birds from the smaller islands of the Pacific coast of western Panama, here termed the Veragua Archipelago, are compiled from documents and specimens collected by Alexander Wetmore. The combined avifauna of these islands is mostly a very depauperate subset of that known from much larger Isla Coiba. The few species from the smaller islands that have not been recorded from Coiba are mainly open-country birds that may be recent colonists. A few species show geographic variation among the islands, the most interesting being two of the distinctive endemic subspecies of Isla Coiba that also occur on Isla Brincanco. Several anomalous distributional patterns are identified.

The avifaunas of the islands off the coasts of Panama have especially rich potential for island biogeography. All these islands are continental and were once continuous with the mainland, so that the species on each island are presumably a subset of the avifaunas found on the adjacent mainland, although each major island group has relictual species that do not occur elsewhere in Panama. The process of isolation invariably reduces species diversity and it becomes important to document which species have survived under insular conditions and which have not. Panamanian islands have already figured importantly in studies of island biogeography (viz. Graves and Gotelli 1983, Wright et al. 1985, Gotelli and Graves 1990) and when data are fully available for all Panamanian archipelagos they will invite valuable comparisons with the well documented loss of diversity in the avifauna of the man-made island of Barro Colorado in Gatun Lake of the Panama Canal (Willis and Eisenmann 1979), which is a likewise a subset of the avifauna of the isthmian lowlands.

The Pearl Islands in the Gulf of Panama have long been the focus of ornithological attention and their avifaunas have been summarized and analyzed by Wright et al. (1985). Wetmore (1952) documented the bird life of the small islands of the Taboga group (Taboga, Taboguilla, and Uravá) near the Pacific entrance of the Panama Canal, based mainly on his work there in 1952. He made another brief visit to the group from 24 to 26 Dec. 1955 and added three species not in his previous report: *Ceryle alcyon*, *Myiopagis viridicata*, and *Vermivora peregrina*. On the Caribbean side, the long-neglected archipelago of Bocas del Toro is currently under study (Olson 1993).

Of the various Panamanian islands on the Pacific coast lying west of the Taboga group (Fig. 1), only the largest, Isla Coiba, has received monographic treatment (Wetmore 1957). The avifauna of Coiba is interesting because of its high degree of subspecific endemism and also for the relictual taxa that occur there. Knowledge of the avifauna of the smaller islands in this region has never been synthesized. These scattered islands have no collective name, so for the sake of convenience and brevity, I shall refer to them as the "Veragua Archipelago," reviving the old term "Veragua" that was once applied to that part of western Panama now consisting mostly of the provinces of Chiriquí and Veraguas. Virtually all knowledge of these avifaunas stems from collecting expeditions of Alexander Wetmore in the early 1960s. Wetmore did not visit all of the islands of the region, but collected on most of the more important ones. Records of many species from these islands are scattered through Wetmore's *Birds of the Republic of Panamá* (Wetmore 1965, 1968, 1972; Wetmore et al. 1984), but not all species that were encountered are specifically mentioned, no island lists were ever published, nor has there been any account of the nature of the islands themselves or of Wetmore's activity there.

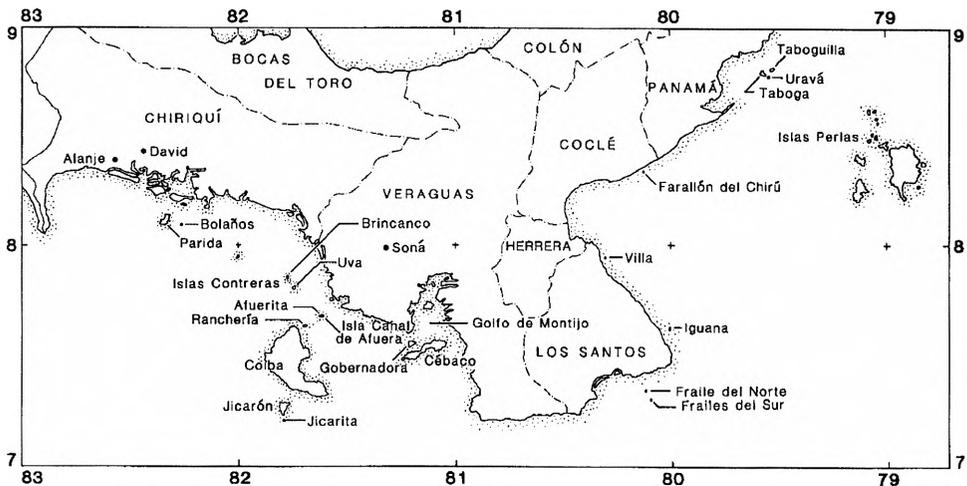


FIG. 1. Map showing the islands of the Pacific coast of Panama and other localities mentioned in the text.

Part of the impetus for determining which species of birds actually occur in the Veragua Archipelago stems from the need to document the fraudulent nature of a large collection of skins labelled as being from virtually all of the smaller islands of the region, supposedly taken there in 1902 by J. H. Batty and sold to Walter Rothschild at Tring, England. The bulk of Rothschild's collection is now housed in the American Museum of Natural History, New York. Although a number of Batty's specimens have been cited in the literature, particularly by Eisenmann (1950), his entire collection from the smaller islands is fraudulently labelled, the specimens having been obtained in 1901 from both montane and lowland localities on the mainland of Chiriquí (Olson MS). Although it is certain that Batty collected on Isla Coiba in 1901, some of the specimens he labelled as being from that island are also fraudulent. He probably never went to the smaller islands and apparently was not in Panama at all in 1902 (Olson MS).

METHODS

Information on the islands of the Veragua Archipelago and their avifaunas was compiled from the field journals and field catalogs of Alexander Wetmore, housed in the Division of Birds, National Museum of Natural History, Smithsonian Institution (USNM). Fortunately, Wetmore included lists or tables of species for each island in his journals that include both specimen and sight records. Some of the latter cannot be confirmed from other entries in his journal so that the only indication of the presence of certain species on an island may be its inclusion in one of these lists or tables. These do not include any unusual occurrences, however. Potentially interesting or unusual specimen records were verified by examination of skins in the USNM collections. The species lists generated in this process were compared with the species accounts in *Birds of the Republic of Panamá* to note any discrepancies, which were mainly in the nature of omissions in the published work.

Doubtless there exist miscellaneous specimens from these islands in other museums. For example, there is a specimen of Laughing Gull (*Larus atricilla*) from Isla Jicarita, an outlier of Isla Coiba, south of Isla Coiba, in the collections of the San Diego Museum of Natural History. But I know of no concerted collecting efforts made in these islands other than Wetmore's, and such incidental records are unlikely to augment significantly the data presented here.

DESCRIPTIONS OF ISLANDS AND HISTORY OF COLLECTING

The dates of Wetmore's activity on all islands west of the Taboga group are summarized in Table 1, where island areas are also given. Areas were determined from digitized computer data from the Department of Defense digital map of the world based on operational navigational charts (ONC).

Miscellaneous Islets and Bird Rocks.—The first four islands in Table 1 are not really in the area of concern of this report, but I include brief mention of them for the sake of completeness.

Farallón del Chirú, off Santa Clara, Coclé Province, is a rocky islet with a triangular point at the landward end and a lower, elongate section seaward. The steep slopes near the crest were clothed with heavy stands of a cereus-like cactus and a few low bushes, whereas the more level section was in long grass. Wetmore noted about 75 Magnificent Frigatebirds (*Fregata magnificens*), some 15 to 20 Brown Pelicans (*Pelecanus occidentalis*), most of them barely-grown young, an Osprey (*Pandion haliaetus*), and a dozen pairs of Blue-footed Boobies (*Sula nebouxii*) with a few young, of which one adult was collected.

Isla Villa, Los Santos, was described by Wetmore as an elongate rock, with an abrupt cliff about 18–25 m high on the south side, but with the northwestern sides sloping so that landing may be possible. The summit was covered with scrub in which there was a colony of 75 to 100 pairs of frigatebirds, about 30 Black-crowned Night Herons (*Nycticorax nycticorax*), and a few pelicans. About a dozen adult Blue-footed Boobies came off the rock, of which a single specimen was shot, the report of the gun startling a flock of about 30 Gray-breasted Martins (*Progne chalybea*) from a hollow in the cliff.

Isla Iguana, Los Santos Province, near the southeastern corner of the Azuero Peninsula, is notable for being home to an endemic subspecies of Yellow Warbler (*Dendroica petechia iguanae*). A description of the island and discussion of the few other

TABLE 1
ISLANDS OF PACIFIC WESTERN PANAMA INVESTIGATED BY
ALEXANDER WETMORE, WITH DATES OF VISITS AND ISLAND AREAS¹

Island	Area	Dates
Farallón del Chirú		1957 Feb 28
Villa		1957 Feb 28
Iguana	(ca. 1 km ²)	1957 Feb 26-27
Frailes del Sur		1956 Feb 6 1957 Feb 26 1962 Mar 18
Cébaco	(83.9 km ²)	1962 Mar 27-28; 1965 Jan 11, 13-20
Gobernadora	(7.6 km ²)	1965 Jan 8-11
Coiba	(502.4 km ²)	1956 Jan 7-Feb 3
Ranchería	(2.2 km ²)	1956 Feb 4
Canal de Afuera	(2.0 km ²)	1962 Mar 20-21, 26
Afuerita		1962 Mar 23-24
Brincanco	(2.9 km ²)	1962 Mar 23-24
Bolaños	(0.7 km ²)	1963 Feb 1,6
Parida	(14.5 km ²)	1963 Feb 2-5, 7

¹Areas are not given for islets too small to appear on the digitized map, which are all probably less than 0.5 km².

species of birds found there may be found in Olson (1980).

Wetmore made observations at the two rocks known as Frailes del Sur, Los Santos, on three occasions. On 6 Feb 1956 he noted hundreds of terns over the larger of the two rocks that he originally took to be Sooty Terns (*Sterna fuscata*), but this was later queried in his journal, probably because he considered the Bridled Tern (*Sterna anaetheta*) to be the more likely species. On 26 Feb 1957 there were only two or three *Sula nebowxii* and an Osprey, and Wetmore speculated in his notes that the terns may have bred earlier than usual. On 18 Mar 1962 he mentioned frigatebirds circling the island and estimated a colony of Sooty Terns on the larger of the two rocks at about 100 pairs, of which he obtained 3 adults and one juvenile. The adults were past breeding and all young were on the wing. He must have forgotten his first observations in 1956 when he wrote (Wetmore 1965:457) that his visit in 1962 was his second to these rocks. This was unfortunate because the 1956 visit provides corroboration of his thesis that Sooty Terns do not breed on an annual cycle here. In 1962 Wetmore noted that the rock known as Fraile del Norte was without vegetation and so low that it would be swept by storms.

Isla Rancheria, Veraguas.—Wetmore included this island, where he spent only part of one day ashore, in his report on Isla Coiba (Wetmore 1957), although he did not provide a separate list of species. He noted that the island was locally called Coibita, but that that name properly applied to another islet. I notice that the name Coibita has recently been used on maps to refer to the island that Wetmore called Ranchería (Atlas Nacional 1988). Of the few species noted here (Table 2), all except *Bubo virginianus* and *Megarynchus pitangua* were also found on Coiba. The specimens of *Turdus* and *Saltator* belong to the distinctive forms found on Coiba. Wetmore's (1957) inclusion of Ranchería in the range of the Coiba endemic *Melanerpes rubricapillus subfuscus* is an assumption without specimen corroboration, as his notes indicate only that he heard "one calling" here. For most of the ensuing discussions, I have considered the avifauna of Ranchería as part of that of Coiba.

Isla Cebaco, Veraguas.—This is the largest and most important of Panama's western Pacific islands, apart from Coiba. It runs diagonally across the mouth of the Golfo de Montijo, on the western side of the Azuero Peninsula. The eastern end is low but the western half on the southern side is high and abrupt down to the water. In 1962, Wetmore landed at the western end, at a bay called Caleta Cayman, and found abrupt rocky slopes that were still forested, with only one small clearing to be seen from the sea, and one area with a considerable stand of *guayacáns* (*Tabebuia guayacan* Bignoniaceae) in bloom. On his first afternoon he set out a mist net that was left overnight and he spent the next two days hunting the wooded slopes with overarching trees. There was a considerable area of level ground that had been cleared for farming and was birdless except for abundant *Columbina talpacoti*. He obtained 27 specimens during this time and remarked on the seeming impoverishment of the avifauna, which he considered sufficiently interesting as to require confirmation by exploring the other end of the island.

This he undertook in 1965, when he and Edwin L. Tyson, who collected mammals, along with several assistants, established a camp at the small village of Platanal at the eastern end of Cébaco. Mist nets were used intensively here, as much for bats as for birds. Extensive areas at this end of the island had been cleared and were either under cultivation or had grown up in brush (*rastrajo*). Nevertheless, original forest remained on steeper slopes along streambeds and on steep hills such as Loma de la Bandera, but was being cut rapidly. Wetmore noted figs as being abundant among the forest trees.

Wetmore had 8 full days of collecting on Cébaco on this trip, in addition to 2 hours of hunting on another day when still camped on Gobernadora. He left a day earlier than planned, with 118 specimens, as he considered that he had sampled the avifauna more than adequately.



TABLE 2

KNOWN DISTRIBUTION OF LAND BIRDS ON ISLANDS OF THE VERAGUA ARCHIPELAGO, INCLUDING ISLA COIBA, PACIFIC COAST OF WESTERN PANAMA¹

	Coiba	Cébaco	Gobernadora	Canal de Afuerita	Brincanco	Bolaños	Parida
<i>Coragyps atratus</i>	0		0				
<i>Cathartes aura</i>	0	0			0	0	0
<i>Sarcoramphus papa</i>	X						
<i>Harpagus bidentatus</i>	X						
<i>Accipiter bicolor</i>	X						
<i>Leucopternus albicollis</i>		0					
<i>Buteogallus anthracinus</i>	X	0		0	X	0	0
<i>Buteo magnirostris</i>	X						0
<i>Morphnus guianensis</i>	0						
<i>Falco rufifularis</i>	X						
<i>Laterallus albigularis</i>	X						
<i>Laterallus exilis</i>	X						
<i>Aramides cajanea</i>	X	X					?
<i>Columba cayennensis</i>	X	X		0	0	0	X
<i>Columbina talpacoti</i>	X	X					X
<i>Claravis pretiosa</i>	X	X					
<i>Leptotila verreauxi</i>		X	X				X
<i>Leptotila battyi</i>	X	X					
<i>Geotrygon montana</i>	X [X]	X					
<i>Ara macao</i>	X [0]			0			
<i>Brotogeris jugularis</i>	X	X					
<i>Pionus menstruus</i>	X	X		0			
<i>Amazona autumnalis</i>	X						
<i>Amazona farinosa</i>	X [0]			0			
<i>Amazona ochrocephala</i>				0			0
<i>Coccyzus minor</i>		0			X	X	X
<i>Crotophaga ani</i>	X						
<i>Crotophaga sulcirostris</i>		X	X				
<i>Tapera naevia</i>		0					
<i>Bubo virginianus</i>	[0]						
<i>Lurocalis semitorquatus</i>		X					
<i>Nyctidromus albicollis</i>		X	X				
<i>Caprimulgus rufus</i>	X						0
<i>Streptoprocne zonaris</i>	X						
<i>Chaetura vauxi</i>	X [0]	0		X	0	0	
<i>Phaeochroa cuvierii</i>	X						
<i>Chlorostilbon assimilis</i>	X	X	X			X	0
<i>Lepidopyga coeruleogularis</i>	X	X					
<i>Hylocharis eliciae</i>	X [X]		X				
<i>Amazilia edward</i>	X						
<i>Amazilia tzacatl</i>	X [X]	X	X	X	X	X	X
<i>Ceryle torquata</i>	X						
<i>Chloroceryle americana</i>	X	X					0
<i>Chloroceryle aenea</i>	X						
<i>Melanerpes rubricapillus</i>	X [0]	X	X				
<i>Veniliornis kirkii</i>	X						

...continued

Coiba Cébaco Gobernadora Canal de Afuerita Brincanco Bolaños Parida
Afuera

<i>Cranioleuca dissita</i>	X							
<i>Thamnophilus doliatus</i>	X							
<i>Procnias tricarunculata</i>		X						
<i>Chiroxiphia lanceolata</i>	X	X	X	X	X			X
<i>Camptostoma obsoletum</i>	X	X			X			
<i>Sublegatus arenarum</i>	X	X	X		X		X	X
<i>Elaenia flavogaster</i>	X				X			0
<i>Elaenia chiriquensis</i>	X	X	X					
<i>Myiopagis viridicata</i>	X							
<i>Mionectes oleagineus</i>	X	X	X					
<i>Leptopogon amaurocephalus</i>	X							
<i>Capsiempis flaveola</i>	X							
<i>Todirostrum cinereum</i>	X							
<i>Contopus cinereus</i>	X	X						
<i>Attila spadiceus</i>	X	X						X
<i>Myiarchus panamensis</i>	X [X]		X		X	X		X
<i>Megarynchus pitangua</i>	[0]	X						
<i>Myiodynastes maculatus</i>	X	X				X	0	X
<i>Tyrannus melancholicus</i>	X	X	X	X				X
<i>Tyrannus savana</i>	0							
<i>Pachyrhamphus polychopterus</i>		X						
<i>Tityra semifasciata</i>	X	X						
<i>Tachycineta albilinea</i>	X	0						
<i>Progne chalybea</i>	X	X			X			
<i>Troglodytes aedon</i>	X	X	0					
<i>Turdus assimilis</i>	X [X]					X		
<i>Turdus grayi</i>		X		0				?
<i>Polioptila plumbea</i>	X							
<i>Cyclarhis gujanensis</i>	X							
<i>Vireo flavoviridis</i>	X [X]	X	0	X	0	X	X	X
<i>Hylophilus flavipes</i>	X							
<i>Parula pitiayumi</i>	X							
<i>Basileuterus rufifrons</i>	X							
<i>Dendroica petechia</i>	X					X	X	0
<i>Thraupis episcopus</i>	X	X			X	X	X	X
<i>Ramphocelus dimidiatus</i>	X	X	X					
<i>Coereba flaveola</i>	X [X]	X	X		X	X	X	X
<i>Cyanerpes cyaneus</i>	X	X	0		X	X	X	0
<i>Saltator maximus</i>		X	X					
<i>Saltator albicollis</i>	X [X]	X				X		
<i>Cyanocompsa cyanoides</i>		X						
<i>Tiaris olivacea</i>	X							
<i>Volatinia jacarina</i>	X	X						
<i>Sporophila americana</i>	X		X					X
<i>Oryzoborus angolensis</i>	X	X						
<i>Arremonops conirostris</i>	X							
<i>Quiscalus mexicanus</i>	X							

¹North American migrants and waterbirds other than rails are omitted but several of the species included here are certainly not breeding residents, viz. *Bubo virginianus*, *Streptoprocne zonaris*, *Tyrannus savana*. Bracketed symbols under Coiba indicate records for Isla Ranchería (= "Coibita"). X = specimen record, 0 = sight record.

Isla Gobernadora, Veraguas.—This fairly large island, lying between Cébaco and Punta Brava on the adjacent mainland, was seen from sea by Wetmore in 1962, when he recorded at least two thirds of the habitat to be in extensive grass land, apparently pasture. In 1965 he camped at the settlement of La Punta, again with E. L. Tyson, and mist nets were in use. In 3 full days of collecting, Wetmore obtained 52 specimens. He mentioned little about the habitat other than that little forest was left. He would work along streambeds and along the beach, where “there was a broad wooded flat . . . facing the sea with no low undergrowth, indication that it was storm swept from time to time.”

Isla Canal de Afuera, Veraguas.—This small island lies between the northeastern tip of Coiba, with its adjacent island of Ranchería, and Bahía Honda on the mainland. The eastern face presents the outline of a low hat with a broad brim, is precipitous, and without beaches. The western face is lower, with three small beaches where Wetmore had two days ashore, obtaining only 11 specimens, partly with the use of a single mist net. He was ashore briefly a few days later but obtained only one additional specimen. The summit and slopes were heavily forested in 1962.

Isla Afuerita, Veraguas.—This is a tiny islet off the western end of Isla Canal de Afuera. Wetmore hunted here on two days in 1962, obtaining a total of 19 specimens. He mentions a stand of spiny palms behind the beach, a steep slope with open woodland to the crest of the ridge, and an interior valley that had been cleared and provided attractive habitat for swifts, swallows, and a brushy “haven for numbers of Philadelphia Vireos.” Farther on, tall woodland with open undergrowth produced no birds.

Isla Brincanco, Veraguas.—This is the northernmost of two major islands (the other being Isla Uva) and several islets that constitute the Islas Contreras, that lie due north of Isla Coiba. Wetmore was ashore on Brincanco for two full days in 1962, where he set out a single mist net. He found that once the steep, rocky slopes to the beach had been crossed there were tall trees with open undergrowth and abundant birds by contrast to what he had found and expected on Canal de Afuera. Specimens numbered 27. On 25 Mar 1962 Wetmore “had a clear view of Isla Pájaros [off the northern side of Brincanco] a steep-sided wooded island with no sign whatever of any birds [presumably meaning any seabirds that would be visible from a boat]. The landward side of [Isla] Uva also was heavily wooded and steep to everywhere. [In his journals Wetmore often used “steep to,” rather than simply “steep,” an expression I have not encountered elsewhere.] There are two small islands without names on the chart, both narrow and the western partly open and partly covered with bushes on the top. Here there was a small colony of frigate-birds.”

Isla Bolaños, Chiriquí.—This is the largest of the islets lying to the east of Isla Parida. Wetmore obtained 14 birds here on two days ashore in 1963. He found it wooded to its height at about 100-110 feet, with undergrowth absent in the trees in a valley that may have been swept by storms, but above this there was heavily vine-entangled undergrowth.

Isla Parida, Chiriquí.—This large island is the southernmost and most isolated of the complex of islands and bays lying to the south of the provincial capital of David. Wetmore was ashore here at places termed Jurel, and Punta Icacos, on 5 days in 1963, during which time he obtained 37 specimens. At various places he reported evergreen gallery forest with trees 100 to 125 feet high, virgin jungle with trees 40 to 60 feet tall, mangrove swamp, clearings and brush (*rastrojo*), and various plantings, including an extensive rice field. He was told that *Aramides* occurred on the island but did not confirm it. He found birds to be scarce, with little diversity.

Sampling effort.—How well have the avifaunas of these islands been sampled? Certainly the collecting effort on Cébaco, the largest and least depauperate of the islands, may be considered adequate, with both ends of the island being sampled and with mist nets being used for both bats and birds over an extended period, with an ample crew to man

them. Although the intensity of the surveys of the other islands varied, and in some instances was little more than perfunctory, in most cases there would be little expectation of adding significantly to the list of resident birds, considering that the islands are so depauperate in the first place and that most of the species that do occur in the archipelago are relatively conspicuous.

Because of the interesting extension of two distinctive Coiba endemics to Isla Brincanco, additional survey of the Islas Contreras, particularly Isla Uva, would be desirable. Another real gap in our knowledge of biogeography is the total absence of information from Isla Jicarón. With an area of 19.2 km², it is the third largest island in the archipelago, after Coiba and Cébaco, and it is also rather high. Because Isla Coiba lies between Jicarón and the mainland, the avifauna of the latter island would probably consist of a subset of that of Coiba, but given the highly endemic nature of the avifauna of Coiba, it would certainly be interesting to know which species and subspecies occur on Jicarón.

Qualifications to the Lists of Species.—The distribution of species of land birds in the Veragua Archipelago is summarized in Table 2. Some of these are certainly or probably not breeding residents, such as *Leucopternis albicollis*, *Bubo virginianus*, *Coccyzus minor*, and *Tyrannus savana*, and on the smaller islands *Ara macao* and the larger Amazon parrots. The Three-wattled Bellbird (*Procnias tricarunculata*) breeds in the highlands but at least some individuals move into lowlands in the non-breeding season, as they have been found on islands and mainland swamps in Bocas del Toro as well as on Cébaco (Wetmore 1972; Olson, unpublished data).

Wetmore (1972:559) recorded *Elaenia flavogaster* from both Cébaco and Gobernadora, but this appears to be a lapsus, as there exists neither a specimen of this species, nor any mention of it from these islands in any of Wetmore's journals, whereas *E. chiriquensis* was collected on both islands (as also recorded in Wetmore 1972). Because *E. flavogaster* might be expected on any of the islands, its absence from all but Afuerita and Coiba is difficult to understand. The apparent absence of *Thraupis episcopus* from Isla Gobernadora is scarcely credible and must be an artifact of one sort or another.

The occurrence of *Bubo virginianus* on Isla Ranchería (Wetmore 1957 1968:163) can only be accidental as there can be few places less suitable for a large predator of medium-sized nocturnal mammals. The mammalian fauna of Coiba is quite depauperate and that of Ranchería is doubtless even more so. The only nocturnal mammals on Coiba of a size appropriate as prey for a Great Horned Owl are possums (*Didelphis*) and young agoutis (*Dasyprocta*) (Thomas 1902). There can hardly be a resident population of this owl on Isla Ranchería so that we must accept that the species may be subject to wandering, at least in southern Central America. There is but one other record of this owl for Panama, an ancient one (1868) from the highlands of Veraguas (Wetmore 1968). If the species were resident in Panama it would surely have been found again, so that this mainland record should also be regarded as a possible vagrant. Slud (1964) stated that only one specimen seemed to exist for Costa Rica and that he never encountered the species there, although Stiles and Skutch (1989:192) refer to it as a "very rare resident." Because they specifically state that there is no breeding record for Costa Rica, one might question the basis for regarding this species as a "resident" in that country. In Nicaragua there are two sight records in lowland pine savanna, where the species was never heard calling or located at night (Howell 1972). In the highlands of Nicaragua there is a single specimen record and a single sight record, from which Howell (in litt. 23 January 1996) suspects that it is a rare resident in the pine forests of the north-central highlands. The Great Horned Owl has been collected frequently in the highlands of Honduras above 900 m, where it is said to be "uncommon to fairly common" (Monroe 1968:156). Here it is probably safe to assume that the species is in fact a resident, breeding bird but its true status in Middle America south

of Honduras otherwise appears to be uncertain. Such sweeping statements as made by the A.O.U. (1983:297) that *Bubo virginianus* "breeds" from Canada and Alaska "south throughout the Americas (except the West Indies and most other islands) to Tierra del Fuego" are meaningless even at the level of country.

There is very little to remark upon regarding waterbirds and wintering species of North American migrants (Table 3) save perhaps that there are so few of the latter. Many wintering species, particularly warblers, are generally confined to higher elevations, however, and would not be expected in the islands. The abundance of Philadelphia Vireos (*Vireo philadelphicus*) may be of some interest. In one instance, Wetmore remarked that he had to abandon attempts to collect around a clearing on Isla Afuerita because this species was so numerous as to impair detection of other species. I have included among the nonresidents a sight record of a "pair" of Rough-winged Swallows (*Stelgidopteryx ruficollis*) among a large flock of swifts over this same clearing even though Wetmore's notes indicate them to have been the tropical form, as it seems likely these were casual visitors, the species not having been recorded from any of the other islands, including Cébaco.

GEOGRAPHIC VARIATION WITHIN THE VERAGUA ARCHIPELAGO

Affinities of Isla Brincanco with Isla Coiba.—The close affinity of the avifauna of Isla Brincanco with that of Coiba has not hitherto been appreciated. This realization makes it all the more regrettable that more is not known about the avifauna of the Islas Contreras, especially Isla Uva, which is about the same size as Brincanco but has never been investigated. One of the more interesting relictual taxa of Coiba is an endemic subspecies of White-throated Robin (*Turdus assimilis coibae*), which more closely resembles birds from South America (Eisenmann 1950) than the subspecies found in western Panama (*T. a. cnephusus*), which is an upland form and thus rather far removed from Coiba. This interesting relictual subspecies also occurs on Isla Brincanco (Wetmore et al. 1984).

When I determined the distribution of subspecies of Streaked Saltator from Panama (Wetmore et al. 1984), I found that two specimens from Isla Brincanco were definitely referable to the distinctive, dark Coiba subspecies *Saltator albicollis scotinus*, which Wetmore (1957) had already established also occurred on Isla Ranchería.

The only other species collected on Brincanco that has supposedly differentiated on Coiba is the Blue-gray Tanager. Wetmore (1957) named the Coiba bird as a new subspecies *Thraupis episcopus cumatilis*, based on its darker coloration, particularly the supposedly bluer sides and flanks. The specimens from Coiba are few, and even within this small series of five there are scarcely two specimens of the same sex that are in comparable plumage. If the Coiba bird can really be differentiated, the differences are very subtle and I would not be prepared to say to which race the two specimens from Brincanco should be assigned without a better series from both islands. Still, the saltator and the thrush show that the very limited known avifauna of Isla Brincanco has a decidedly closer affinity with Coiba than with the mainland.

Leptotila battyi.—This forest dove, which Wetmore (1968) maintained as a species distinct from *L. plumbeiceps*, was first described from Coiba (Rothschild 1901). A single specimen was later taken on the western slope of the Azuero Peninsula and named as a new subspecies, *Leptotila plumbeiceps malae*, supposedly "exactly intermediate between *Leptotila p. plumbeiceps* . . . and *Leptotila battyi*" (Griscom 1927:4). Wetmore (1968:43) obtained three specimens from Isla Cébaco that he assigned to *L. b. malae*, describing the differences in coloration with modifiers such as "very slightly," "slightly," and "faintly," except for the paler forehead. No differences are apparent to me except that

TABLE 3

WATERBIRDS AND NORTH AMERICAN MIGRANTS ON SELECTED ISLANDS OF THE PACIFIC COAST OF WESTERN PANAMA¹

	Cébaco	Gobernadora	Canal de Afuerita	Brincanco	Bolaños	Parida
<i>Pelecanus occidentalis</i>	0	0	0		0	0
<i>Sula leucogaster</i>	0		0		0	
<i>Phalacrocorax brasilianus</i>				0		0
<i>Fregata magnificens</i>	0	0	0		0	0
<i>Tigrisoma mexicanum</i>	0		0			
<i>Egretta thula</i>	0					
<i>Egretta caerulea</i>	0					
<i>Butorides virescens</i>	0					
<i>Nyctanassa violacea</i>	X					
<i>Buteo platypterus</i>	0	0				
<i>Pandion haliaetus</i>	0					
<i>Catoptrophorus semipalmatus</i>	0					
<i>Actitis macularia</i>	0	0	0		0	0
<i>Larus atricilla</i>	0	X				
<i>Sterna maxima</i>					0	0
<i>Ceryle alcyon</i>	X	0				
<i>Empidonax flaviventris</i>	X					
<i>Empidonax virescens</i>	X					
<i>Myiarchus crinitus</i>	X	X		0		X
<i>Myiodynastes luteiventris</i>		X				
<i>Stelgidopteryx ruficollis</i>				0		
<i>Catharus ustulatus</i>	X			X		
<i>Hylocichla mustelina</i>			0			
<i>Vireo flavifrons</i>	X					X
<i>Vireo philadelphica</i>	X	X	0	X		X
<i>Vermivora peregrina</i>	0	X				
<i>Dendroica petechia amnicola</i>	X					
<i>Mniotilta varia</i>	X					
<i>Protonotaria citrea</i>	0	0	X	0		
<i>Seiurus aurocapillus</i>	X	X				
<i>Seiurus noveboracensis</i>	0	X				0
<i>Oporornis formosa</i>	X		X			
<i>Piranga rubra</i>	X	X				
<i>Pheucticus ludovicianus</i>	X					

¹ These records are presented for the sake of completeness; migrants and waterbirds of Coiba and Ranchería are listed in Wetmore (1957). X = specimen record, 0 = sight record.

in two of the Cébaco specimens the foreheads are decidedly white, unlike the gray foreheads in the Coiba series. But the third bird from Cébaco does not seem to differ in this respect. I believe that it is preferable to emphasize the similarity of these populations, rather than a single, inconsistent difference, by regarding *malae* as a synonym of *Leptotila battyi*.

In any case, the distribution of *Leptotila battyi* is plainly relictual and must once have included a greater portion of the mainland, from which it has disappeared, perhaps

only recently through the forest clearing that has been so extensive on the Pacific slope in Veraguas and Chiriquí. Populations were marooned on the outlying islands of Coiba and Cébaco, and the species probably originally occurred on Gobernadora, which has been cleared and where *L. verreauxi* now occurs instead. The same process is occurring on Cébaco (or was, if it has not already run its course), where in 1965 *L. verreauxi* had already moved in but *L. battyi* still persisted where forest had not been cleared.

Melanerpes rubricapillus.—Wetmore (1968) considered that specimens of Red-crowned Woodpecker from Cébaco and Gobernadora were intermediate between *M. r. wagleri* of the mainland and *M. r. subfuscus* of Coiba, which latter is instantly recognizable in being smaller and very dark. This is definitely not true for the pair from Gobernadora, which are perfectly typical of mainland birds. The series of 5 from Cébaco do appear darker below, but there is variation in mainland birds in this respect and some may be equally dark. Wetmore claimed that the combined Cébaco/Gobernadora series was intermediate in size as well but this does not seem to hold, as the average wing length he gives for females is actually a millimeter longer than in *M. r. wagleri*, the larger form. The Cébaco birds may have differentiated slightly, but had there not been a darker form on Coiba that invited comparison, I doubt that this small series would have been noticed as different from mainland birds. If the differences were to prove consistent, they would probably have arisen independently of the birds on Coiba, rather than being due to intergradation.

Camptostoma obsoletum.—Wetmore (1972) referred a single specimen of Southern Beardless Tyrannulet from Isla Afuerita to the Coiba subspecies *C. o. orphnum*, which differs from mainland *C. o. flaviventre* in darker dorsal coloration. This specimen is anomalous in apparently lacking some yellow pigments, so that it is much paler below than in any Panamanian specimen of the species and is grayer, rather than greenish above. The differences between the two subspecies are not especially marked in any case and I do not consider the anomalous Afuerita specimen to be identifiable to one or the other.

Dendroica petechia.—Although Wetmore observed the resident form of this species on Isla Parida, he failed to obtain specimens, and he collected only a pair on Isla Bolaños. It would certainly be interesting to see more material from these islands, because the male from Bolaños is huge, being larger than any other example of the species, and the female is at maximum size for the species (Olson 1980).

Coereba flaveola.—Although the Bananaquit exhibits no endemism in the islands concerned here, two different subspecies are represented that reflect a historical factor that caused an abrupt break on the mainland as well. This provides an excellent illustration of the value of including subspecies, which are frequently maligned, in biogeographical studies.

The two subspecies involved are *C. f. mexicana*, which extends from Mexico to central Panama, and *C. f. columbiana*, which ranges from central Panama through much of Colombia. The differences between these races are not striking (Hellmayr 1935) but they are quite consistent and recognizable. In *columbiana* the underparts are brighter, the dorsum lighter, less blackish, and most conspicuously, the rump patch is more extensive and brighter yellow, less olivaceous, than in *mexicana*. Birds from Parida, Brincanco, and Coiba are clearly referable to *mexicana*, whereas those from Cébaco and Gobernadora are referable to *columbiana*.

It is less clear where the break between subspecies is on the mainland, but specimens identifiable as *columbiana* occur as far west as Soná, Veraguas. I suspect that the boundary is about at this point, a potential barrier being the ridge of low mountains extending south from the Cordillera Central to the tip of the short peninsula that forms the

western border of the Golfo de Montijo. Unfortunately, there are no specimens in USNM from immediately west of here, the nearest being from Alanje, Chiriquí, which are referable to *mexicana*. Such a sharp break between subspecies of an ubiquitous and supposedly vagile species as *Coereba flaveola* is certainly remarkable and deserving of further study.

Sporophila americana.—The so-called Variable Seedeater has a pattern of distribution in the region very similar to that of *Coereba* (Olson 1981). The black-throated subspecies *S. a. hoffmanni* occurs from southwestern Costa Rica to western Veraguas, including Isla Coiba. Birds from Soná, Veraguas, show varying amounts of white in the throat indicating intergradation with the white-throated subspecies *S. a. hicksii*, which is found from eastern Veraguas into Colombia. Of two birds from Gobernadora, one is similar to *hoffmanni* and the other to *hicksii*, indicating that this is also very near the point of contact. It is curious that this species was not recorded on Cébaco.

BIOGEOGRAPHICAL CONSIDERATIONS

Among resident land birds, the families so conspicuously absent on the very large, forested island of Coiba are likewise absent in the rest of the Veragua Archipelago: Tinamidae, Cracidae, Trogonidae, Momotidae, Galbulidae, Bucconidae, Ramphastidae, and Dendrocolaptidae. To these may be added Furnariidae and Formicariidae, so that there is not a single species of tracheophone suboscine in the archipelago outside of Coiba. That there is only one species of antbird on Coiba is strange enough; that there are none at all in the other islands is wondrous. The absence of any wrens except *Troglodytes aedon*, known from a very distinctive subspecies *T. a. carychrous*, on Coiba, where it is a forest inhabitant, and a single specimen of the mainland race *inquietus* from Cébaco, is also noteworthy.

Apart from the crab-eating *Buteogallus* which may be expected in almost any coastal situation, a single *Buteo magnirostris* shot but not recovered on Isla Parida, one individual of *Leucopternis albicollis* seen on Cébaco, and the vagrant *Bubo* discussed above, there are no records of hawks, falcons, or owls in the islands. There are 13 genera that occur on Coiba but not on the other islands: *Phaeochroa*, *Todirostrum*, *Capstiempis*, *Miopagis*, *Leptopogon*, *Polioptila*, *Cyclarhis*, *Hylophilus*, *Parula*, *Basileuterus*, *Quiscalus*, *Tiaris*, and *Arremonops*. That *Amazona autumnalis* should also be absent in the smaller islands, whereas two other species of *Amazona* are present, strikes me as highly peculiar and perhaps artificial because *A. autumnalis* is found on Coiba and is ubiquitous in all of the islands of Bocas del Toro, where it regularly commutes among islands and to the mainland.

There are a few species in the Veragua Archipelago that were not found on Coiba when Wetmore collected there in 1957: *Leucopternis albicollis*, *Leptotila verreauxi*, *Amazona ochrocephala*, *Crotophaga sulcirostris*, *Tapera naevia*, *Lurocalis semitorquatus*, *Nyctidromus albicollis*, *Procnias tricarunculata*, *Megarynchus pitangua* (seen on adjacent Rancharía, however), *Pachyrhamphus polychopterus*, *Turdus grayi*, and *Cyanocompsa cyanooides*. All but four of these were found only on Cébaco, and 2 of the four otherwise occurred only on Gobernadora. Some of these species I have already identified as probably being casual visitors only, or a nonbreeding winterer in the case of *Procnias*. Virtually all of the rest are species associated with open country and they most likely did not colonize Cébaco and Gobernadora until there had been extensive clearing of forest on these islands. It is quite conceivable that some of these species have colonized Coiba in the past 40 years as the result of much felling of forest on that island since Wetmore's visit. It is interesting that the ani on Cébaco and Gobernadora was *Crotophaga sulcirostris*, whereas on Coiba it was *C. ani*.

The Snowy-bellied Hummingbird (*Amazilia edward*) is another species found on Coiba that is absent in the rest of the Veragua Archipelago, although *Amazilia tzacatl* is ubiquitous. The opposite obtains in the Pearl Islands, where *A. edward* is present and *A. tzacatl* is entirely absent, which is truly anomalous. Yet both species occur together on Coiba and on the very much smaller island of Taboga. This defies explanation.

It is of interest that on the Caribbean side of Panama in Bocas del Toro, where *Melanerpes rubricapillus*, *Chiroxiphia lanceolata*, *Ramphocelus dimidiatus*, and *Cyanerpes cyaneus* are absent, the islands of Chiriquí Lagoon are inhabited by *Melanerpes pucherani*, *Manacus vitellinus*, *Ramphocelus passerinii*, and *Cyanerpes lucidus*, whereas these species are absent on any of the Pacific islands, including the Perlas.

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LITERATURE CITED

- A.O.U. 1983. Check-list of North American Birds.
6th ed. American Ornithologists' Union, Lawrence, KS.
- ATLAS NACIONAL. 1988. Atlas nacional de la Republica de Panamá. 3rd ed.
Instituto Geográfico Nacional "Tommy Guardia," Panama.
- GOTELLI, N. J., and G. R. GRAVES. 1990. Body size and the occurrence of avian species on land-bridge islands. *Journ. Biogeogr.* 17:315-325.
- GRAVES, G. R., and N. J. GOTELLI. 1983. Neotropical land-bridge avifaunas: New approaches to null hypotheses in biogeography. *Oikos* 41:322-333.
- GRISCOM, L. 1927. Undescribed or little-known birds from Panama. *Amer. Mus. Novit.*, 280:1-19.
- HELLMAYR, C. E. 1935. Catalogue of birds of the Americas. Part VIII. *Field Mus. Nat. Hist. Zool. Ser.* 13.
- HOWELL, T. R. 1972. Birds of the lowland pine savanna of northeastern Nicaragua. *Condor* 74:316-340.
- MUNROE, B. L., Jr. 1968. A distributional survey of the birds of Honduras. *Ornithol. Monogr.* 7.
- OLSON, S. L. 1980. Geographic variation in the Yellow Warblers (*Dendroica petechia*: Parulidae) of the Pacific coast of Middle and South America. *Proc. Biol. Soc. Washington* 93:473-480.
- _____. 1981. The nature of the variability in the Variable Seedeater in Panama (*Sporophila americana*: Emberizidae). *Proc. Biol. Soc. Washington* 94:380-390.
- _____. 1993. Contributions to avian biogeography from the archipelago and lowlands of Bocas del Toro, Panama. *Auk* 110:100-108.

- SLUD, P. 1964. The birds of Costa Rica; distribution and ecology. *Bull. Amer. Mus. Nat. Hist.* 128:1-430.
- STILES, F. G., and A. SKUTCH. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York.
- THOMAS, O. 1902. On some mammals from Coiba Island, of the west coast of Panama. *Novitates Zoologicae* 9:135-137.
- WETMORE, A. 1952. The birds of the islands of Taboga, Taboguilla, and Uravá, Panamá. *Smithsonian Misc. Coll.* 121(2): 1-32.
- _____. 1957. The birds of Isla Coiba, Panama. *Smithsonian Misc. Coll.* 134(9): 1-105.
- _____. 1965. The birds of the Republic of Panamá. Part 1.—Tinamidae (Tinamous) to Rynchopidae (Skimmers). *Smithsonian Misc. Coll.* 150(1): iv + 483 pages.
- _____. 1968. The birds of the Republic of Panamá. Part 2.—Columbidae (Pigeons) to Picidae (Woodpeckers). *Smithsonian Misc. Coll.* 150(2): v + 605 pages
- _____. 1972. The birds of the Republic of Panamá. Part 3.—Passeriformes: Dendrocolaptidae (Woodcreepers) to Oxyruncidae (Sharpbills). *Smithsonian Misc. Coll.* 150(3): iv + 631 pages
- _____, R. F. PASQUIER, and S. L. OLSON 1984. The birds of the Republic of Panamá. Part 4.—Hirundinidae (Swallows) to Fringillidae (Finches). *Smithsonian Misc. Coll.* 150(4): vi + 670 pages.
- WILLIS, E. O., and E. EISENMANN. 1979. A revised list of birds of Barro Colorado Island, Panama. *Smithsonian Contr. Zool.* 291:1-31.
- WRIGHT, S. J., J. FAABORG, and C. J. CAMPBELL. 1985. Birds form tightly structured communities in the Pearl Archipelago, Panama. Pp. 798-812 *in* P. A. Buckley et al., eds. *Neotropical ornithology*. *Ornithol. Monogr.* 36.

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